The two-dimensional Gabor function adapted to natural image statistics: An analytical model of simple-cell responses in the early visual system

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Abstract

The two-dimensional Gabor function is adapted to natural image statistics by learning the joint distribution of the Gabor function parameters. The joint distribution is then approximated to yield an analytical model of simple-cell receptive fields. Adapting a basis of Gabor functions is found to take an order of magnitude less computation than learning an equivalent non-parameterized basis. Derived learning rules are shown to be capable of adapting Gabor parameters to the statistics of images of man-made and natural environments. Learning is found to be most pronounced in three Gabor parameters that represent the size, aspect-ratio, and spatial frequency of the two-dimensional Gabor function. These three parameters are characterized by non-uniform marginal distributions with heavy tails – most likely due to scale invariance in natural images – and all three parameters are strongly correlated: resulting in a basis of multiscale Gabor functions with similar aspect-ratios, and size-dependent spatial frequencies. The Gabor
orientation and phase parameters do not appear to gain anything from learning over natural images. Different tuning strategies are found by controlling learning through the Gabor parameter learning rates. Two opposing strategies include well-resolved orientation and well-resolved spatial frequency. On image reconstruction, a basis of Gabor functions with fitted marginal distributions is shown to significantly outperform a basis of Gabor functions generated from uniformly sampled parameters. An additional increase in performance results when the strong correlations are included. However, the best analytical model does not yet achieve the performance of the learned model. A comparison with estimates for biological simple cells shows that the Gabor function adapted to natural image statistics correctly predicts some key receptive field properties.

1 Introduction

We know that simple cells in the primary visual cortex have spatially-localized receptive fields, and are tuned to visual stimulus features such as orientation, spatial frequency, and location in the visual field (Swindale, 1996). These simple cells are also the final stage of a mapping of visual stimulus features from the visual field to a retinotopic position on the surface of the primary visual cortex (Durbin and Mitchison, 1990). Simple-cell receptive fields have previously been modeled by the Gabor function (Marcelja, 1980; Daugman, 1985; Jones and Palmer, 1987), which has the unique property of being optimally localized in the space and spatial frequency domains. Models have also been proposed to explain how neural activity and visual experience could lead to the development of simple-cell receptive fields, as well as their larger-scale organization into a cortical map (Swindale, 1996).

Early neural network models described the self-organization of orientation selectivity through Hebbian learning with localized, oriented, input patterns (von der Malsburg, 1973), and uncorrelated random input (Linsker, 1986). More recent models make use of realistic inputs related to natural sensory data. Natural sensory data contains redundancy, and early work by Attneave and Barlow led them to propose that one role of the sensory system is to re-code sensory data in a way that reduces redundancy. This became known as the efficient coding hypothesis (see Olshausen (2013a) and Hyvärinen et. al (2009) for recent reviews). While reducing redundancy may not
be the only (or even main) goal of simple cells, models capable of efficient coding of natural images have been shown to develop realistic simple-cell receptive fields (Olshausen and Field, 1996, 1997; Bell and Sejnowski, 1997; Hyvärinen and Hoyer, 2000; Hyvärinen et. al., 2001; Rehn and Sommer, 2007; Olshausen, 2013b). In this class of models input consists of natural images – i.e., natural sensory data at the level of photoreceptors in the retina, and a Hebbian learning rule implementing an efficient coding strategy results in the adaptation of a set of basis functions according to the statistics of the input. The resulting basis functions (also called “atoms”) are used to efficiently reconstruct natural images, and are closely related to neural receptive fields. The output of these models is a sparse code, meaning that an image can be reconstructed using only a small number of “atoms”.

The efficient coding models just described attempt to find structure in natural images through high-order image statistics. Redundancy in images is the result of strong pixel correlations: natural images are not evenly distributed in pixel-space, unlike images generated from uncorrelated random pixel-values (Field, 1994). Reducing redundancy therefore requires pixel decorrelation. It is known that second-order pixel correlations are completely described by the Fourier amplitude (or power) spectrum, while higher-order statistics is contained in the Fourier phase spectrum (Field, 1994). Efficient coding models generally attempt to remove correlations by seeking a linear (or nonlinear) transformation of the input pixels that reduces their marginal entropy. In models utilizing high-order image statistics this has the result of making the output sparser (Daugman, 1989; Olshausen and Field, 1997; Bell and Sejnowski, 1997; Hyvärinen and Hoyer, 2000; Hyvärinen et. al., 2001; Rehn and Sommer, 2007). Wavelet transforms provide one example of sparse coding through pixel decorrelation (Daugman, 1988; Lee, 1996).

Efficient coding of natural images can also be viewed as attempting to invert the process of image formation. During image formation light is reflected from one or more three-dimensional objects and projected onto a two-dimensional image plane, so that image pixels are correlated in a complicated way that depends on the object viewpoint, lighting, occlusion, and other effects (Horn, 1986; Ullman, 1996). Removing statistical dependencies by generating a sparse code may therefore be a step closer to inverting the process of image formation, and recovering the statistically independent image sources
The aim of this work is to answer the following two questions: can redundancy in natural images be better quantified from the statistical properties of model “simple-cell receptive fields” used for efficient coding? Can these statistical properties be modeled analytically: where the analytical model is capable of generating new “simple-cell receptive fields” with the same statistical properties? I use a computational approach to do this, and assume that: (1) the two-dimensional (2D) Gabor function provides a good description of simple-cell receptive fields, and (2) the efficient coding hypothesis holds; that is, simple-cell receptive fields are adapted to natural image statistics. Simple cells are treated as linear filters to first approximation (Daugman, 1985), so I assume a linear model in this work. The 2D Gabor function could alternatively be used in a nonlinear model to describe, for example, the response properties of complex cells.

