Linear models of simple cells: Correspondence to real cell responses and space spanning properties

GUY WALLIS *

Max-Planck Institute for Biological Cybernetics, D-72076 Tübingen, Germany
School of Human Movement Studies, University of Queensland, St. Lucia, QLD 4072, Australia

Received 3 August 1999; revised 10 June 2000; accepted 17 June 2000

Abstract—Despite their limitations, linear filter models continue to be used to simulate the receptive field properties of cortical simple cells. For theoreticians interested in large scale models of visual cortex, a family of self-similar filters represents a convenient way in which to characterise simple cells in one basic model. This paper reviews research on the suitability of such models, and goes on to advance biologically motivated reasons for adopting a particular group of models in preference to all others. In particular, the paper describes why the Gabor model, so often used in network simulations, should be dropped in favour of a Cauchy model, both on the grounds of frequency response and mutual filter orthogonality.

1. INTRODUCTION

In the 1940s it became clear that cells in the first visual area of cortex were arranged such that the topology of the retina was retained (Talbot and Marshall, 1941). In the 1960s, Hubel and Wiesel (1968) identified a subgroup of these neurons called simple cells, which responded to stationary, spatially localised, oriented contours, i.e. oriented bars and edges. They also discovered that there was a smooth transition in orientation preference between neighbouring sets of these neurons, varying in steps of around 2.5° (Hubel and Wiesel, 1977; Vogels and Orban, 1990). Theorists, struck by this regularity, took the results as evidence that the visual system samples the retinal signal with a family of self-similar filters of differing spatial scale and phase.

*To whom correspondence should be addressed. Perception and Motor Systems Laboratory, School of Human Movement Studies, University of Queensland, St. Lucia, QLD 4072, Australia. E-mail: gwallis@hms.uq.edu.au
However, early hopes that one might be able to replicate all of the characteristics of simple cells with a family of linear filters have, since their heyday in the late 1980s, waned and now all but disappeared. Even before the proposal of such models, it was clear that the cells have non-linear (e.g. Kulikowski and King-Smith, 1973) or at best ‘quasi-linear’ (Kulikowski et al., 1982) characteristics. The sheer variety of simple cell characteristics made it ultimately impossible to draw all of them within one family of functions (Sun and Bonds, 1994). Despite this fact, recent results continue to support the idea that both the spatial and temporal response properties of simple cells can be encapsulated in a linear model which incorporates some form of output non-linearity (Heeger, 1993; Carandini and Heeger, 1994), and that cells with linked spatiotemporal characteristics, may draw their input from cells with linearly separable characteristics (McLean and Palmer, 1989; DeAngelis et al., 1993). Indeed, more recent results, in which changes in membrane potentials were measured rather than the cell firing rate, have helped define the nature of the cells’ non-linearity. This work demonstrates how the afferent input is summed approximately linearly, before being dynamically thresholded and contrast enhanced (Carandini and Ferster, 2000; Carandini, 2000).

These findings have led many researchers in the neural network community to simulate filtering of the retinal image using a family of linear, self-similar filters. By far the most popular model of the last decade has been that of the Gabor filter (Worgotter and Holt, 1991; Pattison, 1992; Lades et al., 1993; Xing and Gerstein, 1993; Pötzsch et al. (1996); Mel, 1997). The aim of this paper is to review much of the literature dealing with the ability of the Gabor filter, amongst others, to fit actual neurophysiological data, and to present new arguments as to why the Gabor is a particularly poor model in comparison to several alternatives. In particular, the paper considers the ability of the filter to form an orthogonal basis set suitable for spanning the input space, and provides evidence that using biologically relevant parameters results in a Gabor filter with low mutual orthogonality and hence limited space spanning properties. The paper concludes that on the basis of currently available neurophysiological data, at least two other models are preferable to the Gabor and all other popular alternatives.

2. THE DEBATE ON SIMPLE CELL MODELS

2.1. Introduction

Several filter shapes have been proposed to perform an image transformation equivalent to that of simple cells. The five filters considered in this paper are described by the difference between two or more Gaussian functions (DoG) (Enroth-Cugell and Robson, 1966; Rose, 1979), Laplacian of a Gaussian ($\nabla^2 G$) (Marr and Hildreth, 1980), Gabor (Marcelja, 1980; Daugman, 1980; Sakitt and Barlow, 1982; Watson, 1983), Cauchy (Klein and Levi, 1985), and the ‘log Gabor’ (Field, 1987; Morrone and Burr, 1988). One of the most influential authors in
this field has been John Daugman. In the mid-1980s he wrote several papers emphasising the attractive mathematical properties of the Gabor filter, specifically in its relation to the minimisation of the joint entropy of spatial location and frequency. This was an extension of the original work of Gabor (1946) who recognised that in a single observation of an information carrying waveform, there exists a trade-off between the amount one can learn about its point of action at a particular moment in time, and its current frequency. Daugman developed Gabor’s work and extended it to two-dimensional images, for which the trade-off lies between spatial location and spatial frequency. Daugman showed that the two-dimensional Gabor filter represents the optimal combination of frequency and space information. This theoretical work went on to receive strong support from both neurophysiological (Kulikowski et al., 1982; Jones and Palmer, 1987) and human psychophysical studies (Harvey and Doan, 1990).

