Orientation tuning curves:
empirical description and estimation of parameters

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Abstract. This paper compares the ability of some simple model functions to describe orientation tuning curves obtained in extracellular single-unit recordings from area 17 of the cat visual cortex. It also investigates the relationships between three methods currently used to estimate preferred orientation from tuning curve data: (a) least-squares curve fitting, (b) the vector sum method and (c) the Fourier transform method (Wörgötter and Eysel 1987). The results show that the best fitting model function for single-unit orientation tuning curves is a von Mises circular function with a variable degree of skewness. However, other functions, such as a wrapped Gaussian, fit the data nearly as well. A cosine function provides a poor description of tuning curves in almost all instances. It is demonstrated that the vector sum and Fourier methods of determining preferred orientation are equivalent, and identical to calculating a least-square fit of a cosine function to the data. Least-squares fitting of a better model function, such as a von Mises function or a wrapped Gaussian, is therefore likely to be a better method for estimating preferred orientation. Monte-Carlo simulations confirmed this, although for broad orientation tuning curves sampled at 45° intervals, as is typical in optical recording experiments, all the methods gave similarly accurate estimates of preferred orientation. The sampling interval, the estimated error in the response measurements and the probable shape of the underlying response function all need to be taken into account in deciding on the best method of estimating preferred orientation from physiological measurements of orientation tuning data.

1 Introduction

Following the discovery of orientation selectivity in visual cortical neurons by Hubel and Wiesel (1959), orientation tuning curves – i.e. graphs of neuronal response *vs* stimulus orientation – have been measured and described in many experiments. These tuning curves are typically approximately symmetric and bell-shaped, with a centre position and width at half-height which varies from cell to cell. Although this much has been known for a long time, few studies have examined what type of mathematical function best describes experimentally obtained orientation tuning data, and little attention has been paid to the related problem of how best to estimate preferred orientation from a series of response measurements made at different orientations. It is of interest to know to what extent orientation tuning curves can be approximated by a mathematical function of some kind, as this can be used to test predictions made by different models. Even though individual tuning curves are known to show idiosyncrasies in shape (Henry et al. 1974) which are unlikely to be captured by a simple mathematical model, they may still show a general tendency to approximate one model function rather than another. Knowing this function is also a prerequisite for deciding how best to estimate the position of the peak of the tuning function from noisy and/or poorly sampled data, as is necessary, for example, in optical recording experiments.

Methods which have been used in the past to describe the shapes of orientation tuning curves and/or to estimate preferred orientation include listening to the response on an audio monitor (e.g. Hubel and Wiesel 1974), linear interpolation or smoothing of adjacent data points (e.g. Henry et al. 1974; Schiller et al. 1976; Vogels and Orban 1990), manual fitting of straight lines (Hammond and Andrews 1978) or curves to data (De Valois et al. 1982) and linear regression of straight lines to each flank of the tuning curve (Rose and Blakemore 1974). More recent methods include calculating the phase angle of the second-order component of the Fourier transform of the tuning curve (Wörgötter and Eysel 1987), vector averaging (e.g. Blasdel and Salama 1986; Bonhoeffer and Grinvald 1991; Blasdel 1992) and least-squares fitting of a Gaussian (e.g. Albright 1984; Maldonado and Grey 1996). The statistical validity of these methods has not been firmly established, however; and there are theoretical objections to using a Gaussian function because orientation tuning is by definition cyclic over the interval 0°–180°, and a Gaussian does not have this property. There are also practical difficulties. For example, both the vector and Fourier methods require that the set of measurement angles be uniformly distributed over a 180° range. Fitting a Gaussian requires that

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the orientation tuning data has to be plotted in such a way that the peak in the tuning function is near the centre of the range of the x-axis values being used and is not split between the left and right edges of the graph.

In this paper I evaluate some of these methods and suggest solutions to the problem of estimating orientation tuning parameters from data which may be noisy or poorly sampled. In order to do this, it is first necessary to have a generally applicable model of the orientation tuning function. I therefore compared the accuracy with which a number of different cyclic functions could describe orientation tuning curves, using data obtained from extracellular, single-unit recordings in area 17 of adult cats. I found that most orientation tuning curves can be accurately described by a wrapped Gaussian function; however, other functions, such as von Mises circular distribution and two variants of it provided slightly better descriptions.

