

Statistics of natural scenes and the cortical representation of color

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ABSTRACT

In this paper we investigate the spatial correlational structure of orientation and color information in natural images. We compare these with the spatial correlation structure of optical recordings of macaque monkey primary visual cortex, in response to oriented and color stimuli. We show that the correlation of orientation falls off rapidly over increasing distance. By using a color metric based on the a-b coordinates in the CIE-Lab color space, we show that color information, on the other hand, is more highly correlated over larger distances. We also show that orientation and color information are statistically independent in natural images. We perform a similar spatial correlation analysis of the cortical responses to orientation and color. We observe a similar behavior to that of natural images, in that the correlation of orientation-specific responses falls off more rapidly than the correlation of color-specific responses. Our findings suggest that: (a) orientation and color information should be processed in separate channels, and (b) the organization of cortical color responses at a lower spatial frequency compared to orientation is a reflection of the statistical structure of visual world.

Keywords: Statistics of natural images, cortical maps, ecological theory of vision

1. INTRODUCTION

The ecological theory of perception states that early sensory processing by the brain is adapted to the statistics of the natural environment. According to the theory, this adaptation, shaped by evolutionary pressure, provides for an efficient transmission of information from the periphery to the higher-order centers of the brain,^{1,2} given unavoidable constraints imposed on the transmission channel in terms of dynamic range, connectivity and number of fibers. These ideas are best exemplified by the processing in the early visual pathway, where the expected redundancies in the input are eliminated. This results in a drastic reduction of the high dimensionality of retinal information arising from sampling of the visual field (from the sheer number of rods and cones), thereby facilitating the transmission of this information by a limited number of fibers. Perhaps the most striking use of this approach was shown by Atick and Redlich,³ who derived the spatial receptive field properties of retinal ganglion cells as an optimal filter for the two-point correlations of contrast in natural images. These correlations, well characterized by a power-law spectrum $s(k) \sim k^{-1}$, imply that nearby retinal receptors are highly redundant,^{4,5} and therefore their information need not be transmitted in full. Similarly, Dan *et al.* showed that a particular sub-population of geniculate cells (x-lagged), are optimal filters for removing temporal redundancies.⁶

In contrast to the relative success of the theory in early processing stages, the cortex has proved more refractory to interpretations based on information-theoretic premises. A prominent property of visual cortical areas is the topographic organization of features such as orientation, color, spatial frequency and direction, whereby nearby units tend to display similar feature preferences.⁷ However, different attempts to reconcile topography with the ecological theory have failed. Sejnowski and Bell have shown that oriented edge detectors are the maximal information filters for the ensemble of natural images,⁸ but these filters cannot be spatially organized on the basis of the similarity of their responses. Indeed, cortical map clustering seems to *preserve* redundancies rather than reduce them, at least when the average firing rate is considered as the coding response*.

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*For a perspective that incorporates fine temporal components of the response, see Ref. 9

Self-organized feature maps, on the other hand, have proved to be a more amenable model of the visual cortex. Kohonen’s self-organized algorithm has been applied successfully to model the process of map formation, under the principle that the topology of the input space should be preserved in the topology of neural space.¹⁰ Maps trained with oriented stimuli recreate to a large extent the spatial organization of primary visual cortex,¹⁰ including selectivity and linear zones punctuated by point and line discontinuities in the case of orientation, and a biologically consistent spatial layout of color selectivity.¹¹ Considered as part of the class of competitive learning algorithms, self-organized maps also have the advantage of a relatively simple physiological interpretation.¹² Moreover, in a seemingly significant departure from the ecological theory, these maps allocate more neural space to more frequent inputs,¹⁰ as opposed to equalize them with the more infrequent ones.

It is pertinent, therefore, to ask the following question: what is the relationship between the *statistics of natural images* and the *spatial structure of cortical maps*? More specifically, is it possible to identify a functional dependence of cortical response maps of orientation and color with the ensemble properties of the corresponding inputs? In the next pages we will present the case for a tentatively positive answer to this question, building on the statistical analysis of natural scenes and on optical imaging data of the mammalian cortex.

