More dark information in natural scenes requires denser mosaics of OFF ganglion cells

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Abstract

The structure and receptive field properties of retinal ganglion cells should reflect statistical properties of the visual world. OFF ganglion cells (which process dark regions in a scene) are smaller and more densely distributed than ON ganglion cells (which process bright regions). Measuring from photographs of natural scenes, we find an excess of dark patches over light patches over a range of spatial scales. This suggests a need for more OFF cells than ON cells. We also quantify the redundancy of information in natural scenes and in ON and OFF channels separately.

Keywords: Retina, information theory, ganglion cells, natural scenes, redundancy

Introduction

A photoreceptor responds with a graded current proportional to local light intensity. However, a ganglion cell (after several stages of retinal processing) discards much of the information about intensity and sends a message to the brain proportional to local contrast. Barlow proposed that the purpose of this transformation is to reduce statistical redundancy [7], a hypothesis which has since been investigated by many authors (reviewed in [14]). Ganglion cells form two main classes, OFF and ON, which rectify, responding selectively to stimuli in their receptive field centers that are, respectively, darker or brighter than the local mean. Both classes also express a "surround" of opposite sign to the center. The center is thought to improve signal-noise ratio by local averaging; whereas the surround is thought to decrease redundancy by subtracting the local mean [18,7,17,5,6,1,12,9].

Although OFF and ON cells have usually been considered purely symmetrical, significant asymmetries are now apparent. Functionally, OFF cells show somewhat slower kinetics, smaller receptive field centers, and stronger rectification [2,3,4,20]. Structurally, OFF cells show smaller dendritic fields and a denser distribution (e.g., [2,3,4,20]), so that in most species the retina contains more OFF than ON cells. We hypothesized that these asymmetries in sampling density and sampling aperture for OFF and ON cells serve to match the ganglion cells to the statistical properties of natural scenes. Our basic technique is to explore the amount of information contained in arrays of model photoreceptors and ON/OFF ganglion cells.

Redundancy of Information in Photoreceptor Arrays

In order to explore the information extracted from bright/dark components of natural scenes the first step is to quantify the redundancy of such scenes as represented by responses of a photoreceptor array. Here we model an ideal array of monochromatic photoreceptors that respond to the intensity of light incident on their receptive fields and consider the spatial intensity variation in static images. Due to the quantal nature of light and random noise, there is a finite number of intensity values I that can be distinguished from a given photoreceptor [16]. The number of values depends on biological factors such as lens characteristics and circuit dynamics, and is fundamentally limited by the randomness of the photon-absorption process. Two intensity values can only be reliably distinguished if their separation is about twice the standard deviation

of the photon count noise in the photoreceptor's receptive field [16]. Thus in brighter conditions, photoreceptors are able to transmit more discriminable intensity levels. Shannon's 1948 theory [13] gives a quantitative measure of the amount of information that such an object can transmit. This is an upper limit on the entropy *H* of the photoreceptor response $H(I) = \log_2(N)$, where *N* denotes the number of intensity levels. Qualitatively, this is the number of binary questions required to determine the intensity *I* [8].

One might expect that an array of two photoreceptors should transmit twice the information, but this is only true if the photoreceptors are encoding independent signals. Generally, the intensities in two nearby photoreceptors are not independent. Rather, knowledge of one intensity value reduces the uncertainty in the other. Then the joint entropy of two photoreceptors with intensity values I_1 and I_2 is $H(I_1, I_2) = H(I_1) + H(I_2 / I_1)$, where $H(I_2/ I_1)$ is the entropy of I_2 given knowledge of I_1. This quantity is always less than or equal to $H(I_1)$, with equality only when the two intensities are completely independent. Similarly, knowledge of two intensity values will reduce uncertainty in a third nearby intensity value, so that the entropy of the three-photoreceptor configuration is $H(I_1, I_2, I_3) = H(I_1) + H(I_2 / I_1) + H(I_3 / I_1, I_2)$, where $H(I_3 / I_1, I_2)$ is the entropy of I_3 given knowledge of I_1 and I_2. It is straightforward to generalize to the entropy of any number of photoreceptors.