2.2. Weaknesses of the Gabor model theory

In many ways the case made by Daugman is very attractive. He takes a renowned constraint on measurable information and applies it to the field of vision, culminating in a filter which appears to fit the available experimental data well. Although many researchers have pointed out shortcomings or weaknesses of his arguments, his work continues to be cited by those outside the field as grounds for using the Gabor model. Some of the issues raised by his critics are discussed in a reply he wrote in 1992 (Daugman, 1992), but there are several points not raised in that paper, which are perhaps more important. Firstly, it is not clear that the visual system is constrained to only make one measurement of an image at one particular location. Indeed, receptive fields of simple cells heavily overlap (Hubel and Wiesel, 1974). This removes the single observation constraint which the original work of Heisenberg and Gabor placed upon their measurements. In addition to this, Daugman’s calculations say nothing about multiple orientation tuning of the filters observed in striate simple cells — a point raised by Field in his work (Field, 1987). And finally, the experimental results supporting the Gabor model were countered by other results; for example, a contemporary study in cats favoured a DoG model (Hegelund, 1986a, b).

A year after the work of Hegelund appeared, Hawken and Parker (1987) reported recordings from monkeys in which they directly compared the Gabor, DoG and $\nabla^2 G$ models. By fitting the models to observed cell sensitivity profiles, they were able to conclude that the $\nabla^2 G$ gave observably poorer fits than the other two distributions. This conclusion concurs with an observation made by Daugman that the $\nabla^2 G$ filter is insensitive to image luminance combinations clearly visible to humans (Daugman, 1988). However, in contrast to Jones and Palmer, Hawken and Palmer further concluded that the Gabor filter fitted their data very poorly, and that on average a DoG filter gave a significantly better fit.
2.3. Symmetry of the amplitude spectrum in log units

Apart from the possible shortcomings of Daugman’s theory mentioned above, there are probably several additional reasons for the discrepancy between the two group’s results. One difference is that Jones and Palmer recorded their data in cats rather than macaque monkeys — the latter being generally regarded as providing a better model for the human visual system. Another, more important difference, is that Hawken and Parker chose to fit their data to the log frequency of the cell’s contrast sensitivity function rather than spatially, as Jones and Parker did. In other words they fitted their data to the log frequency amplitude spectrum of the filter models. Choosing to fit along such dimensions lends great importance to the ability of the model to fit the cell’s low frequency characteristics. This in turn accentuates the failure of a Gabor filter to capture the rapid fall off in response seen in simple cells at low frequencies (Hawken and Parker, 1987).

In practice, the log frequency response profile may be an important characteristic of simple cells. It is certainly true that many simple cells exhibit a striking symmetry in log frequency units about their peak response frequency, which the DoG filter captures and the Gabor does not (see Fig. 1a and 1b).

Many researchers have recognised that the Gabor’s lack of log frequency symmetry is a problem, and have offered various alternatives. Heitger et al. (1992) for example, proposed using a Gabor in which the cosine frequency was attenuated as a function of offset from the centre. Field (1987) chose to use a log Gabor filter (as did Morrone and Burr (1988)), which is perfectly symmetric in the log frequency domain. However, Field does not claim it as a truly representative model of simple cells, presumably realising that such a model would be poor at modelling the smaller percentage of simple cells which exhibit a finite response at D.C., something which the DoG model can also capture by changing the exponent term of the second, negative Gaussian part. On a more practical note, although easily described in the frequency domain, the log Gabor has no convenient expression in the space domain like the DoG or Gabor.

Klein and Levi (1985) also criticised the Gabor for its lack of symmetry in log frequency units, proposing in its stead the use of a Cauchy function. This function has various interesting properties including approximate symmetry (see Fig. 1c). The function can also be conveniently expressed both in terms of its frequency and spatial response profiles. Klein and Levi fit the Cauchy to human contrast sensitivity functions and were favourably impressed by its suitability. The suitability of the Cauchy will hence also be considered in the coming analysis.

As a brief aside, it is worth considering why a Gabor fails to fit the low frequency response of simple cells. The Gabor function is obtained by multiplying a sine function with a Gaussian waveform in the space domain. The equivalent in the frequency domain is a convolution of the two signals. A Gaussian in the space domain has the interesting property of being a Gaussian in the frequency domain too. It also turns out that the width of this Gaussian is inversely related to the width of the Gaussian envelope in the space domain, i.e. the slower the Gabor decays in the
Figure 1. Log scale amplitude spectra for the three filters being investigated, with amplitude scale factor $B$ and frequency scale factor $\sigma$ chosen to provide a peak amplitude of 1 at $f = 1$ in each case. Below, a definition of their form in both spatial and frequency domains. (a) In its current form the DoG function is almost symmetric in log frequency, something typical of many simple cells. (b) The Gabor filter, in contrast, is highly asymmetric. (c) The Cauchy is slightly asymmetric, but clearly more symmetric than the Gabor.

\[ D_x: A_D \left( e^{-\left(\sigma x\right)^2} - \frac{1}{\lambda} e^{-\left(\sigma x/\lambda\right)^2} \right) \]
\[ D_f: B_D \left( e^{-\left(\frac{2\pi f}{\sigma}\right)^2} - e^{-\left(\frac{2\pi f}{\sigma\lambda}\right)^2} \right) \]
\[ G_x: A_G \ e^{-\left(\sigma x\right)^2} \cos\left(2\pi f_\kappa \sigma x\right) \]
\[ G_f: B_G \left( e^{-\left(\frac{\pi f}{\sigma}\right)^2 + f_\kappa \pi} + e^{-\left(\frac{\pi f}{\sigma} - f_\kappa \pi\right)^2} \right) \]
\[ C_x: A_C \ \text{Re}\left[ (1 + i\sigma x)^{-n} \right] \]
\[ C_f: B_C \left( \frac{f}{\sigma} \right)^n e^{-\frac{f}{\sigma}} \]
space domain, the narrower its bandwidth. A cosine function is simply represented by the Dirac function at the appropriate frequency, and convolution results in a Gaussian shifted to the frequency of the sine wave. This has two consequences. First, the even symmetric form of the filter has a non-zero D.C. component. Second, the response profile is always symmetric in the frequency domain, and hence always skewed in the log-frequency domain, as shown in Fig. 1b. To compensate for this, the D.C. response can be made arbitrarily small and perfect symmetry approximated arbitrarily closely by increasing the cosine frequency of the Gabor ($f_k$ in Fig. 1b), or by widening its Gaussian envelope in the space domain. The important question is whether a Gabor function which fits low D.C. and symmetry constraints in the frequency domain also produces a filter of suitable spatial form, with small numbers of peaks beyond the central band for example. As we shall see later, the answer more often than not, is no.