A computational approach has the advantage that more samples, and therefore, better statistics, can be found than is necessarily practical under experimental conditions (Jones and Palmer, 1987) investigated a total of 36 simple cells in their work). In previous computational work, it has been common to estimate the 2D Gabor function parameters for a non-parameterized basis that was in turn estimated from natural images. By learning Gabor parameters directly (see next section) I avoid this situation of an estimate of an estimate. In addition, “controlled learning” is possible, where one has precise control over the learning rates of each Gabor parameter. This leads to the possibility of finding new solutions not seen in other approaches.

The structure of this Article is as follows: In Sec. 2, the Gabor Model is presented and learning rules are derived. In Sec. 3, results from applying the Gabor Model to images of natural and man-made environments are presented. The joint probability distribution of learned Gabor parameters is then modeled in Sec. 4, and analytically-tractable generative models of simple-cell receptive fields are constructed. In Sec. 5, a comparison is made with data from biological simple cells. A brief summary and discussion then follow.
2 The Gabor Model

A model for adapting the two-dimensional (2D) Gabor function to the statistics of natural images is now presented. A linear model for simple cells is assumed here, for reasons discussed in the Introduction. Using the vector \( \mathbf{r} = (x, y) \) to label the discrete pixel coordinates of image \( I(\mathbf{r}) \), an image is assumed to be generated as a linear sum of basis functions \( g(\mathbf{r}, \mathbf{r}') \), and Gaussian noise \( N(\mathbf{r}) \), as

\[
I(\mathbf{r}) = \sum_{\mathbf{r}'} g(\mathbf{r}, \mathbf{r}') a(\mathbf{r}') + N(\mathbf{r}),
\]

where \( a(\mathbf{r}') \) are coefficients. Each basis function is labeled by the vector \( \mathbf{r}' \), and the sum is over the total number of basis functions. In order to investigate simple-cell receptive fields, I choose a parameterized form for the basis functions \( g(\mathbf{r}, \mathbf{r}') \) that is motivated by the work of Daugman (1985), and Jones and Palmer (1987). I start with a 2D Gabor function parameterized in the form:

\[
G(x, y) = A \exp \left[ -\frac{1}{2} \left( \frac{x^2}{\sigma_x^2} + \frac{y^2}{\sigma_y^2} \right) \right] \cos (k \tilde{y} + \varphi),
\]

with

\[
(\tilde{x}, \tilde{y}) = \begin{pmatrix} \cos \phi & -\sin \phi \\ \sin \phi & \cos \phi \end{pmatrix} \begin{pmatrix} x - x_0 \\ y - y_0 \end{pmatrix},
\]

giving a 2D Gaussian with a sinusoidal modulation and eight adjustable parameters. In this parameterization, I have made a single modification from that presented in Daugman (1985), and Jones and Palmer (1987): The wave-vector of the sinusoidal term is always aligned along one of the principal axes of the Gaussian, resulting in one less adjustable parameter. In Eq. (2), I have chosen the wave-vector to be aligned along the \( \tilde{y} \) principal axis so that \( \phi = 0 \) corresponds to a bar or an edge aligned along the \( x \)-axis. The 2D Gaussian envelope is now described by its center position \((x_0, y_0)\), the envelope widths \( \sigma_x \) and \( \sigma_y \), and the orientation \( \phi \) of its principal axes. The sinusoid has wavelength \( \lambda = 2\pi/|k| \) (or spatial frequency \( f = |k|/2\pi \)), phase \( \varphi \), and a wave-vector (propagation direction) along the \( \tilde{y} \) principal axis. The parameter \( A \) is a scale factor.

From the perspective of neuroscience, each of these Gabor parameters tells us something about the receptive fields of cortical simple cells. Receptive-field location is given by \((x_0, y_0)\), while \( \sigma_x \) and \( \sigma_y \) quantify its spatial localization. The parameter \( \phi \) is the
orientation of bar or an edge placed in a receptive field that causes a strong response from the cell. Due to the direction of the wave-vector with respect to the Gaussian principal axes, a basis with $\sigma_y/\sigma_x < 1$ will resolve orientation more sharply than spatial frequency; while a basis with $\sigma_y/\sigma_x > 1$ will resolve spatial frequency more sharply than orientation (Daugman, 1985). The parameter $k$ indicates the preference of a cell for certain spatial frequencies, while $\varphi$ is the receptive-field phase.

The $g(r, r')$ are now parameterized so that each basis function is given by a 2D Gabor function with a unique set of values for five of the parameters:

$$g(r, r') = A \exp \left[ -\frac{1}{2} \left( \frac{\bar{x}^2}{\sigma_x(r')^2} + \frac{\bar{y}^2}{\sigma_y(r')^2} \right) \right] \cos \left[ k(r')\bar{y} + \varphi(r') \right],$$

with

$$\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} = \begin{pmatrix} \cos \phi(r') & -\sin \phi(r') \\ \sin \phi(r') & \cos \phi(r') \end{pmatrix} \begin{pmatrix} x - x' \\ y - y' \end{pmatrix}.$$  \hspace{1cm} (5)

Each 2D Gabor function is centered at $(x, y) = (x', y')$ in the image, so that the Gabor function label $r'$ is given by its center position. If I now choose a single Gabor function to be centered at each discrete pixel location; i.e., $(x', y') = (x, y)$ for each pixel location $(x, y)$, then the set of 2D Gabor functions tiles image space uniformly: each has a unique location and a unique set of parameter values $\phi(r'), \varphi(r'), \sigma_x(r'), \sigma_y(r'), \text{ and } k(r')$. Notice that this basis can still be overcomplete, as discussed in Results. Other choices for the Gabor center positions $(x', y')$ are clearly also possible, but this simplest choice is the one that will be implemented here.

Although it is the basis functions that are chosen to have a Gabor form, receptive fields (given by a Gabor-filter response instead of a Gabor-basis image reconstruction) are similar in form to the basis functions (Olshausen and Field, 1996); and have essentially the same orientation, location, and spatial frequency tuning (Hyvärinen et al., 2009). In the following work, I therefore assume that receptive field parameters and basis function parameters are equivalent.