2. STATISTICS OF NATURAL IMAGES

The scaling analysis of contrast and luminance has been the focus of many studies. Scaling measurements involve studying how the probability of finding a cooccurring pair changes as a function of the relative distance. A classic result in the analysis of natural scenes is that the luminance of pairs of pixels is correlated and that this correlation is scale-invariant.^{1,3,4} This indicates that statistical dependencies between pairs of pixels do not depend on whether the observer zooms in on a small window or zooms out to a broad vista. The scale invariance results from stable physical properties such as a common source of illumination and the existence of objects of different sizes and similar reflectance properties.⁵

Few studies have focused on the structure of long-range correlations of other visual attributes. A report by Sigman *et al.*,¹³ analyzed the spatial distribution of orientation information in natural scenes. They showed that information about the presence of iso-oriented lines in natural images is correlated over relatively short distances, following specific power-law statistics for co-linearity; other pairwise arrangements display shorter correlations. This study also suggested a possible relationship between orientation statistics and the extra-classical receptive field properties of neurons in the visual cortex.

Though the relation between color image statistics and the neural representation of color has been studied before,¹⁴ the primary focus of such research has been on the spectral response properties of the LMS cones, and therefore are not relevant for the question addressed in this manuscript. Several studies have examined the statistical relation between the components of color, as described by three channels comprising a luminance channel, an RG channel and a BY channel.^{5,15} Mante *et al.*¹⁶ showed that luminance and contrast are statistically independent in natural scenes. They demonstrated that the joint probability distribution for luminance and contrast is the product of the marginal probability densities. It is interesting to investigate the joint distribution of orientation and color statistics in natural images. Tailor *et al.* derived the independent components of natural images, and showed that they contain oriented luminance edge filters, and color opponent red-green and blue-yellow filters. The joint probability distribution of orientation and color information was not explicitly computed in their work.

In Section 4 we will present results indicating that orientation and the (L,a,b) color components have significantly different spatial structures of correlations, and that moreover they are statistically independent[†].

[†]The conversion from RGB to CIE $L^*a^*b^*$ coordinates is performed using the ITU recommended D65 white point reference in the ITU BT.709 standard, and using the equations given in Wyszecki and Stiles¹⁷[p. 166]. For the sake of notational convenience, we will use (L, a, b) to denote CIE $L^*a^*b^*$. We also performed our analysis using a calibrated LMS space, as provided by the creators of the image database.¹⁹ The results we obtained were virtually identical for the two color spaces.

2.1 Natural Images Analysis

In order to compute the spatial auto-correlation of orientation and color in natural images, we computed their corresponding fields as described below. For the orientation field:

1. The images were processed with oriented G_1^θ steerable filters¹⁸ with 24 bins of orientation between 0 and 2π . These filters are derived from gaussian functions with standard deviation equal to 3 pixels; this process results in an orientation vector for each pixel, $S(0, \pi/12, \dots, 23\pi/12)$.
2. For each pixel, the best estimate for orientation was computed as the one that maximizes the filter output, $\theta_e = \max \arg S(\theta)$.
3. The orientation field was computed as $\Psi_o(\vec{x}) = S(\theta_e)e^{i\theta_e}$

For the color field:

1. The images were converted into the LAB space, to yield for each pixel the vector (L, a, b) .
2. The color field was computed as $\Psi_c(\vec{x}) = e^{i\theta_c}$, where $\theta_c = \arctan \frac{b}{a}$

Finally, for each field, the autocorrelation function was computed over a representative ensemble of natural images, assuming translational and rotational invariance,

$$c(d) = \sigma^{-1} \left\langle \Re \left[(\Psi(\vec{x}) - \bar{\Psi})(\Psi^*(\vec{x} + \vec{x}') - \bar{\Psi}^*) \right] \right\rangle_{|\vec{x}|=d} \quad (1)$$

where the brackets signify average over \vec{x} and over the ensemble of images, $\bar{\Psi}$ is the average field, $*$ is the complex conjugate operator, \Re the real part operator, and σ the variance, defined as:

$$\sigma = \left\langle \Re \left[(\Psi(\vec{x}) - \bar{\Psi})(\Psi^*(\vec{x}) - \bar{\Psi}^*) \right] \right\rangle \quad (2)$$

where, as in Eq. (1) the average is over \vec{x} and the ensemble of natural images. The invariance assumptions allow for a fast implementation via Fourier transform; we have observed in previous work that rotational invariance might not be fully warranted,¹³ as vertical and horizontal orientations tend to be over-represented. For the sake of completeness, we will show in Section 4 that these differences are present in our database; however, given their measured values, we do not expect them to affect the results on scaling behavior reported here.