2.4. Fitting to cell response data

Having described reasons why the Gabor model might provide poor fits to cell response data this section looks in detail at the quality of fit achieved by the Gabor amongst other models. Although Hawken and Parker’s paper makes a compelling case against the Gabor model, a closer analysis of their results reveals at least one major problem. As they point out, the models which they use to fit their data contain different numbers of free parameters (from 2 to 10), which makes comparison between them a far from trivial operation. One should be wary of selecting a more complicated model for moderate reductions in fitting error, since simpler models are less prone to over-fitting the data, i.e. creating a model which is too sensitive to sampling errors or inherent sample bias. To mitigate this criticism Hawken and Parker suggest that one can at least make a direct comparison between the Gabor and their simplest DoG model, as they both contain four parameters. They have, however, overlooked the fact that by measuring a contrast sensitivity function with drifting gratings their data contains no phase information. This renders the phase term in their equation for the Gabor filter ineffectual in reducing the fitting error — which explains why it is 90° for both example cells given in the paper. The consequence of this is that the Gabor filter has fewer parameters which can freely vary and thus the poorer fitting performance may be attributable to this fact alone.

There does, however, exist an entire literature on the subject of model fitting which can at least give some principled approach to comparing the relative quality of fit achieved by multi-parameter models. Rissanen (1989, pp. 93–95) suggests the application of Akaike’s AIC, a function of the total mean squared error of the model fit to the data, and the ratio of the number of model parameters to the number of data points being fitted. This criterion would still favour the DoG model on the bases of the $\approx 40\%$ reduction in the average fitting error observed in Hawken and Parker’s data.
Klein and Levi (1985) have demonstrated that the Cauchy function fits human psychophysical data well, and its reasonably symmetric form would certainly be better suited to fitting the data of Hawken and Parker than the Gabor. However, it would be informative to see how well it fits measured simple cell response data. It would also be interesting to see how it compares to the DoG and Gabor models listed in Fig. 1. Figure 2 provides data from a cell described by DeAngelis et al. (1993). All three models are afforded three parameters allowing a straightforward comparison of their ability to fit the cell’s sensitivity function.

The obvious conclusion from the figure is that both the Cauchy and DoG capture the form of the simple cell much more closely than the Gabor. There is, however, another twist in the tale. As mentioned in the introduction, many researchers are coming to the conclusion that many simple cells can be described by a linear input model, transformed by some non-linear activation function. That being the case, what researchers have been measuring in firing rates is a distorted version of the true model which the linear filter should actually be attempting to capture, namely, the change in membrane potential. The most recent papers on the topic have explained certain non-linear behaviour seen in the firing rates of cells in terms of the output function alone, adding strength to the argument that the input is summed linearly (Carandini and Ferster, 2000). Apart from changes to the direction selectivity of simple cells, the work generally describes an increase in the breadth of tuning curves. Membrane potentials rise to a broader range of orientations and a wider range of spatial frequencies than the more selective firing rate response would suggest (Carandini and Ferster, 2000; Carandini, 2000). In general, the greater the bandwidth of the cell, the worse the fit achieved by the Gabor, since large bandwidths correspond to larger asymmetries in the log frequency domain. Such changes to the functions being fit will not, however, adversely affect either the Cauchy or DoG models.

2.5. Conclusions and further issues

On the basis of fit to measured data, and the issue of symmetry in the log-frequency response, we now have two good reasons for preferring the DoG and Cauchy models to the Gabor. However, there remains at least one other factor which is important when considering a set of input filters for a neural network, namely, filter orthogonality. Mutual orthogonality is important in that it indicates the ability of a set of functions to form a basis set, spanning the whole range of possible inputs. As Higgins (1977) describes, the ability of a set of non-orthogonal functions to span a space is governed by their ‘nearness’, in a Euclidean sense, to an orthogonal set. Hence, the closer the set is to orthogonality, the closer it will come to spanning the input space.

It should be said that the issue of orthogonality may have had relatively little influence on the design of the visual system, which multiply samples the retinal input, but for simulations in which the sampling will be considerably sparser,
Figure 2. (a) The three filters fit to the frequency response profile of a V1 simple cell (shown as filled circles), as described in DeAngelis et al. (1993). Note the failure of the Gabor to capture the correct peak frequency and its long low frequency tail. The numbers indicate the mean-squared fitting error for each of the models. (b) The three filters transformed into the space domain. The DoG and Cauchy appear very similar, but the Gabor has markedly narrower side bands.
orthogonality will play a role. The lingering doubt about the ability of the three filters to form a reasonably orthogonal basis set prompted the following comparison of their orthogonality.

3. FILTER ORTHOGONALITY

3.1. Introduction

When calculating the orthogonality of a pair of complicated functions it is often tempting to circumvent the mathematics by producing an \( n \)-dimensional vector approximation to them, and to do the test numerically. The main disadvantage of this is that, if the number of dimensions chosen is too small, one may produce very inaccurate results. It turns out that, due to their Gaussian form, the calculations for both the Gabor and DoG are easily derived explicitly. This has the added advantage that one can investigate the role of specific parameters easily.