For a given set of values for the five Gabor parameters at each pixel location, the Gabor Model from Eqs. (3), (4) and (5) could now be used to construct a complete (or overcomplete) set of basis functions. However, to find parameter values consistent with the statistics of natural images, a set of learning rules must be derived. This is carried out in the next section (Section 2.1), which is not essential for understanding the remainder of this work.
2.1 Learning Rules

To derive an appropriate set of learning rules for the parameters in the Gabor model I follow an approach due to Olshausen and Field (1997), and Lewicki and Olshausen (1999). In this approach, the probability of generating a particular image $I$ is assumed to be given by a continuous latent variable model of the form:

$$P(I|\theta) = \int da P(I|\theta, a)P(a),$$

where $a$ are a set of unobserved (latent) variables, and where, for the parameterization used here, $\theta(r) = (\phi(r), \varphi(r), \sigma_x(r), \sigma_y(r), k(r))$ is a vector of the five Gabor parameters for each basis function. In the case of Gaussian noise $N(r)$ with variance $\sigma'$:

$$P(I|\theta, a) \propto \prod_r \exp \left( -N(r)^2/2\sigma'^2 \right),$$

with $N(r) = I(r) - \sum_{r'} g(r, r') a(r')$ from Eq. (1). The marginal distribution for $a$ is assumed to be sparse and to factor:

$$P(a) \propto \prod_r \exp \left( -\beta S(a(r)) \right);$$

where $S(x) = \log (1 + x^2)$ for the Cauchy distribution is assumed here. Other common choices for $P(a)$ are the “logistic” distribution, and the Laplacian distribution.

Estimating parameters in a latent variable model can be done efficiently using the EM algorithm (Dempster et al., 1977). The E-step begins by inferring the latent variables $a$, given $\theta$ and $I$. Using Bayes’ rule, $P(a|I, \theta)$ can be written as

$$P(a|I, \theta) \propto P(I|\theta, a)P(a).$$

However, the expectation over $P(a|I, \theta)$ cannot be evaluated analytically, so approximate inference must be used. One approach, often used in sparse coding, is to assume the Maximum Posterior (MAP) estimate for $a$. Upon defining $E = -\log [P(I|\theta, a)P(a)]$, and using Eq. (7), this can be written as

$$\hat{a} = \arg \max_a P(a|I, \theta),$$

$$= \arg \min_a E,$$

where

$$E = \sum_r \left\{ \frac{1}{2} \left[ I(r) - \sum_{r'} g(r, r') a(r') \right]^2 + \lambda S(a(r)) \right\},$$

with $\lambda = \sigma'^2 \beta$. In this equation all terms independent of $a$ and $g$ (the distribution normalizations do not depend on $a$ or $g$) have been neglected, and $E$ has been re-scaled
by $\sigma^2$. Finding the MAP value for $a$ therefore reduces to simultaneously minimizing the least-squares error and sparseness terms in Eq. (10). For the Cauchy distribution, this can be done efficiently using conjugate gradient descent (Olshausen and Field, 1997).

The M-step involves maximizing $\langle \log P(I|\theta) \rangle$ with respect to the Gabor parameters $\theta$. This average log-likelihood is given by the likelihood function in Eq. (6), averaged over a batch of images. Maximizing this quantity is equivalent to minimizing the Kullback-Leibler divergence between the distribution of images in nature, and the distribution of images generated from the image model (Olshausen and Field, 1997).

Maximizing the average log-likelihood is implemented using gradient ascent. This can be written as

$$\Delta \theta_i(r) = \eta_i \frac{\partial}{\partial \theta_i(r)} \langle \log P(I|\theta) \rangle,$$

$$= \eta_i \left\langle \frac{1}{P(I|\theta)} \frac{\partial}{\partial \theta_i(r)} \int da P(I|\theta, a) P(a) \right\rangle,$$

where $\eta_i$ are the Gabor parameter learning rates, and Eq. (6) has been used for $P(I|\theta)$. It is now convenient to use $P(I|\theta, a) P(a) = \exp(-E)$ from the definition of $E$, allowing Eq. (12) to be written as

$$\Delta \theta_i(r) = \eta_i \left\langle \frac{1}{P(I|\theta)} \int da P(I|\theta, a) P(a) \left( -\frac{\partial E}{\partial \theta_i(r)} \right) \right\rangle,$$

$$= -\eta_i \left\langle \int da P(a|\theta, I) \frac{\partial E}{\partial \theta_i(r)} \right\rangle,$$

$$= -\eta_i \left\langle \frac{\partial E}{\partial \theta_i(r)} \right\rangle_{P(a|\theta, I)},$$

where $E$ is given by Eq. (10). The gradient is given by

$$\frac{\partial E}{\partial \theta_i(r)} = -a(r) \sum_{r'} r(r') \frac{\partial g(r', r)}{\partial \theta_i(r)},$$

where the residual error $r(r)$ is defined as

$$r(r) = I(r) - \sum_{r'} g(r, r') a(r').$$

Using these two expressions in Eq. (15) leads to

$$\Delta \theta_i(r) = \eta_i \sum_{r'} \frac{\partial g^T(r, r')}{\partial \theta_i(r)} \left\langle (a(r) r(r'))_{P(a|\theta, I)} \right\rangle.$$
This is similar to the learning rule of Olshausen and Field (1997) except for the partial derivative term, which allows each Gabor parameter to be learned independently. These terms are provided in Appendix A.

Updating each Gabor parameter therefore requires the calculation of two expectations. The inner expectation in Eq. (18) is with respect to the posterior distribution \( P(a|\theta, I) \) given by Eq. (7) and comprises the E-step. The outer expectation is an average over a batch of images. Adjusting each Gabor parameter according to Eq. (18) is the M-step. The EM algorithm consists of alternating between the E-step and the M-step until convergence is reached (for example, see Bishop, 2006).