Such reductions in uncertainty occur because of statistical redundancy. One way of quantifying this redundancy is to compute the correlation function of pixels separated by some distance *r* in a an ensemble of natural scenes. Classic results in the literature (see the review [14]) show that the Fourier transform of this correlation function has a universal scaling behavior. Here we study a more detailed characterization of local redundancies in natural scenes in which we directly compute the reduction in entropy of local clusters of model photoreceptors due to redundancy in the information they individually convey. This measure will also apply separately to the ON/OFF channels.

Statistical redundancy can be computed given a large collection of photoreceptor inputs, i.e., samples of "typical" visual scenes that can represent the intensity values to which a mosaic of photoreceptors would be exposed. For such samples, we use images from van Hateren's natural stimulus collection [10], a carefully calibrated set of monochromatic 1536x1024 images that are very nearly linear in intensity. We model each pixel as an intensity input, resulting in a square lattice representing some part of the photoreceptor mosaic.

We would like to calculate the entropy of a typical visual scene. The $H = log_2 N$ equation gives an upper bound for the entropy of an independent photoreceptor response, but it is only correct if all intensities found in the collection of visual scenes are equally probable. This is not the case, so we must consider all distinguishable intensity levels $\{i\}$, and determine their individual probabilities. To compute this probability distribution function *p(i)* for image intensities we count the frequency of each intensity value in our set of images and divide by the total number of data points. The resulting distribution, (see Fig.2) rises to a single peak and decays slowly at large intensities. We can calculate the entropy of a single pixel, assuming statistical independence of pixels, as $H(I) = -Sum_i\, p(i)\, log_2[p(i)]$. This entropy depends on the number of different intensity levels *N*; note that *H(I)* becomes infinite as *N* does. For the present purposes we will assume that in our model array a photoreceptor can distinguish *N=50* different intensities. More detailed modeling of specific organisms in different stimulus conditions will require appropriate variation of *N*.

Naive multiplication of this entropy by the number of pixels to obtain the entropy of a typical image ignores any statistical redundancy in the images. A better estimate might consider all collections of two neighboring pixels. Let $p(i,j)$ denote the probability of finding a pair of neighboring horizontal pixels with intensity i on the left and j on the right. Then the entropy of all such pairs in the data set is given by $H(I_1,I_2) = -Sum_{\{i,j\}} p(i,j) \log_2[p(i,j)]$. The generalization to the entropy of some geometry of n pixels is $H(I_1,I_2 \ldots I_n) = -Sum_{(i1 \ldots in)} p(i_1 \ldots i_n) \log_2[p(i_1 \ldots i_n)]$. If all sets of intensity values can be realized, the probability distribution function $p(i_1,...,i_n)$ contains N^n elements in its domain. Ideally, we wish to form this distribution function over the set of all 1536x1024 images, but for even $N=10$, we would need at least $10^{1500000}$ images to do this reliably. Hence we are obliged to consider smaller patches of the image.

Using MATLAB, we computed probability density functions of intensities for geometries of one pixel, two horizontal neighboring pixels, four pixels arranged in a 2x2 square, and 16 pixels arranged in a 4x4 square. We linearly divided the range of intensities in each of 32 images into $N=50$ intensity levels, and calculated the entropy of each configuration. We chose this binning scheme assuming that our model photoreceptors respond linearly and all have the same adaptation pool. Since we have a million pixels in each of 100 images, all quantities are very well estimated. The results for the entropy (information) contained in these image patches are summarized below:

Number of Pixels	Entropy	Entropy per Pixel	(Entropy per pixel)/(Entropy of 1Pixel)
1	4.38	4.38	1
2	6.40	3.20	0.73
4	10.26	2.57	0.59
16	18.82	1.18	0.27

Table 1: *All entropies are listed in bits*

The fourth column measures the amount of statistical redundancy observed when more than one pixel is considered. For patches of 16 pixels, we find that only 27% of the information in each pixel is non-redundant. This calculation is analogous to Shannon's calculation of the entropy of the English language [8], though intensities are more redundant than letters.

Bright/Dark Asymmetry and ON vs. OFF Ganglion Cells

We now seek to separate natural scenes into their bright and dark components. ON and OFF ganglion cells perform this separation by computing local contrasts in a scene [19]. We will explore the differences in the amounts and redundancy of information transmitted via the two kinds of channels.