A standard measure for the orthogonality of two vectors is that of the internal angle, shown as \( \Theta \) below:

\[
\Theta_{\vec{a}_0\vec{a}_1} = \arccos \left( \frac{\vec{a}_0 \cdot \vec{a}_1}{|\vec{a}_0| |\vec{a}_1|} \right).
\]

This formula has an equivalent form for two arbitrary functions of \( x \) and \( y \), which we can call \( g(x, y) \) and \( h(x, y) \), and is given by:

\[
\Theta^{gh} = \arccos \left( \frac{\iint g(x, y) h(x, y) \, dx \, dy}{\sqrt{\iint (g(x, y))^2 \, dx \, dy} \sqrt{\iint (h(x, y))^2 \, dx \, dy}} \right).
\]

This general formula can then be applied to the three filter types. The formula for the difference of Gaussians filter, denoted \( D_{xy} \), is as follows:

\[
D_{xy}(\theta, \lambda, \sigma) = \left( e^{-\left( \frac{\pi \cos \theta + \pi \sin \theta}{\sqrt{2}} \right)^2} - \frac{1}{\lambda} e^{-\left( \frac{\pi \cos \theta + \pi \sin \theta}{\sqrt{2} \lambda} \right)^2} \right) e^{-\left( \frac{\pi \cos \theta - \pi \sin \theta}{\sqrt{2} \lambda} \right)^2}.
\]

It differs from what is often referred to as a difference of Gaussians in the literature, in that it is not circularly symmetric. Simple cells are usually elongated along one axis, with little or no oscillation along this axis, but rather a Gaussian fall-off from a central maximum. Circular DoG filters are often used to model LGN neurons (e.g. Young, 1987), but are unsuitable here. To distinguish the 2D forms of these functions, I refer to the DoG simple cell model as the difference of Gaussian \( \times \) Gaussian model, or DoGG. The general form of the DoGG filter is shown in the...
first plot of Fig. 3. In the formula given above, \( \theta \) controls the filter’s orientation and \( \lambda \) acts as a scaling constant which is included so as to provide a filter which is flexible enough to realise most of the models described by Hawken and Parker in their paper. The parameter \( \sigma \) scales the whole filter, effectively shifting the peak of the frequency response along the frequency axis.

Note that this and all other filters considered here are even symmetric. In fact, visual cortex also contains filters of all phase variations between even- (bar detectors) and odd-symmetric (edge detectors). The orthogonality profiles for each phase value will in general change with phase angle, but I shall only consider their even-symmetric forms in the following analysis. Odd-symmetric filters are guaranteed to be completely orthogonal at an orientation difference of \( \pi/2 \) rad, whereas even symmetric filters are not. I will also not consider the orthogonality of offset receptive fields. Instead, I will only consider what should in practice be the worst case, i.e. identically centred, even-symmetric filters.

For a pair of DoGG filters defined as above, the variables which affect mutual orthogonality are the spatial frequencies, which we can denote as \( \sigma_a \) and \( \sigma_b \), and the difference in orientation, which we can denote as \( \alpha (\theta_a - \theta_b) \). The parameter \( \lambda \) should be constant in any one filtering scheme, and hence must the same for both filters.

The formula for the 2D Gabor filter, denoted \( G_{xy} \) is as follows:

\[
G_{xy}(\theta, \sigma, f_\kappa, \phi) = e^{-((x^2+y^2)\sigma^2)} \cos(2\pi f_\kappa \sigma (x \cos \theta + y \sin \theta) + \phi).
\]

This formula contains two separate scaling terms, \( \sigma \) and \( f_\kappa \). The first, \( \sigma \), governs the spatial frequency of the filter as a whole, and is the equivalent of \( \sigma \) in the expression for the DoGG filter. As before, the spatial frequencies of the two separate filters can be denoted \( \sigma_a \) and \( \sigma_b \). The second term \( f_\kappa \) governs the frequency of the modulating cosine wave which affects the ripple in the Gabor filter profile. The orthogonality of two Gabor filters will vary not only with the difference in orientation \( \alpha \) and the scaling parameters \( \sigma_a \) and \( \sigma_b \), but also with this new parameter \( f_\kappa \). For this reason it is included as an extra dimension of variability in the function describing changes in filter orthogonality. The last three graphs in Fig. 3 depict the Gabor filter for differing values of \( f_\kappa \). Note that just like \( \lambda \) in the DoGG filter, \( f_\kappa \) should ideally be set to one biologically motivated value within any one filtering scheme, and will hence be the same for both filters. The parameter \( \phi \) controls the phase of the filter allowing even- and odd-symmetric filter forms to be generated as-well as all intermediate forms. For the sake of the following calculations \( \phi \) will remain set at zero since only even symmetric forms are being considered, as explained earlier. However, in general, the ability to easily manipulate phase is a useful characteristic not possessed by the DoG function described above.
The formula for the 2D Cauchy filter, denoted $C_{xy}$ is as follows, where $c \equiv \cos \theta$ and $s \equiv \sin \theta$:

$$
C_{xy}(\theta, n, \sigma, \phi) = \cos(n \arctan(2\pi n\sigma (cx + sy)) + \phi) \\
\times \cos(\arctan(2\pi \sigma (cx + sy)))^n e^{-(\sigma (cy - sx))^2}.
$$
This formula contains a scaling term, \( \sigma \) which governs the spatial frequency of the filter and is the equivalent of \( \sigma \) in the expression for the DoGG filter. As before, the spatial frequencies of the two separate filters can be denoted \( \sigma_a \) and \( \sigma_b \). The variable \( n \) governs the overall shape of the filter. In general, as \( n \) rises, the steeper the slopes of the function and the more marked the sidebands become. In practice, the orthogonality of two filters will vary with the difference in orientation \( \alpha \), the spatial frequency terms \( \sigma_a \) and \( \sigma_b \), and \( n \). The last two graphs in Fig. 3 depict the Cauchy filter for two values of \( n \). Note that just like \( \lambda \) and \( f_k \), \( n \) should ideally be set to one biologically motivated value within any one filtering scheme, and will hence be the same for both filters. The parameter \( \phi \) once again controls the phase of the filter and will remain set at zero, as for the Gabor filter.