I also point out that the vector averaging and Fourier transform methods of estimating preferred orientation are mathematically equivalent and identical to calculating a least-squares fit of an angle-doubled cosine function to the tuning curve. However, the cosine function generally does not provide an acceptably accurate description of orientation tuning curves. This means that the Fourier/vector method is likely to be a less accurate estimator of preferred orientation than the best-fitting Gaussian or von Mises function. This result was confirmed by Monte Carlo simulations of well-sampled data with low noise-to-signal ratios. For coarsely sampled noisy data, however, the Fourier/vector method gave estimates that were as accurate, or in some cases better, than curve fitting.

The results suggest that calculating a least-squares fit of a wrapped Gaussian or von Mises function is probably the best way to estimate orientation preference, response strength and tuning selectivity from neurophysiological data. For coarsely sampled data (e.g. 4 samples at 45° intervals), such as that often obtained in optical recording experiments, it may be simpler, and probably just as accurate, to use the vector method to estimate preferred orientation.

2 Methods for determining preferred orientation

2.1 Vector averaging/Fourier transform methods

If responses, $R(x_i)$, are obtained for a set of N test orientations, $x_i, i = 0, 1 \ldots N - 1$, which are uniformly distributed over 0°–180° (e.g. the set of angles 0°, 30°, 60°, 90°, 120° and 150°), then one way of estimating preferred orientation is to calculate the vector average of the responses (Batschelet 1981). This can be done by first calculating two components, a and b, defined by

$$a = \sum_{i=0}^{N-1} R(x_i) \cos(2x_i) \; ; \quad b = \sum_{i=0}^{N-1} R(x_i) \sin(2x_i) \qquad (1a)$$

Preferred orientation, θ, can then be calculated as

$$\theta = 0.5 \arctan(b/a) \text{ if } a > 0$$

or

$$\theta = 180 + 0.5 \arctan(b/a) \text{ if } a < 0 \qquad (1b)$$

The vector magnitude of the responses is defined as

$$L = \left(\frac{1}{N}\right)\left(a^2 + b^2\right)^{1/2} \qquad (1c)$$

where a and b are given by (1a). This quantity is sometimes regarded as a measure of orientation tuning strength in optical recording experiments, although, as discussed below, it does not disambiguate response strength and response selectivity. A better measure of tuning strength (Wögötter and Eysel 1987; Bonhoeffer et al. 1995), which can be used if the responses are always ≥ 0, is given by

$$L = \frac{\left(a^2 + b^2\right)^{1/2}}{\sum_{i=0}^{N-1} R(x_i)} \qquad (1d)$$

For a Gaussian orientation tuning curve, this measure, which lies between 0 and 1, decreases in an approximately linear fashion with increasing width of the tuning curve (see Fig. 5b below), and is insensitive to overall responsiveness.

Wörgötter and Eysel (1987) proposed that orientation preference could be estimated by measuring the phase angle of the second-order term in the Fourier transform of a set of responses $R(x_i)$, with the x_i's uniformly distributed over 360°. A measure of direction preference can be obtained by taking the phase angle of the first-order term. If the method is applied to data obtained with the x_i's distributed over 180°, then the orientation preference is given by the first-order term. (Direction preference, of course, cannot be estimated from such data.) The real and imaginary components, $h(n)$ and $k(n)$, respectively, of the discrete Fourier transform of $R(x_i)$ are given by (Brigham 1974)

$$h(n) = \sum_{i=0}^{N-1} R(x_i) \cos\left(\frac{2\pi n i}{N}\right)$$

$$k(n) = \sum_{i=0}^{N-1} R(x_i) \sin\left(\frac{2\pi n i}{N}\right) \qquad (2)$$

For the 180° degree case, the fist-order components, $h(1)$ and $k(1)$, are identical to a and b obtained by the vector averaging method, because the terms $\pi i/N$ are equal (after conversion from radians to degrees) to the x_i's in (1a). A similar argument applies when the vector averaging method is extended to the case of directional data, where the x_i's span a 360° range. Thus, orientation preferences estimated using the Fourier transform method will be identical to those estimated by vector averaging.

Neither the Fourier transform nor the vector method can be applied if the measured orientations are not equally spaced across a full 180° or 360° range. Nor do the methods weight the data values in accordance with their estimated variances. In the Appendix, I show how the vector sum method can be generalized to cope with these cases. Accordingly, this gives a method for estimating Fourier coefficients from error-weighted, unevenly sampled data.