To calculate the contrast a model ganglion cell would perceive when stimulated with an image, we use a Difference of Gaussians (DOG) model, with the Weber contrast [19]– i.e. we take a Gaussian weighted average of all the intensities surrounding some central point, and subtract a similarly weighted average with a larger variance Gaussian. These center and surround gaussians are weighted equally, so that an image of constant intensity will evoke no contrast response. The size of the excitatory center is defined as the radius where the net weighting is zero. A positive difference (contrast) means that the center was brighter than the surround, i.e. there is a bright patch, and negative contrast means a dimmer center, or a dark patch. Finally, the center-surround difference is normalized with respect to the mean luminance of the center and surround. Such a scheme of divisive normalization models the ganglion cell's adaptive response (see [19] and references therein). In real cells the surround/center ratio is about 5 (reviewed [15]). Fig. 1 shows the percent of positive, negative, and zero contrasts that we encountered in the natural scenes, as a function of the center radius used to calculate them.

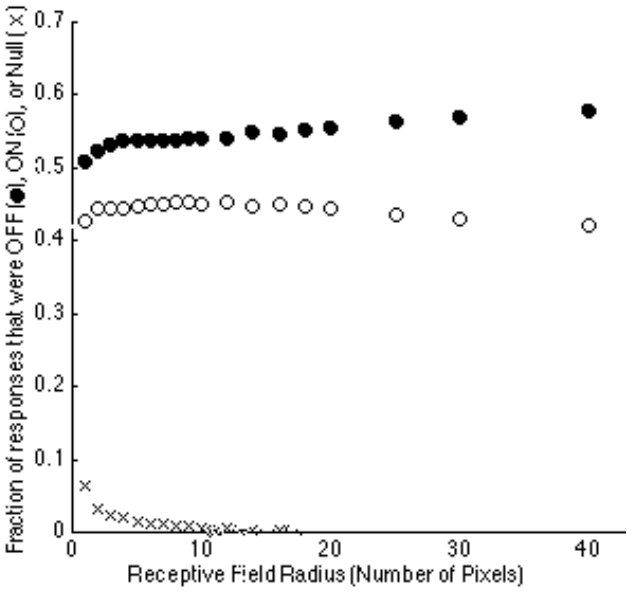

Figure 1: Over the range of center radii, from 1-40 pixels, there are more negative contrasts than positive. Therefore, an OFF cell would tend to respond more frequently to the spatial structure of these scenes than an ON cell. This basic asymmetry in OFF and ON responses shows that over this range of scales there are more dark patches than light patches in a natural scene. We propose this as a basic reason why OFF ganglion cells are more numerous than ON cells.

Information in ON vs. OFF Channels

To study how much information ON and OFF channels convey about a natural scene we should compute the mutual information between their respective contrast images and the intensities in the image. The mutual information is given by $M(I,C) = H(I) + H(C) - H(I,C)$, where M is the mutual information between the intensities I and contrasts C while H is entropy of the appropriate distribution of intensities and contrasts. Note that $H(I,C) = H(I) + H(C/I)$, and since knowledge of the intensities implies knowledge of contrasts in the absence of noise, $H(C/I)=0$. Using this in the expression for M gives $M(I,C) = H(C)$, since we are excluding effects of intrinsic circuit noise in the present ganglion cell model. In short, the entropy of the ON/OFF contrast array is the information it carries about the visual scene.

To compute this entropy we first recognize that a ganglion cell can only transmit a finite number of contrast levels. (This partially includes the effects of noise.) Thus we must bin the contrasts computed by the ON/OFF arrays into a finite number of levels. The maximum information about contrast is achieved when each level encodes an equally probable interval of contrasts [11]. To estimate the maximum information contained in ON/OFF contrast arrays we carry out such a procedure with $N=50$ levels. (We have checked that a cruder scheme of linear division of the contrasts into bins up to to some cutoff maximum gives similar results.) We obtain probability distribution functions for the contrasts at $\approx 10^6$ pixels in each of 100 natural scenes, with results similar to those reported in [19] (see Fig. 2).

