Retina is structured to process an excess of darkness in natural scenes

Charles P. Ratliff, Bart G. Borghuis, Yen-Hong Kao, Peter Sterling, and Vijay Balasubramanian

*Department of Physics and Astronomy, University of Pennsylvania, Philadelphia, PA 19104; 1Department of Ophthalmology, Feinberg School of Medicine, Northwestern University, Chicago, IL 60611; 1Department of Neuroscience, University of Pennsylvania, Philadelphia, PA 19104; and 1Howard Hughes Medical Institute, Janelia Farm Research Campus, Ashburn, VA 20147

Retinal ganglion cells that respond selectively to a dark spot on a brighter background (OFF cells) have smaller dendritic fields than their ON counterparts and are more numerous. OFF cells also branch more densely, and thus collect more synapses per visual angle. That the retina devotes more resources to processing dark contrasts predicts that natural images contain more dark information. We confirm this across a range of spatial scales and trace the origin of this phenomenon to the statistical structure of natural scenes. We show that the optimal mosaics for encoding natural images are also asymmetric, with OFF elements smaller and more numerous, matching retinal structure. Finally, the concentration of synapses within a dendritic field matches the information content, suggesting a simple principle to connect a concrete fact of neuroanatomy with the abstract concept of information: equal synapses for equal bits.

Because neural circuits allocate resources efficiently (14–17), we reasoned that the extra resources devoted to OFF arrays represent specific adaptations to the statistical structure of natural stimuli. We considered that a behavioral decision based on any stimulus is broadly limited by the amount of available information (18, 19). Thus, we reasoned that if negative contrasts contain more information about natural scenes, then this would justify the excess of OFF cells. Furthermore, if dark information is more concentrated spatially in natural scenes, this would justify the OFF cell’s denser distribution of synapses. Thus, we hypothesized that (i) natural scenes contain more regions of negative than positive contrasts; (ii) information in the dark regions is more concentrated, and (iii) the asymmetric organization of paired OFF and ON channels represents an adaptation to this predominance of dark information.

Retinal ganglion cells have spatially extended receptive fields of many different sizes and respond to both spatial and temporal contrast. Thus, to test our hypothesis, we measured spatial contrast in natural images using model center-surround receptive fields and temporal contrast in natural time series with model temporal filters. For temporal contrasts, there was no asymmetry, but for spatial contrasts, there was a marked asymmetry at all spatial scales—favoring negative contrasts. To explore this, we constructed artificial images with the same first- and second-order statistical structure as natural images. These also showed a predominance of negative contrasts. Computing the information represented by mosaics of OFF and ON elements, we found that information peaks when (i) OFF elements are smaller and more numerous, matching retinal structure, and (ii) individual OFF and ON elements represent equal amounts of information. This correlates with the equality in their numbers of synapses. Our results suggest that the retinal mosaic is not simply determined by the required spatial resolution, but by tradeoffs involving the efficient representation of the asymmetric distribution of information in the natural world.

Results

OFF Cells Predominate in Ganglion-Cell Arrays. Differences between OFF and ON cells were known for dendritic-field diameter, cell spacing, and coverage (see Introduction). The difference in dendritic branching had not been quantified but was critical, because in retinal ganglion cells, membrane area sets the number of excitatory synapses received over a given retinal area (12, 13). These numbers, which we now report, could then be compared with the distributions of information across images. We also sought to compare these quantitative aspects of spatial structure

Author contributions: C.P.R., B.G.B., P.S., and V.B. designed research; C.P.R., B.G.B., Y.-H.K., and V.B. performed research; C.P.R., B.G.B., and V.B. analyzed data; and C.P.R., B.G.B., P.S., and V.B. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

1To whom correspondence should be addressed. E-mail: vijay@physics.upenn.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1005846107/-/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.1005846107
Off cells then implies that the OFF array uses on average ~1.7-fold more excitatory synapses.

In summary, the OFF array, containing about 2-fold more cells and synapses than the ON array, allocates more total resources to encoding a scene. An individual OFF cell uses similar resources as an ON cell but concentrates them over a smaller region. On the broad principle that resources are invested according to the likely return, these asymmetries suggest asymmetrical structure in natural images.