2.2 Least-squares fitting of model functions

Given a model function, f, for orientation tuning data, with one or more adjustable parameters p_1, p_2 etc. and data values R_i with estimated variances σ_i^2, this method works by

finding parameter values which minimize the goodness-of-fit

$$\chi^2 = \sum_{i=0}^{N-1} \left(\frac{1}{\sigma_i^2}\right) \{R_i - f(x_i, p_1, p_2, \ldots)\}^2 \qquad (3)$$

From the value of χ^2 it is possible (Press et al. 1994) to estimate the probability that the data can be described by the model and to estimate the probable error in the values of the parameters p_1, p_2 etc.

For certain functions, e.g. where f is a polynomial or a sinusoid, it is possible to derive algebraic formulas from which the parameter values which minimize χ^2 can be calculated explicitly. In many cases, however, it is either necessary, or more expedient, to find parameter values by means of a general purpose minimization method, such as the simplex algorithm. None of these methods is foolproof (Press et al. 1994), and all of them require good initial estimates of parameter values so that they will converge reliably on the minimum value of χ^2.

3 Candidate model functions

3.1 The cosine function

I show in the Appendix that the vector averaging and Fourier transform methods are mathematically identical to calculating a least squares fit to the data of an angle-doubled cosine orientation tuning function

$$\Omega(\theta) = A \cos 2(\theta - \varphi) \qquad (4)$$

where A is the model response at the preferred orientation φ. This model is implied, even if it is not used explicitly, by the vector and Fourier methods.

3.2 The wrapped Gaussian

Orientation tuning curves are often bell-shaped, so an obvious model function is a Gaussian. A Gaussian, however, is not cyclic, and it is inappropriate to attempt to model cyclic data with a non-cyclic function. There are also practical difficulties: a Gaussian cannot be used in a situation in which the peak of the tuning curve is close to zero or $180°$, so that the response is split between the left and right manual ends of the $0°–180°$ axis. Although this problem can be avoided by rescaling the x-axis values so that the peak lies instead somewhere near the middle, this requires an initial estimate of peak orientation, which may be difficult to obtain when the data are noisy or the peak is broad and poorly defined. A solution which works well in practice is to use a wrapped Gaussian (Batschelet 1981) defined as

$$G(\theta) = A \sum_{n=-\infty}^{n=\infty} \exp\left\{\frac{-(\theta - \varphi + 180n)^2}{2\sigma^2}\right\} \qquad (5)$$

where φ is the preferred orientation (in degrees) and σ is a measure of the width to the tuning curve. For most biologically likely values of σ, only a few terms in the sum need be calculated (e.g. $n = -2$ to $+2$ will suffice in most cases).

3.3 Von Mises distribution

A function which is commonly used to model circular distributions in statistical data (Batschelet 1981) is the von Mises distribution, defined here as the function

$$M(\theta) = A \exp\{k[\cos 2(\theta - \varphi) - 1]\} \qquad (6)$$

where A is the value of the function at the preferred orientation, φ, and k is a width parameter, from which the half-width of the tuning curve at half-height, $\theta_{0.5}$, may be calculated (in radians) as

$$\theta_{0.5} = 0.5 \arccos[(\ln 0.5 + k)/k]; \quad k > -0.5 \ln 0.5 \qquad (6a)$$

The von Mises distribution is the circular analogue of the Gaussian distribution in statistics: the vector mean of a set of orientations drawn from the distribution is the maximum likelihood estimate of the mean (Batschelet 1981), a property which it shares with the Gaussian distribution. The von Mises function approximates a Gaussian in shape over a biologically likely range of values of k.

3.4 Flat-topped/sharply peaked von Mises functions

All Gaussian functions have the same shape, in the sense that any two functions can be made identical by appropriate linear magnification of one of them in the vertical and horizontal directions. The shape of a von Mises distribution is determined by a single width parameter k and therefore cannot vary independently of the width at half-height. It is possible, however, that orientation tuning curves might exhibit more shape variations than can be captured by a single width parameter. The function

$$B(\theta) = A \exp\{k[\cos 2(\phi + \nu sin2\phi) - 1]\}$$
$$\phi = \theta - \varphi \, ; -0.5 \leq \nu \leq 0.5 \, ; k > -0.5 \ln 0.5 \qquad (7)$$

where φ is the preferred orientation, A is the response at the preferred orientation, and k and ν are shape parameters, defines a family of symmetric bell-shaped functions in which the slope of the function at half-height can vary independently of the width at half-height. Such curves can be described as being more or less flat-topped or sharply peaked (see Fig. 2c), the degree of flatness being determined by the parameter ν. The width at half-height cannot be given explicitly as an algebraic function, but can be calculated numerically (once parameters A, k, φ and ν have been obtained by least-squares fitting) as the solution to

$$\theta_{0.5} + \nu sin2\theta_{0.5} = 0.5 \arccos[(\ln 0.5 + k)/k] \qquad (7a)$$