If the noise level is zero and the basis is complete, the E-step can be avoided, and the ICA learning rule follows. The Eq. (1) can then be inverted to give \( a(r) = \sum_{r'} g(r, r')^{-1} I(r') \), and the distribution \( P(I|\theta, a) \) in Eq. (6) becomes a delta-function over \( a \). Performing the integral over \( a \) in Eq. (6) then yields \( P(I|\theta) = P(g^{-1} I) \). Maximizing \( \langle \log P(I|\theta) \rangle \) with respect to \( g^{-1} \) forms the basis of the FastICA algorithm (Hyvärinen et al., 2009).

In the presence of Gaussian noise, or for an overcomplete basis, the E-step is usually performed either by sampling from \( P(a|\theta, I) \), or by using its MAP estimate from Eq. (9). For the case of the MAP approach, the learning rule in Eq. (18) becomes

\[
\Delta \theta_i(r) = \eta_i \sum_{r'} \frac{\partial g^T(r, r')}{\partial \theta_i(r)} \langle \hat{a}(r) \hat{r}(r') \rangle,
\]

where \( \hat{r} \) is the residual error from Eq. (17) with \( \hat{a} \) instead of \( a \), and \( \hat{a} \) is the MAP estimate given by Eqs. (9) and (10). The drawback of using MAP in the E-step is encountering a trivial solution given when both terms in Eq. (10) are minimized by a small value of \( a(r') \), and a large value of the \( L_2 \)-norm \( \sum_r |g(r, r')|^2 \); such that \( \sum_r |g(r, r') a(r')|^2 \approx \sum_r |I(r)|^2 \). One way to avoid this solution is to approximate the envelope of each Gabor function as an ellipse: \( x^2/\sigma_x(r)^2 + y^2/\sigma_y(r)^2 = 1 \), and make use of the formula for the area of an ellipse,

\[
A_{\text{ellipse}}(r) = \pi \sigma_x(r) \sigma_y(r).
\]

Now the parameters \( \sigma_x(r) \) and \( \sigma_y(r) \) can be updated according to the variance of \( \hat{a}(r) \).
by modifying a rule used in Olshausen and Field (1997):

$$A_{\text{ellipse}}(r)^{\text{new}} = A_{\text{ellipse}}(r)^{\text{old}} \left[ \frac{\langle \hat{a}(r)^2 \rangle}{\sigma^2_{\text{goal}}} \right]^\alpha,$$

(20)

$$\sigma_x(r) = A_{\text{ellipse}}(r)^{\text{new}} / \pi \sigma_y(r),$$

(21)

$$\sigma_y(r) = A_{\text{ellipse}}(r)^{\text{new}} / \pi \sigma_x(r).$$

(22)

The fixed point of this learning rule is reached when the variance of $\hat{a}(r)$ over an image batch achieves a goal value $\sigma^2_{\text{goal}}$, preventing $g(r, r')$ from either growing too big or too small.

3 Results

The learning rules given by Eqs. (19)–(22) are now applied to batches of 100 image patches, with each image patch being $16 \times 16$ pixels, taken at random from natural images. The ten natural images used here come from the McGill Calibrated Colour Image Database (Olmos and Kingdom, 2004), and include images from the categories for flowers, foliage, landscapes, textures, and shadows. These images were converted to grayscale, and then underwent whitening and dimensionality reduction using the method described in Olshausen and Field (1997). The E-step in the EM algorithm was implemented using the Cauchy prior with conjugate gradient descent.

The first objective is to show that application of the learning rules to natural images leads to a set of basis functions that are oriented, localized, and bandpass: as originally shown in Olshausen and Field (1996). The Gabor parameters are initially drawn from uniform distributions of random numbers: $\phi$ is uniform over $(0, \pi)$, $\varphi$ is uniform over $(-2\pi, 2\pi)$; and the spatial parameters $\sigma_x$, $\sigma_y$, and $\lambda (=2\pi/|k|)$ are each uniform over $(0.2, 0.4)$ in dimensionless units. Note that 1 dimensionless unit is equal to one image patch side-length (16 pixels). This parameter choice is mostly an uninformed choice for natural images.

Applying the learning rules to natural images adapts the Gabor parameters to the statistics of natural images. The resulting basis of 256 Gabor functions (one Gabor function per pixel in a $16 \times 16$ image patch) is shown in Fig. 1. It is clear from this figure that the learned basis functions are oriented, localized, and bandpass. The basis
Figure 1: A basis of 256 Gabor functions learned from natural images. Histograms of the Gabor parameters are shown in Fig. 2.

is also approximately 1.4-times over-complete: its singular values become relatively small after about 180 dimensions.