The database of natural images consists of 850 color calibrated pictures from the McGill Calibrated Colour Image Database, and includes pictures of animals in their environment, foliage, land and water landscapes, shadows in natural and man-made settings, close-ups of natural and fabricated textures, close-ups of flowers, fruits and vegetables, and city scenes;¹⁹ two examples are shown in Fig. 1.

3. STATISTICS OF CORTICAL MAPS

The visual cortex is perhaps the most researched brain area; in particular, its response to orientation has been very well characterized at the single-cell as well as the population levels, revealing a spatial structure of orientation columns, punctuated by point and line discontinuities.⁷ Other visual attributes such as visual field position, spatial frequency, direction and ocular dominance are mapped in similar fashion. Some features of these maps can be understood in terms of the broad topology of the input space: specifically, self-organized map formation predicts that an intrinsically circular variable such as orientation will create point-discontinuities (known as pinwheels), as any continuous map of $S^1 \times R^2$ (i.e. orientation and retinotopy) onto R^2 will be non-invertible.²⁰

In comparison with orientation, the cortical response to color attributes in the visual field has been more difficult to characterize. Functional brain imaging studies in humans have uncovered cortical areas that are preferentially activated by chromatic stimuli. Moreover, psychophysical and lesion reports suggest the existence of a specialized color processing system that is, to some extent, unconcerned with the processing of other visual features. The pioneering work of Livingstone and Hubel²¹ revealed that the cytochrome oxidase dense blobs

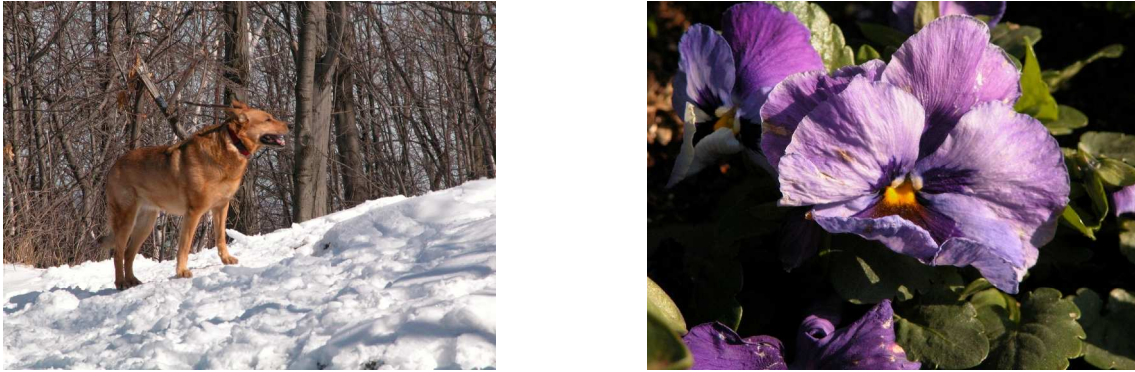


Figure 1. Representative images from the ensemble used to estimate the statistics of natural images.

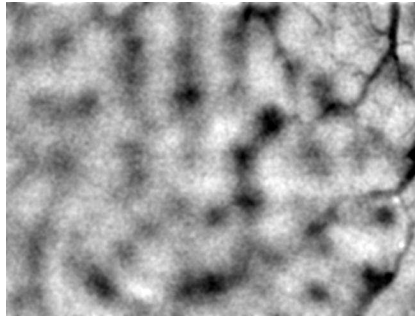


Figure 2. Optical recording of macaque cortex, visual area V1 showing the response to a uniform color patch. The image size is 652x492 pixels at 6μ /pixel.

in the primary visual cortex (V1), and the regions between them (interblobs), contain populations of neurons that differ in their selectivity for color or orientation. More recently, Xiao *et al.* demonstrated, using optical imaging, that color information is reliably encoded by spatial patterns of activity across V1 and the extra-striate area V2; moreover, color and orientation are mapped in segregated compartments, and display different spatial properties.^{22–25} Using a support-vector machine (SVM) methodology to identify regions that contained the most information in discriminating color and orientation, they showed that areas that process orientation are relatively small, and distributed at a high spatial frequency. On the other hand, areas that process color are comparatively larger and distributed at a lower spatial frequency. In the present study, we demonstrate that these differences can be quantified, and (tentatively) related to the statistical properties of natural images.