3.5 A skewed von Mises function

The flanks of orientation tuning curves sometimes appear to differ significantly in slope. Such an asymmetry cannot be captured by any of the preceding functions, which are all symmetric around the preferred orientation. The von Mises function can be modified to introduce a component of skewness, or asymmetry, as follows:

$$S(\theta) = A \exp\{k[cos2(\phi + \nu[cos2\phi - -1]) - 1]\}$$
$$\phi = \theta - \varphi \; ; \quad -0.5 \leq \nu \leq 0.5 \; ; \quad k > -0.5 \ln 0.5 \quad (8)$$

As in the other functions, A is the maximum value of $S(\theta)$, which occurs at the preferred orientation, i.e. when $\theta = \varphi$. The amount of skewness is determined by the value of ν. When $\nu = 0$, both the flat-topped (7) and skewed (8) functions are identical to the von Mises distribution.

The widths of the function at half-height are given by the solutions to

$$\theta_{0.5} + \nu(\cos 2\theta_{0.5} - 1) = \pm 0.5 \arccos[(\ln 0.5 + k)/k] \quad (8a)$$

Alternatively, a single width parameter, which will lie between the two half-widths when $\nu \neq 0$, can be calculated from (6a).

3.6 Straight lines

Some authors (e.g. Rose and Blakemore 1974; Hammond and Andrews 1978) have modelled tuning curves by fitting straight lines to the flanks of the curve. Visually, this often appears to be a good description. Orientation preference can be defined as the position where the lines intersect, and the model function defined as

$$S(\theta) = R[m_1(\theta - \varphi) + A] \; ; \; \theta < \varphi$$
$$S(\theta) = R[m_2(\theta - \varphi) + A] \; ; \; \theta \geq \varphi \quad (9)$$
$$R(x) = x, x \geq 0 \; ; \quad\quad R(x) = 0, x < 0$$

where m_1 and m_2 are the slopes of the two flanks, and A is the value of the function at the preferred orientation φ. This function has four free parameters and can be fitted to data values by the simplex method, which does not require evaluating the derivatives of the function (which are undefined at three points).

4 Experimental data

4.1 Measurement of orientation tuning curves

Orientation tuning curves were obtained from extracellular recordings of single unit responses in area 17 in a series of adult cats. Results from some of these, and other, experiments done on the same units have been reported elsewhere (Swindale and Mitchell 1994; Swindale 1995). In the experiments, cats were anaesthetized by inhalation of 70% N_2O and 30% O_2, supplemented either by halothane or isoflurane gas (0.5%–1.5%) or by intravenous (i.v.) infusion of sodium pentobarbital at a rate of 1 mg/kg·h. In the experiments in which sodium pentobarbital was used as the supplementary anaesthetic, acepromazine was used as an initial sedative, and paralysis during artificial respiration was produced by continuous i.v. infusion of flaxedil (10 mg/kg·h). In the experiments in which halothane or isoflurane was used, oxymorphone was used as an initial sedative and was also infused i.v. (0.01–0.035 mg/kg·h) together with the paralyzing agent pancuronium bromide (0.2 mg/kg·h) throughout the experiment. In all cases, the agents infused were dissolved in lactated Ringers, delivered at an overall rate of 5

ml/kg·h. These variations in procedure were not believed to have any significant effect on the orientation tuning parameters studied here. Other aspects of the surgical preparation are described in more detail in Swindale (1995).

Visual stimuli were generated by a Picasso image synthesizer (Innisfree, Cambridge, MA) connected to a Tektronix 608 monitor and consisted of moving bright bars, with length (typically 1.5°–4°), width (typically 0.2°–0.4°) and velocity (typically 1.0–5.0°/s) chosen to elicit near optimal responses from the unit being studied. The brightness of the bars was about 60 cd/m², and the background brightness was about 9 cd/m². Tuning curves, obtained under computer control, were measured for sets of orientations, spaced typically at intervals of 10°–20°, presented in pseudo-random order. Each stimulus was presented 4–16 times, and from the resulting data, a mean response, from which an estimate of spontaneous activity was subtracted, and an estimate of the error in the mean at each test orientation were obtained.