Histograms of the learned Gabor parameters are shown in Fig. 2. Instead of showing the histogram for $k$, I show the histogram for wavelength $\lambda$ in order to be consistent with the units of $\sigma_x$ and $\sigma_y$. Each of the five Gabor parameters has 256 data points, however, a subset of this data was used to generate Fig. 2. The histograms for $\phi$ and $\varphi$ appear to be approximately uniform, as they were initially chosen to be. In contrast, histograms for the three spatial parameters $\sigma_x$, $\sigma_y$, and $\lambda$ appear to be highly non-uniform and to have long tails. This seems to be where most of the learning has taken place. Looking back at Fig. 1 it is clear that the non-uniform histograms are responsible for the multiscale nature of the Gabor functions: i.e., there are many smaller Gaussian envelopes, and fewer larger ones. There will be more to say about these histograms, and correlations between the spatial parameters, in Sec. 4. The sixth histogram is the Gabor function aspect-ratio, given by the parameter ratio $\sigma_y/\sigma_x$. This histogram has a mean value close to 0.5, and $0 < \sigma_y/\sigma_x < 1$ means the Gabor functions resolve orientation more sharply than spatial frequency, as discussed in Sec. 2.
Figure 2: Histograms of learned Gabor parameters corresponding to the Gabor functions shown in Fig. 1. The wavelength $\lambda = 2\pi/|k|$ is displayed instead of $k$. Histograms were generated from 236 (out of 256) data points satisfying $\sigma_x \leq 1$. 
Performance on image patch reconstruction is compared in Fig. 3. Given an input image $I$, Eqs. (9) and (10) are used to find the output $a$ for a given basis $g$. The ratio $S(a)/S(I)$ then measures the relative sparseness of the output $a$ compared with the input image $I$. A value less than 1 means the output is more sparse than the original input image, which is the desired outcome of finding a sparse code. However, finding a sparse code leads to a least squares error penalty in the image reconstruction. The sparser the output (the smaller the $S(a)/S(I)$ value), the larger the image reconstruction error will be. The values shown in Fig. 3 are found by averaging the error of reconstructing 400 test image patches at each value of $S(a)/S(I)$ displayed (by using different values of $\lambda$ in Eq. (10)).

It is seen in Fig. 3 that uniformly distributed Gabor parameters result in high reconstruction error across all sparseness levels. However, after just 200 iterations of Eqs. (19)–(22), the learned Gabor parameters have significantly reduced the reconstruction error across all sparseness levels. Further iterations lead to little improvement, and performance starts to degrade after 320 iterations. This is most likely due to the approximation used for the area of a Gabor function in the MAP approach. Notably, the reconstruction error for the basis of Gabor functions after 200 iterations is seen to be comparable to that for a non-parameterized basis learned using the rule of Olshausen and Field (1997) with 2000 iterations, which is shown for comparison. Adapting Gabor functions is therefore highly efficient, requiring an order of magnitude less computation (and less data) than a non-parameterized basis. The Gabor basis does not do quite as well as the non-parameterized basis at sparsity levels approaching 1, but appears to do better at sparsity levels approaching 0.5.

Having established this benchmark it is now possible to explore Gabor parameter statistics that result from other types of images. Ten images of man-made environments that include buildings and vehicles were collected from the man-made category in the McGill Calibrated Colour Image Database. Applying the learning rules to the same initial conditions as previously, leads to the basis of 256 Gabor functions shown in Fig. 4 and the histograms of Gabor parameters shown in Fig. 5. The Gabor parameter histograms in Fig. 5 are seen to be quite different to those in Fig. 2. The most obvious difference is the 3 large peaks at $\phi = 0$, $\pi/2$, and $\pi$: indicating that most Gabor functions are aligned either horizontally or vertically (this can be seen in Fig. 4). In fact,
man-made structures in this image set contain a majority of horizontal and vertical components – where pixels are strongly correlated along one direction, and anti-correlated along another – such as images that contain tall buildings or window frames. Another key feature in these histograms is the smaller range of values for $\sigma_x$, $\sigma_y$, and $\lambda$: and the corresponding reduced multiscale behavior in the size distribution of Gabor functions in Fig. 4. The scale invariance usually observed in natural images most likely breaks down for man-made structures, leading to a set of characteristic length scales. These results show the learning rules given by Eqs. (19)–(22) are capable of adapting Gabor parameters to the statistics of different image sets.

The learning rules for $\sigma_x$ and $\sigma_y$ are completely symmetric in $x$ and $y$ (see the partial derivatives in Append. A), reflecting the symmetry in $x$ and $y$ in the 2D Gaussian envelope. However, in order to learn the basis in Fig. 1, it was necessary to break this symmetry by setting different values for the learning rates: the learning rate for $\sigma_x$ was five times larger than that for $\sigma_y$. This leads to the necessary question: what happens if these two rates are interchanged? The result of doing this, and learning on the original set of natural images, is shown in Fig. 6. The Gabor function aspect-ratio given by $\sigma_y/\sigma_x$ (not shown) now has a mean close to 2 instead of 0.5. The majority of these
Figure 4: A basis of 256 Gabor functions learned from images of man-made environments. Histograms of the Gabor parameters are shown in Fig. 5.

Gabor functions satisfy $\sigma_y/\sigma_x > 1$, meaning they now resolve spatial frequency more sharply than orientation – the opposite property of the Gabor functions in Fig. 1. The Gabor parameter histograms look similar to those in Fig. 2, with the histograms for $\sigma_x$ and $\sigma_y$ interchanged.

A basis learned in a sparse coding model does not usually look like the basis in Fig. 6. To determine whether this basis might simply be a local minimum that is difficult to observe in practice, it was chosen as an initial condition in the learning rule of Olshausen and Field (1997), and iterated 2000 times. The result is shown in Fig. 7. The difference between Figs. 6 and 7 indicates that the basis in Fig. 6 is not a stable solution of the Olshausen and Field learning rule applied to natural images. This method was also used to confirm that the basis in Fig. 1 is a stable solution.

4 Analytical Models of Simple Cell Response

In the previous section, a set of learning rules was used to adapt Gabor parameters to the statistics of natural images, yielding a basis of Gabor functions that could be used for efficient reconstruction of natural images. Alternatively, these Gabor functions can
Figure 5: Histograms of learned Gabor parameters corresponding to the Gabor functions in Fig. 4. The wavelength $\lambda = 2\pi/|k|$ is displayed instead of $k$. Histograms were generated from 251 data points satisfying $\sigma_x \leq 1$. 

$\phi/\pi$ vs. Frequency

$\varphi/\pi$ vs. Frequency

$\sigma_x$ vs. Frequency

$\sigma_y$ vs. Frequency

$\lambda$ vs. Frequency

$\frac{\sigma_y}{\sigma_x}$ vs. Frequency
Figure 6: A basis of 256 Gabor functions learned from natural images after interchanging the learning rates for $\sigma_x$ and $\sigma_y$.