Our results are computed with a center size of 2 (roughly 13 pixels in the excitatory center) and a surround/center ratio of 5. In addition, notice the asymmetry between the distributions of positive and negative contrasts. The asymmetry is statistically significant. We use the density functions in Fig. 2 to equally divide the contrasts into *50* response levels for each cell type following the methods of [11]. An ON or OFF response is created by assigning a value from *1* to *50* for a positive or negative contrast, and 0 for zero contrast.

We calculate the entropy of arrays of model ON and OFF cells using the same methods we applied to model photoreceptors. Specifically we construct an array of model ON/OFF cells centered under pixels in the image with an array spacing s (the distance in pixels between adjacent cells) which is of order the center size. This roughly reflects the organization of ganglion cell mosaics. We then compute the entropy per cell by considering 1x1, 1x2 and 2x2 patches of ganglion cells to assess information content and redundancy of the contrasts they measure.

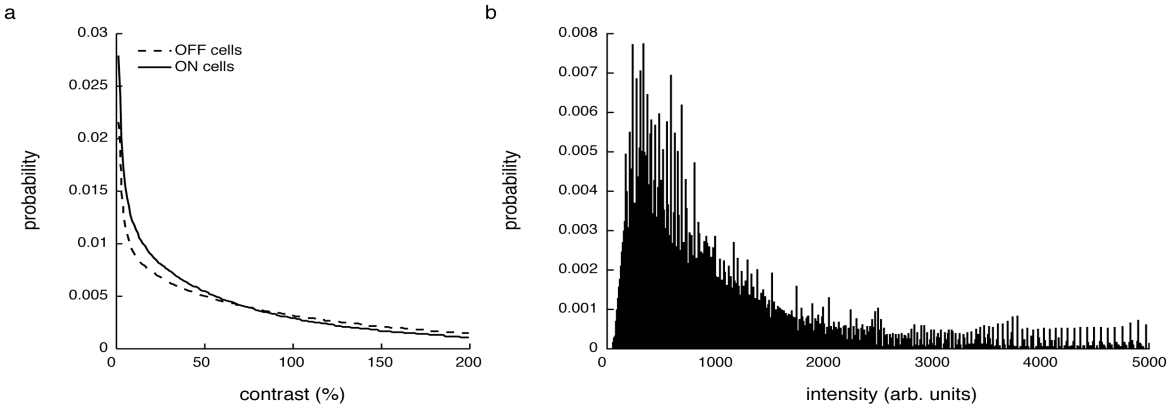

Figure 2: ***Contrast distributions vs. Intensity Distributions***

Table 2 shows several interesting results. First, the entropy of the cell arrays increases as the array spacing increases. This is because cells that are spaced further apart are observing parts of the image that are more statistically independent and their responses are therefore less redundant. Secondly, even when the array spacing is only 1 pixel (so that the cell spacing is the same as the photoreceptor spacing) the entropy per cell in 1x2 and 2x2 patches of ON/OFF ganglion cells is a large fraction of the information in cells studied individually. This shows directly that the contrast image is much less redundant than the intensity image: for example, the 2x2 ON (OFF) array with unit spacing retains 77% (75%) of its information per pixel, compared with 59% for photoreceptor arrays. At an array spacing of four pixels the ON (OFF) array retains 96% (95%) of the information possible. Finally, for any center size and array spacing OFF arrays contain more information than ON arrays. The difference is statistically significant given the size of our data set

Array Spacing	1	2	3	4	5	6	7	8	9	10
1 cell										
ON	3.45	-	-	-	-	-	-	-	-	-
OFF	4.09	-	-	-	-	-	-	-	-	-
1x2 cell array										
ON	3.02	3.26	3.36	3.40	3.41	3.41	3.42	3.42	3.42	3.42
OFF	3.55	3.83	3.95	4.01	4.03	4.04	4.05	4.05	4.05	4.05
2x2 cell array										
ON	2.64	3.07	3.25	3.32	3.34	3.36	3.37	3.37	3.37	3.38
OFF	3.08	3.59	3.81	3.90	3.94	3.96	3.97	3.98	3.98	3.99