Because these tuning curves were obtained for moving bars, it is, strictly speaking, incorrect to describe them as orientation tuning curves, and to attempt to describe them by functions that are cyclic in a 180° interval. Most cells in the cat visual cortex show some degree of direction selectivity and give different responses to bars moving in opposite directions. Thus, a proper description of their responses would be a directional tuning function with two peaks of different heights (and possibly different widths), spaced about 180° apart. The orientation tuning curve might be defined as the tuning curve obtained by summing the responses to pairs of stimulus presentations moving in opposite directions. For simplicity, this distinction will be ignored, as it has been in nearly all other studies of orientation tuning. What is really half of a directional tuning function which is cyclic over 360° will be analysed here as if it was an orientation tuning function which is cyclic over 180°.

Data from a total of 63 single units were selected for analysis. Units with responses which were weak or erratic, or whose receptive fields were incompletely traversed by the stimulus, were not included. Of the 63 units, 14 were classified as simple, 35 as complex, while the remaining 14 were not, or could not be, classified. Curve fitting of the six different model functions was done using a simplex algorithm (Press et al. 1994). Correct convergence was tested by restarting with a new, slightly different set of initial parameter estimates, and by perturbing the values after the fit appeared to be stable, to ensure repeated convergence onto the same values. Error-weighted fits were done by setting σ_i (3) equal to the calculated standard error in the mean of the response at each orientation. Unweighted fits were done by setting $\sigma_i = 1$ for all data values.

Goodness-of-fit between model functions and the data was calculated in two ways: (1) when error-weighted fits were done, the χ^2 value (3) was used to calculate the probability that the data were consistent with the model function; (2) to reveal possible systematic differences between the average shape of the orientation tuning curve of the entire sample and the model function shape, normalized residuals were calculated according to the formula

$$y_i = 100[R_i - f(\theta_i)]/A \quad (9a)$$
$$x_i = (\theta_i - \varphi)/\omega \quad (9b)$$
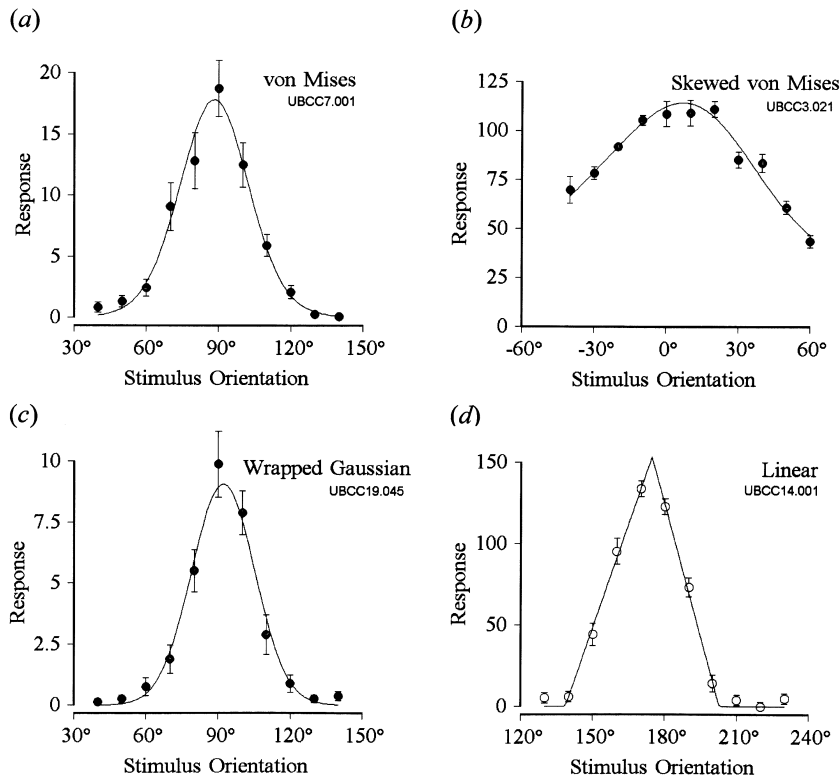
Fig. 1a–d. Four orientation tuning curves, chosen at random from the complete set of 63 used for analysis, together with examples of best fitting model functions