Figure 7: A basis that results from choosing the Gabor functions in Fig. 6 as an initial condition in the learning rule of Olshausen and Field (1997), and then iterating 2000 times. The difference between Figs. 6 and 7 indicates the basis in Fig. 6 is not a stable solution for natural images.
be considered as a model of simple-cell responses to visual stimulus inputs.

In this section, I approximate the joint distribution of the five learned Gabor parameters in order to construct an analytically-tractable generative model of Gabor functions that can be used for efficient coding or modeling of simple-cell receptive fields. The first step is to approximate the marginal distributions of the five Gabor parameters. This is done by fitting continuous distributions to the histograms in Fig. 2. As mentioned in Sec. 3, the Gabor parameters $\phi$ and $\varphi$ are well approximated by uniform distributions. The three spatial Gabor parameters $\sigma_x$, $\sigma_y$, and $\lambda$ are best approximated by a non-uniform distribution with a heavy tail. Using the exponential distribution, for example, yields a generative model that does not perform well on image reconstruction. The distribution must have a tail that decreases more slowly than exponential. With these considerations, I choose the Log-Normal distribution:

$$ p(x|\mu, \sigma) = \frac{1}{x\sigma\sqrt{2\pi}} \exp\left( -\frac{(\ln x - \mu)^2}{2\sigma^2} \right), \tag{23} $$

where $\ln x$ has mean $\mu$, and standard deviation $\sigma$; and the Pareto distribution:

$$ p(x|\alpha, \beta) = \begin{cases} 
\frac{\alpha\beta^\alpha}{x^{\alpha+1}} & x \geq \beta, \\
0 & x < \beta,
\end{cases} \tag{24} $$

with scale parameter $\beta$, and shape parameter $\alpha$. These are both heavy-tailed distributions, and the tail of the Pareto distribution is also scale-invariant due to its power law structure. These distributions are shown as solid curves in Fig. 8, where Maximum-Likelihood estimates of the parameter values were used. The Log Normal was fitted to the histogram for $\sigma_x$, while the Pareto was fitted to the histograms for $\sigma_y$ and $\lambda$.

Gabor parameters are clearly not independent of each other, as can be seen in the histogram of $\sigma_y/\sigma_x$ in Fig. 2. Therefore, the next step is to try to model dependencies in the joint distribution. It is found that only three out of the ten pairwise correlations for five Gabor parameters are large. These three largest correlations are between the three spatial Gabor parameters. Scatter plots for these parameters are shown in Fig. 9 along with the line of best fit to each data set. In fact, one of the three correlations is redundant. That is, if we know the value of one spatial parameter, we can use any two of the three correlations to find the remaining two spatial parameters. The two most obvious correlations to understand is that between $\sigma_x$ and $\sigma_y$: which is necessary for an oriented Gabor function with the correct aspect-ratio, and that between $\sigma_y$ and $\lambda$: which
Figure 8: Normalized histograms of the three spatial Gabor parameters from Fig. 2 and fitted distributions (solid curves) from Table 1.
Figure 9: Scatter plot, and line of best fit, for each pair of Gabor parameters that are strongly correlated. Correlation coefficients and line-of-best-fit parameters are given in Tables 2 and 3.

correctly correlates wavelength with window-size so that larger Gabor functions do not have too many subfields, and smaller Gabor functions do not have zero subfields.

It is now possible to construct generative models that approximate, to an increasing degree of accuracy, the joint distribution of learned Gabor parameters. The first model (called First Gabor Model) is detailed in Table 1, and only includes the marginal distribution of each Gabor parameter; no correlations are introduced. The first column lists the Gabor parameter, the second column gives the distribution used to model that parameter, the third column lists the inverse CDF (cumulative distribution function) used to draw random samples from that distribution, while the final column lists the parameter estimates used for each distribution. The relevant distributions are the Uniform, Log-Normal, and Pareto distributions previously discussed.

In the second model (Second Gabor Model) listed in Table 2, values for each of the Gabor parameters are drawn from their fitted marginal distributions, as in the First Gabor Model. Correlations between the three spatial Gabor parameters are also included using a Gaussian copula [Embrechts, 2001] with three correlation coefficients $\rho_1$, $\rho_2$, and $\rho_3$. 
| Gabor Parameter | Marginal Distribution | Sample Generator | Parameter Estimate |
|-----------------|-----------------------|------------------|--------------------|
| φ               | Uniform               | φ = πU           |                    |
| φ               | Uniform               | φ = −2π + 4πU    |                    |
| σx              | Log Normal            | σx = exp (μ + σZ) | μ = −1.269         |
|                 |                       | μ = −1.269       |                    |
|                 |                       | σ = 0.3771       |                    |
| σy              | Pareto                | σy = β1(1 − Y)^{(1/α1)} | α1 = 1.592 |
|                 |                       | Y = Φ (ρ1Z1 + ρ2Z2) | β1 = 0.0750 |
|                 |                       | β1 = 0.0750      |                    |
| λ               | Pareto                | λ = β2(1 − Z)^{(1/α2)} | α2 = 2.751 |
|                 |                       | Z = Φ (ρ2Z1 + ρ1ρ2Z2 + ρ3Z3) | β2 = 0.1987 |
|                 |                       | β2 = 0.1987      |                    |
|                 |                       | ρ1 = 0.8054      |                    |
|                 |                       | ρ2 = 0.7432      |                    |
|                 |                       | ρ3 = 0.7279      |                    |

Table 1: First Gabor Model: Values for each of the five Gabor parameters are drawn from the distributions listed in the table. Here, U is drawn from the standard uniform distribution, and Z, from the standard normal distribution. No correlations are modeled.