3.1 Optical Image Analysis

The data used here[‡] were derived from optical recordings in macaque V1, upon presentation of oriented black and white square wave drifting gratings (for orientation), and uniform field color stimuli (for color). Figure 2 shows a typical optical image recording from macaque monkey cortex visual area V1.

For orientation and color we computed *information fields*, based on the SVM-obtained classification of the cortical response to the corresponding stimulus modality. Given a two-class data set $\{\bar{y}_i, c_i\}$, where \bar{y} represent

[‡]Detailed information about the experimental protocol is available in Ref. 25

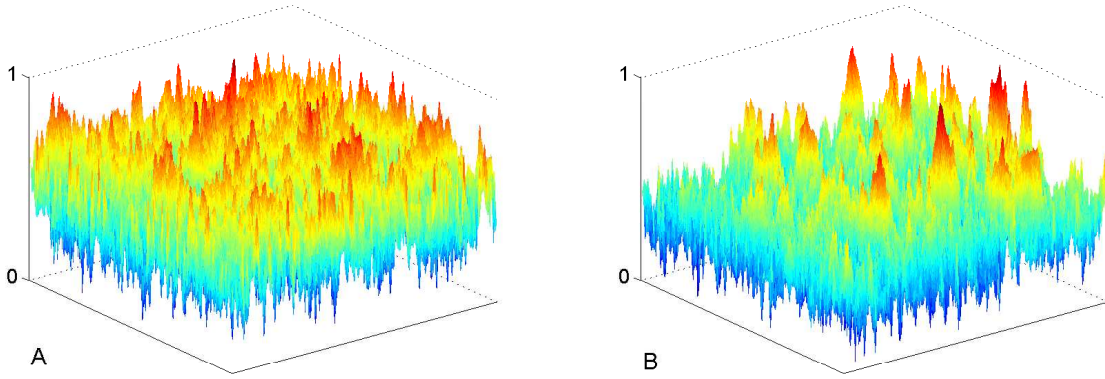


Figure 3. Cortical information fields for orientation (A) and color (B). The fields were normalized to their maximal value; the resolution is 400x400 pixels, and each pixel corresponds to 6 μm over the cortical surface.

the data and $c = \{-1, 1\}$ the classes, the objective of SVM is to minimize the norm of the weight vector associated (perpendicular) with the separating hyperplane, constrained to a good separation between the classes. Formally, it is equivalent to the following optimization problem:

$$\text{minimize: } \|\vec{w}\| + \lambda \sum_i \epsilon_i, \text{ subject to: } c_i(\vec{w} \cdot \vec{y}_i - b) \geq 1 - \epsilon_i \quad (3)$$

where ϵ is a misclassification or slack variable, λ a constraint on misclassifications, and b is an offset constant in case the data are not centered.

The orientation (color) classification consisted of two-group classifications, one for each of the possible pairs of different stimulus orientations (color). Each two-group classification was associated with a weight \vec{w}_n . For each pair, the i -th component of the weight vector w_{ni} represents the relative contribution that the given pixel makes to the given two-group classification. To estimate the relative contribution of each pixel to the entire process of classification, we calculated the *relative information field* for orientation (color) as:

$$\Phi(\vec{x}(i)) = \sqrt{\sum_n w_{ni}^2} \quad (4)$$

where $\vec{x}(i)$ represents the two-dimensional coordinates corresponding to the i -th pixel. Figure 3 shows information fields for orientation (3A) and color (3B). The fields have been normalized to their maximum value; note that differences in the spatial structure of the fields are evident to the naked eye.

Similarly to Eq. (1), we computed the auto-correlation function for each field as follows:

$$c(d) = \sigma^{-1} \langle [(\Phi(\vec{x}) - \bar{\Phi})(\Phi(\vec{x} + \vec{x}') - \bar{\Phi})] \rangle_{|\vec{x}|=d} \quad (5)$$

$$\sigma = \langle [(\Phi(\vec{x}) - \bar{\Phi})^2] \rangle \quad (6)$$

where as before $\bar{\Phi}$ is the mean field, and the average is over all cortical positions.