Table 1. Goodness-of-fit to different models, from χ^2 values

Model	No. of orientation tuning curves			
	$P < 0.001$	$0.001 \leq P < 0.01$	$0.01 \leq P < 0.1$	$0.1 \leq P < 1$
Skew	3	3	9	43
von Mises	6	1	11	40
Flat-topped	6	3	6	43
Gaussian	6	3	11	38
Linear	8	10	13	27
Cosine	54	2	1	1

where θ_i is the orientation at which response R_i was measured, A is the value of the fitted function at the preferred orientation φ, and ω is a width parameter. For a Gaussian, $\omega = \sigma$; for the cosine (which does not have a variable width parameter) $\omega = 1$; for all the other functions, $\omega = \theta_{0.5}$.

Equation (9a) expresses the difference between each measured response, R_i, and the value estimated from the curve fit, as a percentage of the parameter A, the peak of the fitted function; (9b) rescales the θ values from tuning curves of different widths and peak orientations as if the y_i values all came from tuning curves of the same width. If the data set is well described by the model function, the y_i's should be small, and a graph of the points (x_i, y_i) should be scattered above and below the horizontal axis of the graph. Systematic deviations of the experimental tuning curves from the model functions will be revealed if the mean of the y_i values differ significantly from zero at different points along the x-axis. Goodness-of-fit was measured as the root mean square (rms) value of the y_i values.

5 Results

5.1 Comparison of the different model functions

Figure 1 shows four examples of orientation tuning curves, selected at random from the complete set, together with examples of best-fitting model functions. Table 1 shows the goodness-of-fit, expressed as a probability, of each of the six model functions to the complete data set, obtained from the χ^2 value (3) following error-weighted least-squares fits of the model functions to the tuning curves. Note that in this case, a high rather than a low probability value is desirable, i.e. a value close to 1 indicates a good fit of the model to the data. The probability that a χ^2 value as large as the one obtained might have been due to chance, assuming that the data were derived from the model function, subject to the estimated errors, was calculated, and the number of tuning curves falling into each of four probability ranges was counted. The calculation of probability values from the χ^2 statistic takes into account the number of degrees of freedom in the fit, that is, the difference between the number of points on the measured tuning curve and the number of free parameters in the model function concerned. Therefore,

Table 2. Goodness-of-fit to different models, using residuals

Model function	No. of free parameters	rms value of residuals (%)	
		weighted	unweighted
Skew	4	6.5	5.5
Flat-topped	4	6.8	5.8
Linear	4	7.2	5.8
von Mises	3	7.4	6.6
Gaussian	3	7.6	6.7
Cosine	2	177	27.1

model functions with a larger number of free parameters do not automatically perform better with this test.

Tuning curves in column 4, with P values in the range 0.1–1.0 can be regarded as well described by the model function concerned. Tuning curves in column 3, with P values in the range 0.01–0.1 are less well described, although given that over 50 curves were analysed, some values should be expected to fall into this range. It might be regarded as at least questionable whether tuning curves with P values between 0.001 and 0.01 are acceptably described by the model, whereas curves in column 1, with P values < 0.001 might be regarded as definitely inconsistent.

This measure of goodness-of-fit depends on the estimate of the variance in the mean of each data point, so that if the estimated variances are small, the χ^2 value is correspondingly large. Thus, paradoxically, tuning curves determined with high reliability (e.g. those obtained with relatively large numbers of stimulus repetitions) may give low P values, whereas a larger, and apparently better, P value may be obtained from noisier data, although the visual impression of goodness-of-fit may be much the same in both cases. The method does, however, allow an unbiased comparison of different models, since they have all been applied to the same data set. On this basis, the skewed von Mises function performs best, although the flat-topped, plain von Mises, and wrapped Gaussian functions perform almost equally well, with perhaps a slight advantage in favour of the flat-topped and von Mises functions over the Gaussian. A linear function appears to do significantly less well, while a cosine function provides an unacceptable fit in almost all cases.

Table 2 shows the rms value of the differences between fitted and measured values, expressed as a percentage of the maximum height of the tuning curve, for each of the models. This measure was obtained for both error-weighted and unweighted fits: it can be expected to be slightly larger when error-weighted fits are done, and to decrease, other things being equal, as the number of free parameters increases. As with the χ^2 measure, these results suggest that the skewed von Mises function approximates the data slightly better than the flat-topped, von Mises or Gaussian functions. The linear function also does well on this test, possibly because, like the skewed function, it is able to accommodate asymmetries in the shapes of the tuning curves. As also shown by the χ^2 measure, the cosine function is unacceptable as a model by this criterion. Figure 2 plots the residuals for several of the models.