| Gabor Parameter | Marginal Distribution | Sample Generator | Parameter Estimate |
|-----------------|-----------------------|------------------|--------------------|
| φ               | Uniform               | φ = πU           |                    |
| φ               | Uniform               | φ = −2π + 4πU    |                    |
| σx              | Log Normal            | σx = exp (μ + σX) | μ = −1.269         |
|                 |                       | μ = −1.269       |                    |
|                 |                       | σ = 0.3771       |                    |
| σy              | Pareto                | σy = β1(1 − Y)^{(1/α1)} | α1 = 1.592 |
|                 |                       | Y = Φ (ρ1Z1 + ρ2Z2) | β1 = 0.0750 |
|                 |                       | β1 = 0.0750      |                    |
| λ               | Pareto                | λ = β2(1 − Z)^{(1/α2)} | α2 = 2.751 |
|                 |                       | Z = Φ (ρ2Z1 + ρ1ρ2Z2 + ρ3Z3) | β2 = 0.1987 |
|                 |                       | β2 = 0.1987      |                    |
|                 |                       | ρ1 = 0.8054      |                    |
|                 |                       | ρ2 = 0.7432      |                    |
|                 |                       | ρ3 = 0.7279      |                    |

Table 2: Second Gabor Model: Values for each of the five Gabor parameters are drawn from their fitted marginal distributions, and correlations are modeled using a Gaussian copula with 3 correlation coefficients. Here, Φ(x) = 0.5 (1 + erf(x/√2)) is the CDF of the standard normal; while U is drawn from the standard uniform distribution; and Z1, Z2, and Z3 are independent draws from the standard normal distribution.
Table 3: Third Gabor Model: Values for $\phi$, $\varphi$, and $\lambda$ are drawn from their fitted marginal distributions, and correlations are modeled using a line of best fit. Here, $U$ is drawn from the standard uniform distribution.

In the third model (Third Gabor Model) listed in Table 3, only $\phi$, $\varphi$, and $\lambda$ are drawn from their fitted marginal distributions. Correlations are modeled using a line of best fit. This was done by fitting a straight line to the scatter plots for $\sigma_x$ versus $\lambda$, and $\sigma_y$ versus $\lambda$. Now, given a value of $\lambda$ drawn from its fitted marginal distribution, values for $\sigma_x$ and $\sigma_y$ can then be determined. Marginal distributions for $\sigma_x$ and $\sigma_y$ are therefore of the same type as for $\lambda$.

The performance of each Gabor model on image patch reconstruction is compared in Fig. [10]. From this figure it is seen that the First Gabor Model, with its fitted non-uniform marginal distributions, performs significantly better than sampling Gabor parameters from uniform distributions. An additional increase in performance comes from including correlations, as can be seen from the performance of the Third Gabor Model. Surprisingly, the more complex model given by the Second Gabor Model (with 9 fitted parameters) does little better than the First Gabor Model. The Gaussian copula in the Second Gabor Model is a simple and versatile multivariate copula for modeling linear dependence. However, it does not appear to model dependence in the heavy tails of the joint distribution very well. A large body of literature exists on this topic, so it may be that finding a better copula leads to a significantly better model with improved performance. Conversely, the line of best fit approach in the Third Gabor Model does appear to be a reasonable model of this dependence. However, this is at the expense of not
Figure 10: Mean error of image reconstruction at different sparseness levels for uniformly distributed Gabor parameters (squares), the Gabor model in Table 1 (circles), the Gabor model in Table 2 (triangles), the Gabor model in Table 3 (plus signs), and the learned Gabor parameters from Fig. 3 (crosses).

modeling the fitted marginal distributions of \( \sigma_x \) and \( \sigma_y \).

It is clear that an appreciable performance gap still exists between the best analytical model (given by the Gabor Model in Table 3) and the learned Gabor parameters of Sec. 3. A model that can handle both dependency in heavy tailed distributions, and use the best fitting distributions for the marginals (i.e., through a better choice of copula), is expected to significantly reduce this gap. A basis of Gabor functions generated from the Gabor Model in Table 3 is shown in Fig. 11. This basis looks qualitatively similar to that in Fig. 1. Matlab code for generating this basis is available at Loxley (2014).

5 Comparison with Estimates for Biological Simple Cells

In Sec. 3, the two-dimensional Gabor function was adapted to the statistics of natural images to yield an efficient coding strategy for this data. These results are now compared with results from fitting the two-dimensional Gabor function to simple-cell
receptive fields of cat (Daugman, 1985; Jones and Palmer, 1987), and macaque monkey (Ringach, 2002).

One of the main findings of Daugman (1985) was that for cat simple cells, the width and length of a Gabor function are strongly correlated: yielding a narrow range of width/length aspect-ratio values from 0.25 to 1. The Gabor Model presented here predicts exactly this result (shown in the bottom-right panel of Fig. 2 and top-left panel of Fig. 9). This correlation implies orientation is better resolved for these cells than spatial frequency.

Another prediction from both Daugman (1985), and Jones and Palmer (1987), was that the phase parameter has a uniform distribution. This is also predicted by the Gabor Model (shown in the top-right panel of Fig. 2). Finally, Daugman (1985) found that the wave vector and principal axis are strongly correlated (aligned), which I already assumed in the parameterization of the Gabor Model.