### 3.2. Contrasting filter orthogonality

The derivation of expressions for the orthogonality of both the Gabor and DoGG filters appear in the appendices. The Cauchy filter does not lend itself to such analysis however, and so numerical techniques were used. The expressions are henceforth denoted \( \Theta^D \), \( \Theta^G \) and \( \Theta^C \) respectively and will be measured in the range 0° to 90° to distinguish them from orientation difference \( \alpha \), which will be measured in radians. In this section, I compare orthogonality over a range of biologically motivated parameter values.

The first parameter to consider is \( \lambda \), the scaling parameter which controls the relative height and width of the DoGG filter. Figure 4a shows the surface described by \( \Theta^D \) as a function of \( \lambda \) and the difference in filter orientation \( \alpha \). Notice that the two spatial frequencies are chosen to be identical i.e. \( \sigma_a = \sigma_b \) on the assumption that orthogonality is lowest for filters tuned to the same spatial frequencies — an assumption which will be confirmed later.

The general trend which emerges is that orthogonality drops as the angle between the filters is reduced, as one might expect for an orientation-tuned filter. Of more interest is the change in orthogonality seen as the size of \( \lambda \) is altered. The highest measure of orthogonality is achieved at values close to unity, suggesting that a low value of \( \lambda \) is desirable. In order to decide upon a reasonable value we can turn to the results of Hawken and Parker for data from real cells. In their results for DoGG filters, the value of \( \lambda \) generally falls within the range 3 < \( \lambda \) < 4. Henceforth, the value 3.5 will be used.

The next parameter to consider is \( f_k \), the cosine frequency term of the Gabor filter. Figure 4b shows the surface described by \( \Theta^G \) as a function of \( f_k \), and the angle of separation \( \alpha \), once again setting \( \sigma_a = \sigma_b \). Clearly, for values of \( f_k < 1 \) this term has a very great affect upon filter orthogonality over the entire range of filter orientations. Similarly, for the Cauchy filter, the parameter \( n \) plays an important role in controlling filter orthogonality, as shown in Fig. 5a. As \( n \) increases, so orthogonality increases across all differences in orientation \( \alpha \).

Figure 5b shows several curves from all six orthogonality surfaces. From this latest graph it is clear that the value of \( f_k \) and \( n \) used will be crucial in deciding
whether the filter is more or less orthogonal than a DoGG filter. However, before considering what would be a reasonable value of $f_x$ or $n$, it is worth checking that filter orthogonality reaches a minimum across all $\alpha$ when the spatial frequencies, $\sigma_a$ and $\sigma_b$ of the two filters, are the same. Figure 6 shows the change in orthogonality with relative spatial frequency and angle of separation $\alpha$ for all of the filters.
Figure 5. (a) Orthogonality of two Cauchy filters, $\Theta^C$ as a function of the parameter $n$, and the difference in orientation $\alpha$. (b) Three values from this surface compared with the orthogonality of a DoGG filter and a Gabor filter. Orthogonality of the Gabor and Cauchy exceed that of a DoGG at $f_k \geq 0.7$ and $n \geq 5$ respectively.
Figure 6. Orthogonality surfaces for filters of different spatial scales defined by $\sigma_a$ and $\sigma_b$ for a typical DoGG filter, a Gabor filter and a Cauchy filter.
plots do indeed support the earlier assumption, revealing that differently spatially tuned filters exhibit almost complete orthogonality even when oriented in the same direction.

It now only remains to find realistic values for the Gabor cosine frequency $f_c$ and the Cauchy variable $n$. For $f_c$ we can turn to Hawken and Parker’s paper. Typical values quoted by them for best fitting Gabor profiles are $x_c \approx 2.0'$ or 0.033 deg and $f_c \approx 3.0$ c deg$^{-1}$, where their one dimensional Gabor is defined as follows, ignoring both the variable amplitude and phase terms:

$$G_x(x_c, f_c) = e^{-(x/x_c)^2} \cos(2\pi f_c x).$$

The overall cosine frequency equivalent to $f_c$ is gained by taking the product of $f_c$ and $x_c$, and so $f_c = f_c x_c = 0.1$. This typical value for $f_c$ is so low that two Gabor filters would be highly non-orthogonal even at a separation of $\pi/2$ rads.

As pointed out in the previous section, it may well be the case that Hawken and Parker’s decision to fit log frequency responses plays a large role in fixing such an unexpectedly low value of $f_c$. Other criteria based on spatial appearance may have produced a higher value. The best fitting value of $f_c$ for the cell shown in Fig. 2 was $f_c = 0.43$. What is more, Fig. 5b reveals that a value of $f_c$ approaching 1 would provide much higher orthogonality than the DoGG filter. Inspection of Fig. 3, however, reveals that the cosine term then oscillates rapidly enough to cause sizable side excitatory regions, something true of relatively few simple cells.

With regard to the Cauchy function, as with $f_c$, $n$ must remain fairly low in order to prevent significant sidebands emerging. On the other hand, $n$ must be high enough to keep the log frequency profile reasonably symmetric and the level of mutual orthogonality high. From Fig. 1 $n$ should be at least 3, though preferably 5. As it happens, Klein and Levi suggest a good fit with human contrast sensitivities can be achieved with these values of $n$. Such Cauchy functions will be only slightly skewed in log frequency and fit simple cell forms very closely. The value of $n$ used to fit the cell in Fig. 2 was exactly in the correct range ($n = 4$).