4. RESULTS

The results of the spatial auto-correlation analysis for orientation and color in natural images, and for the cortical response to orientation and color are presented in Fig. 4 and Fig. 5, respectively. In the case of natural images,

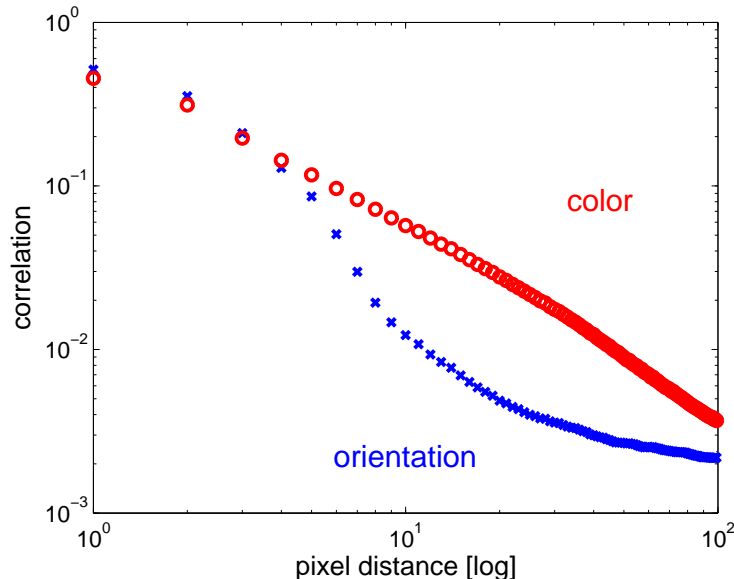


Figure 4. Spatial auto-correlation of the orientation and color fields in natural images.

the plot shows that the color correlation decays with a long tail; indeed, it approaches a power-law (i.e. algebraic) scaling, evident by the linear stretch in the double-log plot. In contrast, the orientation field decays much faster, which can be approximated by an exponential function (data not shown).

For the cortical responses, both orientation and color decay in a quasi-exponential form, but the orientation field decays at a rate approximately two to three times higher than the color field, until it reaches its plateau at $300 \mu m$. The plot looks remarkably similar to that of natural images in terms of the scaling behavior. It must be noted that the cortical response plot is semi-log, whereas that for natural images, as mentioned above, is double-log. The reason for presenting the data in this form is that the visual cortex maps the retinal space through a *conformal* logarithmic transformation $c = \log(z + z_0)$, where z is distance to the fovea, c cortical distance to the foveal representation, and z_0 a constant.²⁶ We cannot make a precise statement about the location of the fovea in the cortical fields and therefore the comparison between the plots is only qualitative at this point; nevertheless, the fact that for both natural images and cortical responses color has a significantly longer tail than orientation is independent of our choice of double-log and semi-log for the respective plots.

In order to compare the results summarized by Fig. 4 to a null hypothesis, we compared the correlation structure of natural images with a specific type of man-made images, which consisted of five paintings of the American painter Jackson Pollock. We chose these paintings as they are considered to be abstract art, and the apparent lack of correlation structure in them. We applied the same methodology as before to compute the correlation statistics for orientation and color. The result is shown in Fig. 6. Next, we randomized the pixel locations in these paintings, and computed the correlation statistics, as shown in Figure 7. The results in Fig. 6 show that over larger spatial scales (say 10 pixels and beyond), the correlation behavior of color and orientation is very similar, and this holds true for both the original and randomized versions of the images. Moreover, the correlation in this case decays much faster than for natural images, five decades versus three decades for the same two decades of pixel distance.

It appears that there are relatively few studies that examine the statistical relation between orientation and color, and this prompted us to explore this question. We computed the joint statistics of orientation and color as follows. We estimated the pairwise joint probability distributions of orientation angle θ_e with each of the color (L, a, b) values, giving rise to three distributions, (θ_e, L) , (θ_e, a) and (θ_e, b) . We used the same binning procedure as before with 24 bins for θ_e , L, a, b. More sophisticated procedures can be used if necessary such as the use of splines to smooth the binning.²⁷ The plots in Figure 8 clearly indicate that the pairwise product of the