In Ringach (2002), macaque monkey simple cells were also found to have a correlation between the Gabor-function spatial dimensions. This data is shown as the circles in Fig. 12, where the dimensionless quantities $n_x = \sigma_x/\lambda$, and $n_y = \sigma_y/\lambda$ have been plotted. The positions of the data points indicate that some cells were broadly tuned for orientation and low-pass for spatial frequency (receptive fields like circular blobs),
Figure 12: Distribution of receptive field shapes from data for macaque monkey simple cells (Ringach, 2002), compared with predictions from the Gabor Model (from results displayed in Figs. 1-3). Circular “blob-like” receptive fields occur near the origin of the \((n_x, n_y)\)-plane, while receptive fields with several subfields occur away from the origin. While others were more sharply tuned for orientation and high-pass for spatial frequency (oriented receptive fields with multiple subfields). Circular “blob-like” receptive fields occur near the origin of the \((n_x, n_y)\)-plane, while receptive fields with several subfields occur away from the origin. For comparison, data from the Gabor Model (from Figs. 1-3) is shown as the triangles in Fig. 12. Due to a difference in the parameterization used in Ringach (2002), it was necessary to plot \(n_x = \sigma_y / \lambda\), and \(n_y = \sigma_x / \lambda\) for the Gabor Model data. It is seen in Fig. 12 that the Gabor Model predicts oriented receptive fields with multiple subfields: no circular blob-like receptive fields are predicted. These results seem to be a general property of many sparse coding models, as pointed out in Ringach (2002), rather than an artifact of the Gabor Model itself. Examples of sparse coding models predicting a more diverse set of receptive fields are given by the works of Rehn and Sommer (2007), and Olshausen (2013b). The first model includes a form of “hard-sparseness” and predicts blob-like receptive fields as seen in the Ringach data. The second model includes a 10-times overcomplete basis and predicts center-surround (difference of Gaussians) receptive fields, among others, which are clearly not possible in a purely Gabor-parameterized model.
Finally, Ringach (2002) found that the phase parameter clusters towards even and odd-symmetric functions (0 and multiples of $\pm \pi/2$ in $\varphi$) for macaque monkey, opposite to the findings for cat. While the Gabor Model results agree with those for cat.

6 Summary and Discussion

The two-dimensional (2D) Gabor function describes response properties of simple cells and provides an elementary description of natural images. In this work, the 2D Gabor function was adapted to the statistics of natural images in order to develop an efficient coding strategy. Approximating the joint distribution of learned Gabor parameters yielded analytical models that could be used for efficient coding or modeling of simple-cell receptive fields.

Adapting the 2D Gabor function to natural image statistics was shown to be highly efficient – requiring an order of magnitude less computation (and less data) than a non-parameterized basis. The derived learning rules were shown to be capable of adapting Gabor parameters to the statistics of images of man-made and natural environments. Learning was found to be most pronounced in three Gabor parameters that represent the size, aspect-ratio, and spatial frequency of the 2D Gabor function. These three parameters were characterized by non-uniform marginal distributions with heavy tails – most likely due to scale invariance in natural images – and all three parameters were strongly correlated: resulting in a basis of multiscale Gabor functions with similar aspect-ratios, and size-dependent spatial frequencies. However, the orientation and phase parameters did not appear to gain anything from learning over natural images. Each of these parameters approximately maintained an initial distribution that was chosen as uniform over the range of allowable values. This result may present an alternative way of thinking about the finding of Eichhorn et. al. (2009) that orientation selectivity does not yield a large contribution to redundancy reduction in these kinds of models.

Different tuning strategies were also found by controlling learning through the Gabor parameter learning rates. This is not possible in a non-parameterized model. Specifically, interchanging the learning rates of the Gaussian envelope parameters led to opposing tuning strategies where either orientation was well-resolved, or spatial frequency was well-resolved.
One of the main points of this work was to develop an analytical model of simple-cell receptive fields and basis functions for efficient coding. On image reconstruction, I showed that a basis of Gabor functions with fitted marginal distributions outperformed a basis of Gabor functions generated from uniformly sampled parameters. An additional increase in performance was found when strong correlations between three Gabor parameters were included. However, the best analytical model does not yet achieve the same performance as the learned model. Reasons for this were suggested.

I also compared model results with those from fitting the 2D Gabor function to the receptive fields of cat and monkey simple cells. Some of the receptive field shapes were predicted by the model, and correlations yielding the Gabor function aspect-ratio were found to be in very good agreement. Model predictions for the phase parameter agreed with findings for cat, but not for monkey.

Improvements to the models include: learning the parameters for the Gabor-function center positions; replacing MAP inference with efficient sampling to eliminate some of the approximations required; and using a second-order method for the parameter learning instead of gradient ascent in order to avoid having to choose a learning rate for each Gabor parameter. Using a “hard” form of sparseness in the objective function, as done in Rehn and Sommer (2007), should result in finding a more diverse set of receptive fields within the Gabor framework. The analytical models could be improved by finding a better way of modeling multivariate dependencies in heavy-tailed joint distributions.

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Appendix

The partial derivatives required in Eqs. (18) and (19) are given here:

\[
\frac{\partial g^T(r, r')}{\partial \phi(r)} = g^T(r, r') \left( \frac{1}{\sigma_x(r)^2} - \frac{1}{\sigma_y(r)^2} \right) \tilde{x} \tilde{y} - h^T(r, r') k(r) \tilde{x},
\]

\[
\frac{\partial g^T(r, r')}{\partial \sigma_x(r)} = g^T(r, r') \frac{\tilde{x}^2}{\sigma_x(r)^3},
\]

\[
\frac{\partial g^T(r, r')}{\partial \sigma_y(r)} = g^T(r, r') \frac{\tilde{y}^2}{\sigma_y(r)^3},
\]

\[
\frac{\partial g^T(r, r')}{\partial k(r)} = -h^T(r, r') \tilde{y},
\]

\[
\frac{\partial g^T(r, r')}{\partial \phi(r)} = -h^T(r, r'),
\]

where \( g^T(r, r') = g(r', r) \) is the transpose of \( g(r, r') \), and \( h^T(r, r') = h(r', r) \) is the transpose of

\[
h(r, r') = A \exp \left[ -\frac{1}{2} \left( \frac{\tilde{x}^2}{\sigma_x(r')^2} + \frac{\tilde{y}^2}{\sigma_y(r')^2} \right) \right] \sin \left[ k(r') \tilde{y} + \phi(r') \right],
\]

and \((\tilde{x}, \tilde{y})\) are defined as in Eq. (5).

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