5.2 Accuracy of parameter estimates

The mathematical functions described above are useful not just as potential models, but as different estimators of physiological parameters of interest. In the present paper, a main concern is to find the best estimator of preferred orientation from physiologically obtained orientation tuning data, although other parameters such as the response maximum and tuning width are also of interest. If the errors in the data measurements are normally distributed, and if the data are well described by a model function in a statistical sense, then a least-squares fit of the model function to the data is likely to provide a good estimate of the parameters of interest. The preceding section showed that several different model functions, including a wrapped Gaussian, the von Mises function, and two variants of it, provide statistically acceptable descriptions of real orientation tuning curves in a substantial majority of the cells studied. Estimates of preferred orientation derived from least-squares fits of these functions ought therefore to be as close to accurate as it is possible to obtain from the data. The curve-fitting procedures do not yield directly an estimate of likely error in the fitted parameter values, but it is possible to estimate the errors by a Monte Carlo method in which new tuning curves are generated by substituting each data value in a given tuning curve with a new value chosen at random from a distribution with the same mean and variance as that measured experimentally. The assumption is that such a curve is equally likely to have been obtained, were the experiment repeated. A new set of parameter values is measured from a curve fit, and the procedure repeated until estimates of the variance in the parameter values of interest have been obtained. This was done to estimate the error in the measurement of orientation preference. These errors were usually small and ranged from $\pm 0.41°$ to $\pm 3.2°$ over the whole sample.

Table 3 shows how well the estimates of preferred orientation, made from the same tuning curve by the five different methods, agree with each other. It is to be expected that best-fitting wrapped Gaussian and von Mises functions, which are usually very similar in shape, should give similar estimates, and this was found to be the case. Because the linear and cosine functions fit the data less well, they would be expected to give estimates which differ more from each other, and this was also found to be the case. This is consistent with the probability that these procedures provide less accurate estimates of preferred orientation, although the fact that two different methods give similar results does not mean that they are both accurate.

Least-squares fitting to a cosine function and vector averaging provided estimates that were similar to within about $0.0014°$ and in no case was greater than $0.009°$ for both error-weighted and unweighted versions of the procedures. This agreement provides a test of the numerical accuracy of the calculations, because the two methods are mathematically equivalent (see Appendix) despite being computationally different and should yield identical estimates.

5.3 The skewness parameter

Figure 3 graphs values of the skewness parameter, ν, determined by least-squares fits of the skewed von Mises function

(a)

(b)

(c)

(d)
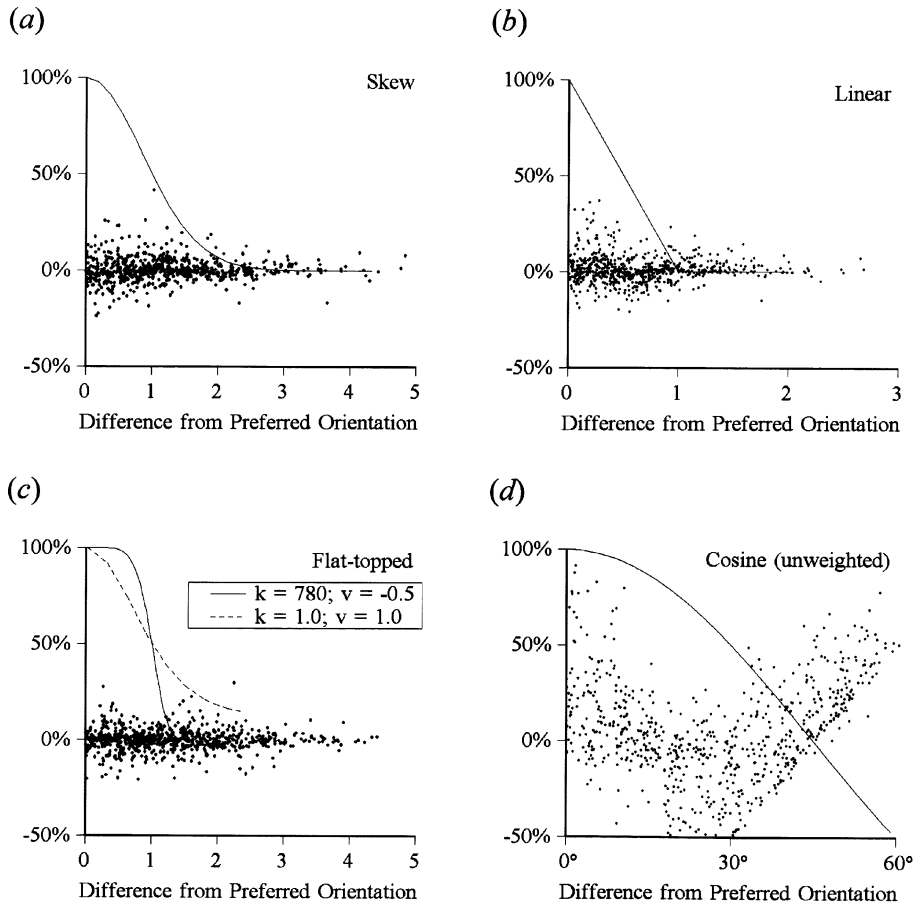
Fig. 2a–d. Residuals for four of the different model functions calculated according to (9a, b). Each point is a single measured response from a cell to a particular stimulus orientation. The y-axis value of each point shows the difference between the measured response at a given orientation and the value determined from the best-fitting model function, expressed as a percentage of the maximum response. With the exception of Fig. 9d, distances along the x-axes are rescaled according to the width of the best-fitting tuning curve: a distance of 1 equals the half-width of the tuning curve at half-height for **a**, **b** and **c**. All the data points are shown, with the exception of **d** where some outliers have been removed. *Continuous lines* show examples of model functions