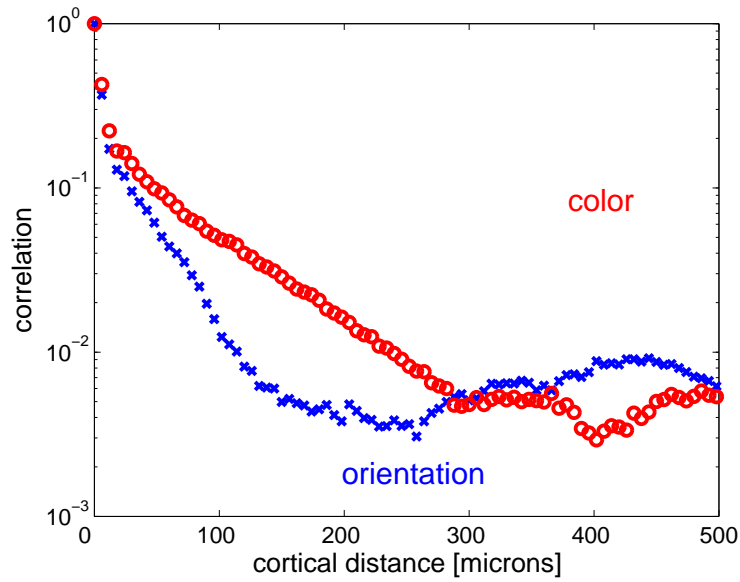


Figure 5. Spatial auto-correlation of the orientation and color fields in the macaque visual cortex. The fields were obtained by applying a classification approach to the response to color and orientation stimuli.²⁴ The distance is measured in microns over the cortical surface.

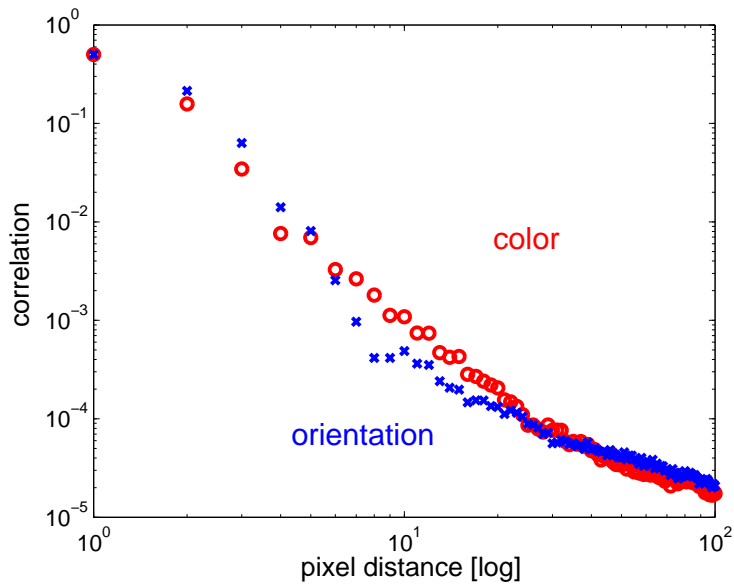


Figure 6. The correlation statistics gathered over five Jackson Pollock paintings.

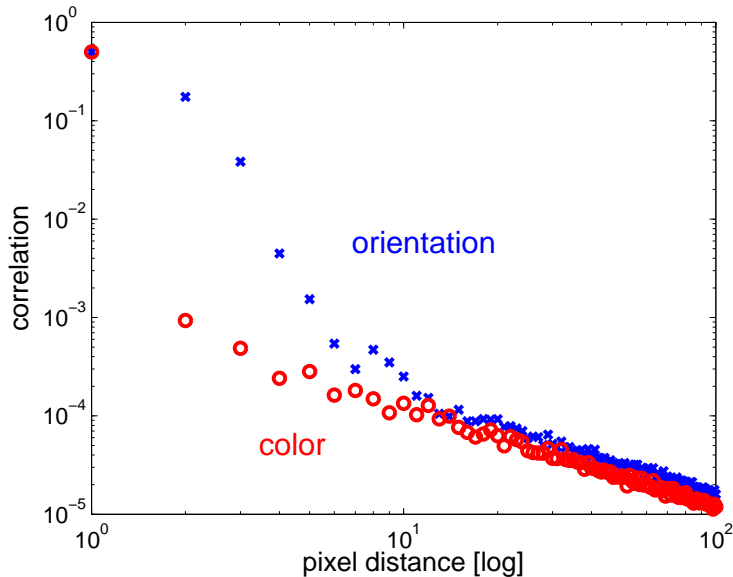


Figure 7. The correlation statistics computed over randomized versions of Jackson Pollock paintings.

marginal probability density functions is equal to the joint probability distribution functions $P(\theta_e, L)$, $P(\theta_e, a)$ and $P(\theta_e, b)$. Thus, $P(\theta_e, L) = P(\theta_e)P(L)$, where $P(\theta_e)$ is the probability density function of θ_e and $P(L)$ is the probability density function of luminance, L .