**Natural Images Contain More Negative Spatial Contrasts.** ON and OFF ganglion cells respond selectively to positive and negative spatial contrasts (locally bright and dark regions). Thus, we asked if the predominance of OFF cells in retinal mosaics might reflect an adaptation to an excess of negative spatial contrasts in natural images. To measure the distribution of bright and dark regions, we modeled the ganglion cell’s center-surround receptive field as a diversely normalized difference of Gaussians filter (22). This filter measured contrast at an image point \((x, y)\) as

\[
\text{Contrast}(x,y) = \frac{I_c(x,y) - I_s(x,y)}{I_d(x,y)}
\]

Here, \(I_c\), \(I_s\), and \(I_d\) are intensities measured by unit-normalized center, surround, and divisive normalization Gaussian filters centered at \((x, y)\). Center and surround were weighted equally so that a spatially uniform image evoked no response. Divisive normalization captured ganglion-cell adaptation to local mean intensity (23). Thus, the filter measured contrast as a percent difference in intensity between center and surround relative to a divisive adaptation pool. A positive response meant that the center was brighter than the surround.

From a standard set of calibrated monochrome natural images (24), we selected 50 rural images. Image resolution was 1 arc-min per pixel, corresponding to roughly two cone-receptive field diameters in the human fovea. We convolved these images with model receptive fields to measure contrast at every location (Fig. 2). The surround SD was taken to be 1.5 times the center SD, matching previous measurements (10), and the adaptation pool was taken to be of the same size as the surround (the SD of \(I_d\) was set equal to the SD of \(I_c\)). For each filter size (parameterized by center SD), we constructed a probability distribution of contrasts by convolution with the image ensemble. Here, we report the distribution of contrasts obtained after averaging over all images. To avoid edge artifacts, contrasts calculated within 100 pixels of an image edge were discarded.

The distributions of local contrast peaked at 0, with sharper peaks for narrower filters (Fig. 2C). For all filter radii, negative contrasts (dark regions) were more numerous. To quantify this asymmetry, we measured the proportion of negative contrasts, setting response threshold to match measurements from ganglion cells (25–27). As filter width increased, the contrast distributions flattened, causing the number of subthreshold responses to decrease. However, at all spatial scales, negative contrasts were substantially more numerous (Fig. 2D). The excess of negative contrasts was independent of the adaptation pool size, the power of \(I_d\) appearing in the denominator in Eq. 1 and the precise shape of the center-surround filter \((SI Tar)\). This is because divisive normalization by a positive number does not change the sign of the center response minus the surround response. Thus, the fraction of dark contrasts exceeded the fraction of bright contrasts even without divisive normalization. These findings extend early reports of specific instances of a skew to negative contrasts (15, 28, 29).

**Excess Negative Contrasts Arise from Skewed Intensities and Spatial Correlations.** To determine what causes the dark/bright asymmetry in natural images, we constructed several types of artificial image. First, control images were established by drawing pixel patterns that matched previous measurements (10), and the adaptation pool was taken to be of the same size as the surround (the SD of \(I_d\) was set equal to the SD of \(I_c\)). For each filter size (parameterized by center SD), we constructed a probability distribution of contrasts by convolution with the image ensemble. Here, we report the distribution of contrasts obtained after averaging over all images. To avoid edge artifacts, contrasts calculated within 100 pixels of an image edge were discarded.

The distributions of local contrast peaked at 0, with sharper peaks for narrower filters (Fig. 2C). For all filter radii, negative contrasts (dark regions) were more numerous. To quantify this asymmetry, we measured the proportion of negative contrasts, setting response threshold to match measurements from ganglion cells (25–27). As filter width increased, the contrast distributions flattened, causing the number of subthreshold responses to decrease. However, at all spatial scales, negative contrasts were substantially more numerous (Fig. 2D). The excess of negative contrasts was independent of the adaptation pool size, the power of \(I_d\) appearing in the denominator in Eq. 1 and the precise shape of the center-surround filter \((SI Tar)\). This is because divisive normalization by a positive number does not change the sign of the center response minus the surround response. Thus, the fraction of dark contrasts exceeded the fraction of bright contrasts even without divisive normalization. These findings extend early reports of specific instances of a skew to negative contrasts (15, 28, 29).
intensities independently from a Gaussian distribution. Probing with the same filters used on natural images (Fig. 2), we found, across spatial scales, equal numbers of OFF and ON responses (Fig. 3 A and C). Next, images were created by drawing intensities from natural distributions, which are highly skewed (30). Probing these with the same filters, we found substantial asymmetries, with more OFF than ON responses (Fig. 3 B and D).