4. DISCUSSION

This paper has provided evidence that either the difference of Gaussian $\times$ Gaussian or Cauchy models of cortical simple cells should be chosen in preference to several alternative models, including the Gabor. The paper has argued this case both from the standpoint of neurophysiological evidence and new quantitative measures of filter orthogonality. These reasons can be summarised as follows:

- All of the neurophysiological studies mentioned here regard the Laplacian of a Gaussian as providing the worst fit to measured data.
- The Gabor filter is not symmetric in log frequency, whereas the DoGG and Cauchy filters, as described here, are.
- The Gabor model gives a poorer fit to measured data than the DoGG or Cauchy.
The Gabor model provides a less orthogonal set of functions than the DoGG or Cauchy for biologically relevant parameter values.

As the earlier analysis showed, if mutual filter orthogonality were the only constraint for choosing a filter, one could increase the cosine frequency \( f_\kappa \), in the Gabor function beyond its biologically relevant range, or raise the value of \( n \) in the Cauchy function. Alternatively, one could consider generating a new family of Gabor-like wavelets which are completely orthogonal (see Sheng et al. (1992) for a review). The main reason for not considering such functions here is the lack of data on how well they fit simple cell data, but also because there is no a priori reason for supposing that orthogonality would be preferable for our visual system. In practice, the representational redundancy inherent in a non-orthogonal set of filters may well provide enhanced tolerance to noisiness in input signals. This in itself is clearly a desirable property of any element in a system set to analyse real-world images (Sheng et al., 1992; Field, 1994). Within the context of this paper, orthogonality is seen as a useful property, but it should not be made artificially high at the expense of being able to reproduce cellular response properties.

A final point worth considering when choosing a model is simply its ease of use. The ability of the Cauchy function to easily generate different phase shapes via the phase term, \( \phi \), sets it apart from the DoGG. Apart from the fact that cells do appear in the whole spectrum of phases, it also allows the generation of models like those discussed by Ohzawa et al. (1997), which rely on pairing opposite phase cells to select for binocular disparity. Given the indistinguishably good fit produced by both the DoGG and Cauchy to real cell responses, the Cauchy is probably preferable in practice to the DoGG.

In summary, we can say that none of the models proposed here fully describe the action of simple cells. Any such model would need to take account of issues such as the diversity of receptive field form, cell interaction, temporal change and non-linearity (Kulikowski et al., 1982; DeAngelis et al., 1993; Sun and Bonds, 1994). On the other hand, there is no question that linear filters do capture a great deal of the form of simple cell receptive fields, and that they therefore represent a useful starting point for larger scale network models of visual cortex (McLean and Palmer, 1989; DeAngelis et al., 1993). Indeed, there are several successful models of invariant object recognition which use Gabor (Lades et al., 1993; Mel, 1997) or DoGG (Wallis and Rolls, 1997) filters to sample the input array. As Jacobson et al. (1993) point out, by combining a linear model with a non-linear output/activation function (such as a sigma function), and with some degree of lateral inhibition between neighbouring neurons, a good deal of simple cell function can be captured. They approve of the combined model described by Heeger (1993), a variant of which is implemented by Wallis in his model (Wallis and Rolls, 1997).

To conclude, the main point which this paper seeks to make is that used in the correct manner, with appropriate inhibition and output non-linearities, linear models form a useful starting point to modelling visual cortical processes. However, if one wishes to justify the use of such models on the grounds that they are ‘inspired by’
or ‘consistent with’ biology, it is important to use biologically relevant parameters. By applying this constraint, the Gabor model becomes much less attractive than other models, and both the DoGG and Cauchy model emerge as more suitable alternatives.

NOTES

1. The two most highly parameterised models which they propose are not considered here because of this problem.
2. Indeed that appears to be true of the Gabor filters used by Pötzsch et al. (1996) which, by inspection of their Fig. 1b, have large side peaks.

Acknowledgements

I am grateful to the editor, Jian Yang, to Miguel García-Pérez and to the other, anonymous reviewer for helpful comments. Thanks also to Michael Hucka for initiating an informative discussion on this topic on CVNet in 1995, and to all of the researchers who contributed to the debate.

REFERENCES


APPENDIX A: ORTHOGONALITY OF TWO DOGG FILTERS

From the general expression for function orthogonality $\Theta^{gh}$ given in the main text, we can write an expression for the orthogonality of two DoGG filters, denoted $\Theta^D$. If we define:

$$\Omega^D(\alpha, \lambda, \sigma_a, \sigma_b) = \int \int D_{xy}(0, \lambda, \sigma_a) D_{xy}(\alpha, \lambda, \sigma_b) \, dx \, dy,$$

then

$$\Theta^D(\alpha, \lambda, \sigma_a, \sigma_b) = \arccos \left( \frac{\Omega^D(\alpha, \lambda, \sigma_a, \sigma_b)}{\sqrt{\Omega^D(0, \lambda, \sigma_a, \sigma_a)} \sqrt{\Omega^D(0, \lambda, \sigma_b, \sigma_b)}} \right).$$

Note that for infinite positive and negative limits the integral of the square of $D_{xy}$ is the same for any orientation $\alpha$, which allows us to conveniently set $\alpha$ to zero in the second integral of the denominator. Also note that now, the terms in the denominator are both just special cases of the numerator in which $\sigma_a$ and $\sigma_b$ are equal, and $\alpha$ is set to zero, which means that we need only calculate the general case of $\Omega^D$.