Table 2: *Entropy per cell in NxM size arrays of ON and OFF model ganglion cells. The 1x2 array cells are on a horizontal line. The 2x2 arrays are square. All center sizes are 2 pixels and all center/surround ratios are equal to 5.*

Summary: By analyzing patches of model photoreceptors and ganglion cells, we quantified the degree of local redundancy in natural image intensities. Thus 4x4 patches carry only 27% of the information expected if the photoreceptor signals were independent. Second, we quantified the reduction of this redundancy by ganglion cell arrays. Third, we found that at any spatial scale natural scenes contain more dark than light patches. Model OFF arrays processing dark patches

transmit more information per ganglion cell about a given scene than ON arrays. These asymmetries should help explain why real OFF ganglion cells are smaller and form denser arrays than ON cells.

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[1] J.J. Atick and A.N. Redlich, Towards a theory of early visual processing, Neural Computation Vol. 2 (1992) 308-320.
[2] E.J. Chichilnisky and R.S. Kalmar, Functional Asymmetries in ON and OFF Ganglion Cells of Primate Retina, The Journal of Neuroscience Vol 22(7) (2002) 2737-2747.
[3] D.M. Dacey and M.R. Petersen Dendritic field size and morphology of midget and parasol ganglion cells of the human retina, Proc. Natl. Acad. Sci. USA Vol 89 (1992) 9666-9670.
[4] A.M. Derrington and P. Lennie, Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque, J. Physiol. Vol. 357 (1984) 219-240.
[5] R.M. Balboa and N. Grzywacz, The Minimal Local Asperity Hypothesis of Early Retinal Lateral Inhibition, Neural Computation Vol. 12 (2000) 1485-1517.
[6] R.M. Balboa and N. Grzywacz, The role of early retinal lateral inhibition: More than maximizing luminance information, Visual Neuroscience Vol 17 (2000) 77-89.
[7] H.B. Barlow, Possible principles underlying the transformation of sensory messages, in: W.A. Rosenblith ed., Sensory Communication (Cambridge, MA: MIT Press, 1961) 217-234.
[8] T. Cover and J. Thomas, Elements of Information Theory, (John Wiley & Sons 1991).
[9] D.J. Field, What is the goal of sensory coding?, Neural Computation Vol. 6 (1994) 559-601.
[10] J.H. van Hateren and A. van der Schaaf, Independent component filters of natural images compared with simple cells in primary visual cortex, Proc.R.Soc.Lond. B Vol. 265 (1998) 359-366.
[11] S. Laughlin, A simple coding procedure enhances a neuron's information capacity, Z. Naturforsch Vol. 36 (1981) 910-912
[12] S.T. McCarthy and W.G. Owen, Preferential representation of natural scenes in the salamander retina, Investigative Opthamology and Visual Science Vol. 37 (1996) S674.
[13] C.E. Shannon, A mathematical theory of communication, Bell System Technical Journal 27 (July 1948) 379-423 and (October 1948) 623-656.
[14] E.P. Simoncelli and B.A. Olshausen, Natural image statistics and neural representation, Annu. Rev. Neurosci. 24 (2001) 1193-1216
[15] R.G. Smith & P. Sterling, Cone receptive field in cat computed from microcircuitry, Vis. Neurosci. 5 (1990) 453-61.
[16] A. Snyder, S. Laughlin and D.G. Stavenga, Information Capacity of Eyes, Vision Res. Vol. 17 (1977) 1163-1175.
[17] M.V. Srinivasan, S.B. Laughlin and A. Dubs, Predictive coding: a fresh view of inhibition in the retina, Proc.R.Soc.Lond. B Vol. 216 (1982) 427-459.
[18] P. Sterling (2003) How retinal circuits optimize the transfer of visual information, in: LM Chalupa, JS Werner eds., The Visual Neurosciences (MIT Press, 2003).
[19] Y. Tadmor and D.J. Tolhurst, Calculating the contrasts that retinal ganglion cells and LGN neurones encounter in natural scenes, Vision Research Vol. 40 (2000) 3145-3157.
[20] K.A. Zaghloul, K. Boahen, J.B. Demb, Different circuits for ON and OFF retinal ganglion cells cause different contrast sensitivities, J. Neurosci. 23 (2003) 2645-54.