Artificial images lacking the natural power-law correlations (1/ power spectrum) (31) showed more subthreshold responses with increasing filter size (Fig. 3 A and B). This results from averaging over more uncorrelated pixels, as expected from the central-limit theorem, and holds equally for images created from Gaussian- or skewed-intensity distributions. However, when images constructed from either intensity distribution included the natural power-law correlations, the fractions of negative, positive, and subthreshold contrast responses were constant at all spatial scales (Fig. 3 C and D). Thus, the artificial images that most closely mimicked the distribution of OFF and ON responses for natural images were those that combined the natural-intensity distribution and the natural power-law correlations (Fig. 3D).

Thus, the excess of negative contrasts arises from the skewed-intensity distribution in natural images (i.e., because the mean intensity is greater than the median). This excess is maintained across scales by the spatial correlations.

Temporal Contrasts Are About Equally Positive and Negative. Besides spatial contrasts, ganglion cells also respond to temporal contrasts—caused by local increments or decrements in light intensity. Thus, we wondered whether the predominance of OFF cells might also indicate differences in the natural occurrence of increments and decrements. To test this, we first measured the statistics of light increments in 12 standard natural time series of intensities representing optic flow arising from viewer motion (32). We binned the intensities over a range of time intervals (0.8 ms to 1 s) and measured the probability of encountering an increase or decrease in intensity from one interval to the next. At each temporal scale, the distribution was symmetric around 0 (results for 100-ms bins in Fig. 4A), and the numbers of light increments and decrements were equal. To test whether this result was specific to optic flow, we constructed artificial time series by simulating fixational eye movements on static images (Materials and Methods). Again, at all temporal scales, the distribution of increments and decrements was symmetric (Fig. 4A).

Ganglion cells do not simply respond to light increments and decrements binned at some scale—rather they encode temporal contrast, understood as the response of temporal receptive fields that takes the form of a band-pass filter. Thus, we tested if there might be a predominance of negative temporal contrasts measured in this way. We constructed model temporal receptive fields as band-pass filters described by a difference of cascades of low-pass filters, \( p_1(t/\tau_1)e^{-n(t/\tau_1 - 1)} - p_2(t/\tau_2)e^{-n(t/\tau_2 - 1)} \), where \( \tau_1 < \tau_2 \) were time constants and \( n \) was the order of the two low-pass filters (7). Using a spatial binary white-noise stimulus, we measured temporal filters at the center of the spatial receptive field for a population of 77 brisk-transient cells (42 OFF and 35 ON) (Fig. 4B). We fit parameters to minimize root mean-squared error (RMSE). The mean RMSE was 0.027—comparable with noise fluctuations in the data. Mean values of \( n \), \( \tau_1 \), and \( \tau_2 \) were, respectively, 6, 67 ms, and 97 ms.

We found no significant difference in the fit parameters for ON vs. OFF cells. The mean time to peak of the measured ganglion cell filters—a primary measurement, not a fit—was 65 ms for OFF cells and 68 ms for ON cells. Thus, the temporal filters for ON and OFF brisk-transient cells are opposite in sign but otherwise approximately equal. This agrees with refs. 6 (ground squirrel), 33 (primate), and 34 (guinea pig). Slightly faster kinetics have been reported for ON parasol cells in primate (7) and for OFF cells in salamander (35).