In order to make the measurement of independence more rigorous, we computed the pairwise mutual information between (θ_e, L) , (θ_e, a) and (θ_e, b) respectively. The mutual information between two variables A and B is defined in terms of their entropies, $H(A)$ and $H(B)$ as follows. Let A possess N finite states, $\{a_1, a_2, \dots, a_N\}$. The entropy $H(A)$ is given by

$$H(A) = - \sum_{i=1}^N p(a_i) \log p(a_i) \quad (7)$$

The entropy $H(B)$ is similarly defined, where B possess M finite states. The joint entropy $H(A, B)$ is defined by

$$H(A, B) = - \sum_{i=1}^N \sum_{j=1}^M p(a_i, b_j) \log p(a_i, b_j) \quad (8)$$

The mutual information, $MI(A, B)$ is defined by

$$MI(A, B) = H(A) + H(B) - H(A, B) \geq 0 \quad (9)$$

The mutual information is zero when A and B are statistically independent.

We estimated the pairwise mutual information $MI(\theta_e, L) = 0.0022$ bits, $MI(\theta_e, a) = 0.0019$ bits, and $MI(\theta_e, b) = 0.0029$ bits. We also measured the mutual information between θ_e and the hue angle, $\theta_c = \arctan \frac{b}{a}$ to be $MI(\theta_e, \theta_c) = 0.0028$ bits. Since these pairwise mutual information measures are close to zero, we conclude that orientation is independent of the (L, a, b) color components. This observation indicates that orientation and color information should be processed in separate pathways, as seems to be true in human and primate visual systems.

Taylor *et al.*²⁸ demonstrated that the independent components of natural images contain oriented edge and color filters consisting of blue-yellow and red-green opponent receptive fields. Our results are in agreement with this finding, though we used a different approach, where color (L, a, b) values were explicitly computed. Furthermore, we used a considerably larger number of natural images for our statistical analysis, 850, as compared to 20 used by Taylor *et al.*