Substituting the formula for $D_{xy}$ and factorising:

$$\Omega^D(\alpha, \lambda, \sigma_a, \sigma_b) = \omega_1^D + \omega_2^D + \omega_3^D + \omega_4^D,$$

for

$$\omega_1^D = \int \int \exp \left( -x^2 \left( \frac{\sigma_a^2 \lambda^2 + \sigma_b^2 \sigma_c^2 + \sigma_b^2 \sigma_s^2}{2 \lambda^2} \right) - xy \left( \frac{\sigma_b^2 \sigma_c (\lambda^2 - 1)}{\lambda^2} \right) \right) \, dx \, dy,$$

$$\omega_2^D = -\frac{1}{\lambda} \int \int \exp \left( -x^2 \left( \frac{\sigma_a^2 \lambda^2 + \sigma_b^2 \sigma_c^2}{2 \lambda^2} \right) - y^2 \left( \frac{\sigma_a^2 + \sigma_b^2}{2 \lambda^2} \right) \right) \, dx \, dy,$$
where \( c \equiv \cos(\alpha) \) and \( s \equiv \sin(\alpha) \).

It is now possible to express the exponent values in matrix form:

\[
\begin{pmatrix}
(x \ y)
\end{pmatrix}
\begin{pmatrix}
A_{xx} & A_{xy} \\
A_{yx} & A_{yy}
\end{pmatrix}
\begin{pmatrix}
x \\
y
\end{pmatrix}
\]

This then allows the application of the general result that for any symmetric matrix \( A \):

\[
\int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} e^{-(x^2+y^2)(A)^2} \ dx \ dy = \frac{\pi}{\sqrt{|A|}}.
\]

The respective matrix determinants can thus be evaluated:

\[
|A_{\omega_1^p}| = \frac{1}{4\lambda^4} \left( (\sigma_a^4 + \sigma_b^4 s^2) \lambda^4 + (\sigma_a^4 + 2\sigma_a^2 \sigma_b^2 c^2 + \sigma_b^4 c^4 \\
+ \sigma_b^4 s^4 + 2\sigma_b^2 s^2 c^2) \lambda^2 + \sigma_a^2 \sigma_b^2 s^2 \right),
\]

\[
|A_{\omega_2^p}| = \frac{1}{4\lambda^4} \left( (\sigma_a^4 + \sigma_b^4 s^2) \lambda^2 + \sigma_a^2 \sigma_b^2 c^2 + \sigma_b^4 \right),
\]

\[
|A_{\omega_3^p}| = \frac{1}{4\lambda^4} \left( (\sigma_b^4 s^4 + \sigma_a^4 \sigma_b^2 + \sigma_b^4 c^4 + 2\sigma_b^2 s^2 c^2) \lambda^2 + \sigma_a^2 \sigma_b^2 + \sigma_b^4 \right),
\]

\[
|A_{\omega_4^p}| = \frac{1}{4\lambda^4} \left( (\sigma_a^4 + 2\sigma_a^2 \sigma_b^2 + \sigma_b^4) \right).
\]
These relate to the formulae for the $\omega_{1-4}^D$ as follows:

\[
\begin{align*}
\omega_1^D &= \frac{\pi}{\sqrt{|A_{\omega_1^D}|}}, & \omega_2^D &= -\frac{\pi}{\lambda \sqrt{|A_{\omega_2^D}|}}, \\
\omega_3^D &= -\frac{\pi}{\lambda \sqrt{|A_{\omega_3^D}|}}, & \omega_4^D &= \frac{\pi}{\lambda^2 \sqrt{|A_{\omega_4^D}|}}.
\end{align*}
\]

By substituting the values for $\omega_{1-4}$ into the expression for $\Omega^D$, we obtain the following expression:

\[
\Omega^D(\alpha, \lambda, \sigma_a, \sigma_b) = \frac{\pi}{\sqrt{|A_{\omega_1^D}|}} - \frac{\pi}{\lambda \sqrt{|A_{\omega_2^D}|}} - \frac{\pi}{\lambda \sqrt{|A_{\omega_3^D}|}} + \frac{\pi}{\lambda^2 \sqrt{|A_{\omega_4^D}|}},
\]

which, with reference to the first two equations of this appendix, gives us an explicit expression for the change in orthogonality between two DoGGs as a function of the filter spatial frequencies $\sigma_a$ and $\sigma_b$, the scaling constant $\lambda$, and the angular separation $\alpha$.

APPENDIX B: ORTHOGONALITY OF GABOR

As for the DoGG filter, we first define $\Omega^G$ as follows:

\[
\Omega^G(\alpha, \sigma_a, \sigma_b, f_k) = \int \int G_{xy}(0, \sigma_a, f_k) G_{xy}(\alpha, \sigma_b, f_k) \, dx \, dy,
\]

then the expression for the orthogonality of two Gabor filters is:

\[
\Theta^G(\alpha, \sigma_a, \sigma_b, f_k) = \arccos \left( \frac{\Omega^G(\alpha, \sigma_a, \sigma_b, f_k)}{\sqrt{\Omega^G(0, \sigma_a, \sigma_a, f_k) \Omega^G(0, \sigma_b, \sigma_b, f_k)}} \right).
\]