To compute the distribution of temporal contrasts encountered by real ganglion cells, we convolved the natural and simulated time series of intensities described above with the average measured temporal filters. In both cases, the filter responses peaked at 0, were highly kurtotic (Fig. 4C), and showed a slight excess (1–3%) of negative responses (Fig. 3D). To test whether this result depended on the temporal kinetics of the receptive field, we computed the responses for a range of \( \tau_1 \) while keeping the ratio \( \tau_2 / \tau_1 \) fixed. The slight excess of negative responses persisted (Fig. 4D).

The excess in negative temporal contrast was small compared with the excess of negative spatial contrasts (10–15%) (Fig. 2 and SI Text). This suggests that the excess of OFF cells is driven by asymmetric spatial statistics. To test this, we studied model mosaics selective for negative and positive spatial contrasts.

Optimal Mosaics Have More OFF Elements. Given the measured excess of negative spatial contrast in natural scenes, a simple argument suggests that a mosaic with more OFF elements would transmit the most contrast information. Consider a retina with a single ganglion cell: contrast information transmitted by this retina will be maximized if this is an OFF cell, because the excess of negative contrasts makes it more likely to respond when another factor is equal. When the number of OFF ganglion cells is increased, the responses will have redundancies because of correlations in the natural visual input. This will decrease the relative advantage of OFF over ON cells. Eventually, adding ON cells will become equally useful, and therefore, the mosaic transmitting the most information should contain a mixture of OFF and ON cells but more OFF cells, as seen in the retina.
that all detailed response models embody. These features were (i) limited dynamic response range, (ii) a rectifying, saturating nonlinearity that fills this response range, (iii) noise, which effectively discretizes the response levels, and (iv) fixed amount of overlap within ON and OFF mosaics (about 2 SDs of the receptive-field centers) (6, 10).

**Information in a Mosaic of ON and OFF Elements.** We considered a mosaic of $N = N_{ON} + N_{OFF}$ retinal ganglion cells in spatially independent ON and OFF arrays, each covering area $A$. Elements were spaced evenly within each array and independently between arrays. The total information about a visual input conveyed by the array’s responses is $I = I_{ON} + I_{OFF} = M$, where $I_{ON}$ and $I_{OFF}$ give the mutual information between the natural-scene input and the arrays and $M$ is the mutual information between the OFF and ON arrays.

If ganglion cells were independent encoders, information in an array would equal the number of elements in the array multiplied by the information conveyed by a single element. Because contrast as measured by ganglion cells is uncorrelated, even at modest separations, ganglion-cell redundancy is largely a result of receptive-field overlap (10). Therefore, we can write $I_{ON, OFF} = p_{ON, OFF}N_{ON, OFF}I^{f_1}$, where $I^{f_1}$ is the information in single cell responses and the coefficient $0 < p < 1$ discounts for redundancy in information encoded by overlapping receptive fields (10). Thus, total information is $I = p_{ON, OFF}N_{ON}I^{f_1}_{ON} + p_{OFF, OFF}N_{OFF}I^{f_1}_{OFF}$. Receptive overlap is constant across cell types, because cell spacing is about two times the SD of the central receptive field (6, 10). We scaled receptive-field sizes with array spacing to maintain this degree of overlap. Thus, redundancy caused by overlap ($p$) was constant, independent of the cell density.

We took $I^{f_1}$ to be information in the response of a balanced filter (i.e., center and surround with equal normalization so that uniform illumination did not produce a response). Measured with spatiotemporal white noise, the surround is reported to be somewhat weaker than the center (7). We omitted this, because the balanced center-surround (contrast) component of filter responses dominates the information content of large arrays (10).

Information in the single-cell response was modeled by recognizing that the limited dynamic range and response noise together lead to an effectively finite number of signaling levels (firing rates). Larger receptive fields sum over more cones, and hence, the signal to noise ratio should grow as the square root of the number of summed elements (i.e., square root of the receptive-field area) (10, 36, 37). Hence, we took the number of signaling levels in the ON and OFF channels to be $l_{ON, OFF} = \beta_{ON, OFF}(A_{ON, OFF})^{1/2}$, where $A_{ON, OFF}$ is the receptive-field area and $\beta$ is a measure of the intrinsic signal to noise ratio of the channel. Taking the ON and OFF arrays to be evenly spaced, $l_{ON, OFF} = p_{ON, OFF}(A/N_{ON, OFF})^{1/2}$, where $A$ is the fixed area of the retinal patch being considered.