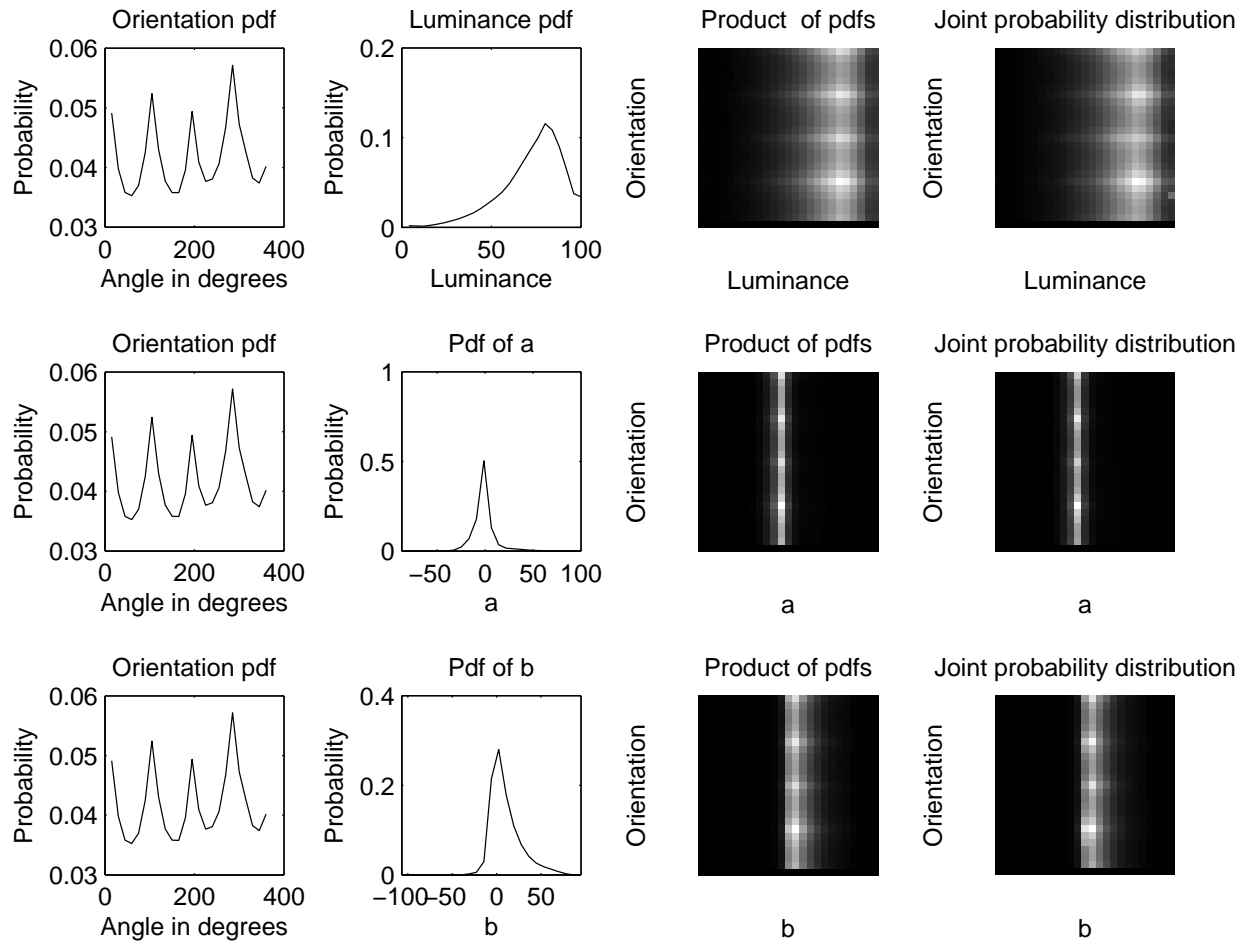


Figure 8. The marginal probability density functions are displayed in the first two columns. The probability density function for orientation $P(\theta_e)$ is shown in the first column. The second column contains probability density functions for L, a and b. The third column shows the pairwise product of the two marginal probability density functions in the first two columns. The fourth column shows the joint probability distribution for the variables in the first two columns. These plots show that the joint probability distribution appear similar to the marginal probability density functions, suggestive of statistical independence of the variables represented in the first two columns.

5. DISCUSSION

We have presented novel results showing that orientation and color attributes in the ensemble of natural images display different spatial structure of auto-correlations, whereby color is significantly correlated over longer distances than orientation. At the same time, we showed that this qualitative difference between the statistics of orientation and color has a parallel in the spatial structure of the cortical responses (as measure by the information fields) to the same attributes; i.e. the patterns of response to color stimuli are significantly more spatially correlated than those for orientation. These results are preliminary, and we cannot conclude that the qualitative match of the correlational structures in the input and cortical spaces is the result of a causal relationship. In particular, more statistics need to be collected for a thorough characterization of the cortical response to color. Though orientation has been much more studied than color, the specific question that we have asked in the present manuscript, that of the relationship between the spatial properties of visual attributes and that of their cortical responses, also requires a new look at the well-established properties of orientation maps.

We also demonstrated the statistical independence of orientation and color information in natural images. This indicates that it would be necessary to process orientation and color information in separate channels, as is observed in the human and primate visual systems. The spatial correlation structure of orientation and color information may also govern the spatial organization of units in the orientation-processing and color-processing channels respectively.

We explicitly motivated our approach on the ecological theory of perception. This theory has been dominated by information-theoretic concepts, i.e. the idea the function and architecture of the nervous system needs to maximize information transmission in the context of biological constraints. At present, experimental confirmation of this theory has come from local neural features, such as the response properties of individual neurons. Our results point, however, to a more general interpretation of the ecological theory, in which the input space shapes the organization of neural responses at a population level. This organization might be ultimately related to the satisfaction of information-theoretic constraints, but it seems more likely that it is the result of processes with explicit spatial constraints. In particular, models of cortical organization that emphasize the role of spatial structure in coding and processing can make testable predications about the relationship between the input ensemble and the neural map of responses.

One plausible consequence of our results is that, if color and orientation information are coded by separate populations of cortical neurons,²¹ then color-coding units should have larger receptive fields than the orientation-coding ones. This prediction is based on an additional assumption that the receptive field size of each unit should be as large as the visual field within which the value of the attribute coded by the given unit tends to be relatively constant in natural scenes. A large receptive field reduces photon noise, and might also reduce the number of units required to sample the entire scene, as compared with a small receptive field. Our prediction is supported by a recent finding that the average receptive field size of color-selective neurons in V1 is 1.5 times as large as that of orientation-selective ones.²⁹

Finally, we would like to emphasize that even though we focused on orientation and color, the ideas developed in the present manuscript should be valid for other significant visual attributes, as well as the other primary perceptual modalities.

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