Substituting the formula for $G_{xy}$ with $\rho = 2\pi f_k$, and factorising:

\[
\Omega^G(\alpha, \sigma_a, \sigma_b, f_k) = \omega_1^G + \omega_2^G + \omega_3^G + \omega_4^G,
\]

for

\[
\begin{align*}
\omega_1^G &= \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2) x^2 + i \rho (\sigma_b c + \sigma_a) x} e^{-(\sigma_a^2 + \sigma_b^2) y^2 + i \rho \sigma_b s y} \, dx \, dy, \\
\omega_2^G &= \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2) x^2 + i \rho (\sigma_b c - \sigma_a) x} e^{-(\sigma_a^2 + \sigma_b^2) y^2 + i \rho \sigma_b s y} \, dx \, dy, \\
\omega_3^G &= \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2) x^2 - i \rho (\sigma_b c + \sigma_a) x} e^{-(\sigma_a^2 + \sigma_b^2) y^2 - i \rho \sigma_b s y} \, dx \, dy, \\
\omega_4^G &= \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2) x^2 - i \rho (\sigma_b c - \sigma_a) x} e^{-(\sigma_a^2 + \sigma_b^2) y^2 - i \rho \sigma_b s y} \, dx \, dy.
\end{align*}
\]
All of the above equations can be expressed in the following general form:

\[
\omega_n^G = \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2)(x^2 + 2\xi_x x)} e^{-(\sigma_a^2 + \sigma_b^2)(y^2 + 2\xi_y y)} \, dx \, dy
\]

\[
= \frac{1}{4} \int \int e^{-(\sigma_a^2 + \sigma_b^2)(x + \xi_x)^2 - \xi_x^2} e^{-(\sigma_a^2 + \sigma_b^2)((y + \xi_y)^2 - \xi_y^2)} \, dx \, dy
\]

\[
= \frac{1}{4} e^{(\sigma_a^2 + \sigma_b^2)(\xi_x^2 + \xi_y^2)} \int e^{-(\sigma_a^2 + \sigma_b^2)(x + \xi_x)^2} \, dx \int e^{-(\sigma_a^2 + \sigma_b^2)((y + \xi_y)^2 - \xi_y^2)} \, dy,
\]

where the values of \(\xi_x\) and \(\xi_y\) are:

<table>
<thead>
<tr>
<th>Factor</th>
<th>(\xi_x)</th>
<th>(\xi_y)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\omega_1^G)</td>
<td>(-i \rho \frac{(\sigma_a c + \sigma_a)}{2(\sigma_a^2 + \sigma_b^2)})</td>
<td>(-i \rho \frac{\sigma_b s}{2(\sigma_a^2 + \sigma_b^2)})</td>
</tr>
<tr>
<td>(\omega_2^G)</td>
<td>(-i \rho \frac{(\sigma_c c - \sigma_a)}{2(\sigma_a^2 + \sigma_b^2)})</td>
<td>(-i \rho \frac{\sigma_b s}{2(\sigma_a^2 + \sigma_b^2)})</td>
</tr>
<tr>
<td>(\omega_3^G)</td>
<td>(i \rho \frac{(\sigma_b c + \sigma_a)}{2(\sigma_a^2 + \sigma_b^2)})</td>
<td>(i \rho \frac{\sigma_b s}{2(\sigma_a^2 + \sigma_b^2)})</td>
</tr>
<tr>
<td>(\omega_4^G)</td>
<td>(i \rho \frac{(\sigma_c c - \sigma_a)}{2(\sigma_a^2 + \sigma_b^2)})</td>
<td>(i \rho \frac{\sigma_b s}{2(\sigma_a^2 + \sigma_b^2)})</td>
</tr>
</tbody>
</table>

By a change of variables \(z_x = \sqrt{2(\sigma_a^2 + \sigma_b^2)}(x + \xi_x)\) and \(z_y = \sqrt{2(\sigma_a^2 + \sigma_b^2)} \times (y + \xi_y)\) we have:

\[
\omega_n^G = \frac{1}{8(\sigma_a^2 + \sigma_b^2)} e^{(\sigma_a^2 + \sigma_b^2)(\xi_x^2 + \xi_y^2)} \int e^{-\frac{1}{2}z_x^2} \, dz_x \int e^{-\frac{1}{2}z_y^2} \, dz_y.
\]

Each integrand is now in the form of a standard Gaussian distribution which allows the application of the following result:

\[
\int_{-\infty}^{+\infty} e^{-\frac{1}{2}z^2} \, dz = \sqrt{2\pi},
\]

which yields an expression for \(\Omega^G\):

\[
\Omega^G(\alpha, \sigma_a, \sigma_b, f_k) = \frac{\pi}{2(\sigma_a^2 + \sigma_b^2)} e^{\frac{z^2 f_k^2 \sigma_a^2 \sigma_b^2}{(\sigma_a^2 + \sigma_b^2)^2}} \left( e^{-\frac{(\pi^2 I^2(\sigma_b c + \sigma_a)^2}{(\sigma_a^2 + \sigma_b^2)^2}} + e^{-\frac{(\pi^2 I^2(\sigma_c c - \sigma_a)^2}{(\sigma_a^2 + \sigma_b^2)^2}} \right).
\]

In the special case \(\sigma_a = \sigma_b\) and \(\alpha = 0\):

\[
\Omega^G(0, \sigma_a, \sigma_a, f_k) = \frac{\pi}{4\sigma_a^2} \left( 1 + e^{-2\pi^2 f_k^2} \right).
\]

Substituting these results into the original expression for the change in orthogonality between two Gabor filters, denoted \(\Theta^G\), yields the following final expression
in terms of $\alpha$, the angular separation, $\sigma_a$ and $\sigma_b$, the spatial frequencies, and $f_k$, the cosine modulation frequency:

$$\Theta^G(\alpha, \sigma_a, \sigma_b, f_k) = \arccos \left( \frac{2\sigma_a \sigma_b e^{-\left(\frac{\pi^2 f_k^2 \sigma_a^2}{(\sigma_a^2 + \sigma_b^2)}\right)} \left( e^{-\left(\frac{\pi^2 f_k^2 (\sigma_b e^{-i\alpha} + \sigma_a)}{(\sigma_a^2 + \sigma_b^2)}\right)} + e^{-\left(\frac{\pi^2 f_k^2 (\sigma_b e^{-i\alpha} - \sigma_a)}{(\sigma_a^2 + \sigma_b^2)}\right)} \right)}{(\sigma_a^2 + \sigma_b^2)(1 + e^{-2\pi^2 f_k^2})} \right).$$