For simplicity, we took all signaling levels to be equally used. Similar results follow for any reasonable pattern of use (e.g., an exponential distribution of firing rates). With this simple encoding model, applying Shannon’s formula for response entropy gave $I^{f_1}_{ON} = - (1-p_{ON}) \log(1-p_{ON}) - \sum_{i=1}^{l_{ON}} (p_{ON}/l_{ON}) \log p_{ON}/l_{ON} = p_{ON} \log l_{ON} - p_{ON} \log p_{OFF} = p_{OFF} \log p_{OFF}$ and was similar for OFF cells, where $p_{ON}$ is the probability of encountering a positive contrast in natural scenes and $p_{OFF} = 1 - p_{ON}$ is the probability of negative contrasts. We assumed that the model receptive field responded to its input so that the entropy of the output was informative about the input. Loss of information to noise was included in the discretization of the signaling levels. We assumed that noise in each response level is roughly the same, and therefore, the frequency of finding each equal noise-response level is given by $p_{ON}/l_{ON}$. Thus, $I^{f_1}_{ON}$ measured the mutual information between the input and the ON receptive-field output.
The last step was to estimate mutual information $I$ shared between ON and OFF arrays. To do this, we observed that ON and OFF cells with disjunct receptive fields have uncorrelated responses and hence, do not share any information (10). However, when ON and OFF receptive fields overlap, their responses are anticorrelated. Thus, to approximate the interaction of ON and OFF arrays, we supposed that if an ON cell fails to respond, the overlapping population of OFF cells will do so and vice versa. Thus, the entropy of nonresponse of ON cells (the $\rho_{OFF}$ log $\rho_{OFF}$ term in $I^{ON}_{ON}$) duplicates information that is already conveyed by the OFF array and vice versa. Thus, the mutual information between the ON and OFF arrays could be subtracted by simply dropping this term. This gave

$$I \approx \rho_{ON}N_{ON}I^{(1)}_{ON} + \rho_{OFF}N_{OFF}I^{(1)}_{OFF},$$

with $I^{(1)}_{ON,OFF} = \rho_{ON,OFF}\log\rho_{ON,OFF} - \rho_{ON,OFF}\log\rho_{ON,OFF}$ with $\rho_{ON,OFF}$ as above. This simple expression captured the essential features of contrast encoding by retinal ganglion cells.

**In the Optimal Mosaic, ON and OFF Elements Carry Similar Information.** The balance between ON and OFF elements that maximizes contrast information can be evaluated by maximizing $I$ with respect to $N_{ON}$ while holding the retinal area $A$ and the number of mosaic elements $N$ fixed: $(dI/dN_{ON})|_{N_{ON}} = 0$. This gave

$$I^{(1)}_{OFF} - I^{(1)}_{ON} = \frac{1}{2}(\rho_{OFF} - \rho_{ON})$$

that characterized the optimal mosaic of OFF and ON elements.

To understand the meaning of this expression, observe that ON and OFF ganglion cells differ only slightly in their receptive-field overlap (6, 10), and as a consequence, the difference in their redundancy is negligible. Thus, taking $\rho_{ON} \approx \rho_{OFF}$,

$$I^{(1)}_{OFF} - I^{(1)}_{ON} \approx \frac{1}{2}(\rho_{OFF} - \rho_{ON})$$

in the optimal mosaic. The left-hand side is the difference in independent information encoded by individual OFF and ON elements ($\sim 0.5$ bits each in the optimal mosaic with typical parameters) (Fig. 5a) when $\rho_{OFF} - \rho_{ON} \sim 0.1$ (Fig. 2D). Thus, the difference in information between an ON–OFF pair, divided by the total, is $\sim 0.05/3 = 1.5\%$. In other words, in the optimal mosaic, individual OFF and ON elements convey similar amounts of information.

**Mosaics with More OFF Elements Maximize Contrast Information.** To evaluate the fraction of OFF elements in the optimal mosaic, we recalled that the signal-to-noise ratios (SNRs) of ON and OFF receptive fields and redundancies within their arrays are similar (10, 27). Thus, it was helpful to define parameters that characterized both the average of the number of signaling levels in ON and OFF channels, $I = [(\rho_{ON} + \rho_{OFF})/2]4(A/N)^2$, and the fractional difference in their redundancy and intrinsic SNR, $\gamma = (\rho_{OFF} - \rho_{ON})/(\rho_{OFF} + \rho_{ON})$ and $\mu = (\rho_{OFF} - \rho_{ON})/(\rho_{OFF} + \rho_{ON})$.

Solving the optimization condition (3) to linear order in the small parameters $\gamma$ and $\mu$ gave the optimal OFF fraction $N_{OFF}/N = (1/2) + (\rho_{OFF} - \rho_{ON})[\log(2) - 3/2] + \mu + \gamma[\log(2) - 1/2]$.

Assuming similar intrinsic SNRs and redundancies in the ON and OFF pathways ($\mu \approx 0; \gamma \approx 0$), $\sim 10$ signaling levels ($\sim 10$) (27) and $\rho_{OFF} - \rho_{ON} \sim 0.1$ (Fig. 2) then gives

$$N_{OFF}/N \approx 0.64 \text{ or } N_{OFF}/N_{ON} \approx 1.77.$$

This ratio is in the measured range.

Receptive-field profiles and overlap, and noisiness of OFF and ON cells might vary between cell types and species. This could change the fraction of negative contrast responses ($\rho_{OFF}$), the relative redundancy ($\gamma$), the relative SNR ($\mu$), and the average numbers of signaling levels ($l$). Hence, we varied these parameters in the model and asked how they affect the optimal OFF fraction. We found that a significant excess of OFF elements persists in the optimal array over substantial variations of the parameters [5% $\leq \rho_{OFF} \leq 20\%$, $5 \leq l \leq 15$, and 20% variations in relative redundancy ($\gamma$) and relative SNRs ($\mu$) of OFF an ON cells] (Fig. 5).

**Discussion**

All vertebrate retinas rectify cone signals into OFF and ON circuits. An explanation for this architecture is that it doubles the dynamic range (38). It may also be metabolically efficient, because both types respond sensitively to small variations while maintaining low firing rates. Maintaining low rates is important, because information rates increase sublinearly with the spike rate (39) and energy cost and axonal volume increase supraneously with firing rate (39–41). Thus, space and energy efficiency (bits/μm²; bits/ATP) improve when contrast signals are rectified into lower rate ON and OFF channels.

Our results suggest another reason to use separate OFF and ON mosaics: to allow structural adaptation to natural scenes. OFF arbors, being smaller, are nearly 2-fold more numerous than ON arbors (Fig. 1), a difference that holds across cell types of markedly different spatial and temporal bandwidths and across species. This hinted that OFF and ON arrays might be adapted to match an excess of dark contrasts in natural scenes. That is what we found (Figs. 2 and 3). Given that dark and bright contrasts in natural images distribute unequally, separate circuits matched to the characteristic distributions will use the retina’s resources more efficiently (Fig. 5).

Because our concise model captures key general features of the ganglion-cell contrast response, these results should generalize to more detailed models also. We omitted the maintained firing rate and resulting gentler (i.e., less rectifying) nonlinearity reported for ON cells in some species [primate (7) and guinea pig (34)], because, although it imbues an ON cell with a small OFF response, we measured that this component contributes negligibly to contrast detection by an ideal observer (10). This occurred because
the OFF response of ON cells, arising from a depression of the maintained firing rate, was noisy and largely redundant with the stronger response in the OFF array. Our model also omitted a firing threshold beyond ON/OFF rectification. Including it would have little effect, because the key result is driven by the excess of negative contrasts, and this persists even in the presence of a threshold (result for a 1% threshold shown in Fig. 2). Within our model, a purely excitatory array of OFF ganglion cells would have a substantially higher threshold than ON cells or if ON cells devoted a significant fraction of their bandwidth to OFF responses, but neither of these matches measurements.

We showed that optimal mosaics are organized so that individual OFF and ON elements transmit equal amounts of information. This correlates with our finding that OFF and ON dendritic arbors, despite a 2-fold difference in retinal area, count equal numbers of excitatory synapses (Fig. 1 B and C). Perhaps a simple principle connects a concrete fact of neuroanatomy with the abstract concept of information: equal synapses for equal bits.

**Materials and Methods**

**Anatomy.** Retinas were harvested from adult guinea pigs and prepared for anatomy in accordance with the guidelines of the University of Pennsylvania and National Institutes of Health (13). Ganglion cells were identified by staining with Syto 13, and the larger somas were injected with DiI (1% dissolved in absolute ethanol). Injected cells were imaged by confocal microscopy (40x; oil-immersion objective). To prevent shrinkage, retina was kept moist (0.1 M phosphate buffer), and to prevent compression, a spacer (~200 μm) was placed between the slide and coverslip. ON brisk-transient cells had large somas (15–20 μm), which were multicascade of dendrites exiting laterally; vs. OFF brisk-transient cells, which were smoothly rounded because of dendrites exiting vertically. Cell type was validated by dendritic morphology and stratification depth.

**Physiology.** Extracellular spikes were obtained from brisk transient ganglion cells in vitro, responding to photopic white noise projected from a CRT monitor at 60 Hz (10). Cells were selected based on soma size (15–20 μm) and transient response to a light flash. White noise was a 16 x 16 checkerboard (75 x 75 μm per patch) in a gray background. The intensity of each patch was updated on alternate monitor frames according to a random binary sequence.

**Setting Response Thresholds.** To set a 4% contrast threshold (~1% to model measurements) (25), we first measured a ganglion-cell filter’s center radius from its zero-crossing. Then, we made a spot of this radius that was 4% brighter than background. The response of the divisively normalized filter centered on this spot was set as the threshold for model cell response.

**Artificial Image Construction.** Gaussian noise images (Fig. 3A) had pixels drawn independently from a Gaussian (with an offset to avoid negative intensities). Natural noise images (Fig. 3B) had pixels drawn from the natural-intensity distribution (24). Pink noise (Fig. 3C) was constructed by convolving Gaussian noise with a 1/f filter. Natural pink noise (Fig. 3D) remapped intensities in pink noise to the natural-intensity distribution while preserving pink-noise correlations.

**Naturalistic Time-Series Construction.** Fixational time series were random walks through natural images—at each time step, the nearest neighbor of the current pixel was randomly selected. To match the ~0.5%/s velocity of fixational eye movements (42) and because image pixels were separated by 1/60°, we required the expected displacement of the random walk to be 30 pixels/s. A random walk of M steps has a mean displacement of √M—thus, we required √N ~ 900 and took each time step to be 1/900 s.

**ACKNOWLEDGMENTS.** We thank B. Backus and R. Smith for discussions and S. Fina for help with figures. We were supported by National Institutes of Health Grant RO1 EY08124 (to B.G.B., Y.-H.K., and P.S.), National Science Foundation Grant IBN-0344678 (C.P.R. and V.B.), and National Institutes of Health Training Grants T32-07035 and T32-07128 (to C.P.R.). During this work, V.B. was the Helen and Martin Chooljian Member at the Institute for Advanced Study, Princeton and visited the Aspen Center for Physics.


9. Jin JZ, et al. (2008) We off and on elements transmit equal amounts of information. This correlates with our finding that OFF and ON dendritic arbors, despite a 2-fold difference in retinal area, count equal numbers of excitatory synapses (Fig. 1 B and C). Perhaps a simple principle connects a concrete fact of neuroanatomy with the abstract concept of information: equal synapses for equal bits.


15. Jin JZ, et al. (2008) We off and on elements transmit equal amounts of information. This correlates with our finding that OFF and ON dendritic arbors, despite a 2-fold difference in retinal area, count equal numbers of excitatory synapses (Fig. 1 B and C). Perhaps a simple principle connects a concrete fact of neuroanatomy with the abstract concept of information: equal synapses for equal bits.