Table 3. Agreement between different estimators in the values of preferred orientation. Values are the rms values of the difference between the estimates for each tuning curve, in degrees

| Estimator	Skew	Flat-topped	von Mises	Gaussian	Linear	Cosine	Vector sum
Skew	0						
Flat-topped	3.71	0					
von Mises	3.58	0.58	0				
Gaussian	3.75	0.58	0.33	0			
Linear	3.69	4.18	4.12	4.22	0		
Cosine	5.68	6.34	6.22	6.2	7.25	0	
Vector sum	5.68	6.34	6.23	6.2	7.25	0.0014	0

(8), against the corresponding value of the half-width of the tuning curve at half-height, determined from the best-fitting value of k according to (6a). Estimates of the errors in ν, determined using the Monte Carlo method described above, are also shown for some of the points. The figure suggests that at least some of the measured tuning curves had a significant degree of skewness. This is consistent with the slightly better overall fits to the data provided by the skewed function.

5.4 Effects of sampling density and noise on estimates of preferred orientation

In optical recording experiments, orientation preference is usually estimated by vector averaging of signals that are noisy and coarsely sampled in the orientation domain: mea-

surement from four samples, at 45° intervals, is typical. It would be useful to know how accurate the estimates made with this method are likely to be. The results in the previous section also raise the possibility that curve-fitting of a more suitable model function than a cosine might be a better estimator of preferred orientation than vector averaging. To answer these questions, I simulated orientation tuning data, varying the noise in the signal, the sampling interval, and the width of the underlying tuning function. I then calculated the rms error in the estimates of preferred orientation obtained by applying the vector averaging and curve-fitting methods.

The wrapped Gaussian function (5) was used to generate the simulated data, with values of preferred orientation, φ, chosen with uniform probability in the range 0°–180°. The
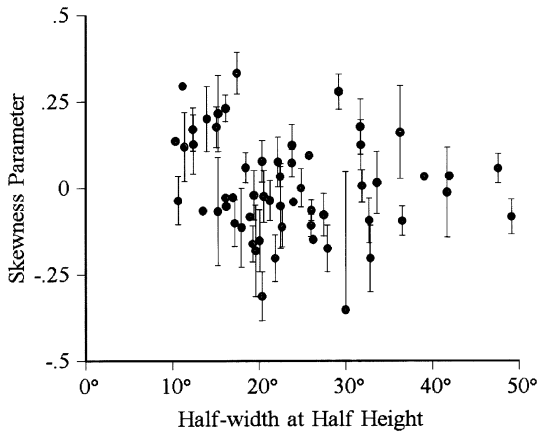
Fig. 3. Values of the skewness parameter, ν, determined from the error-weighted best-fits of the skewed von Mises function (8) to 58 of the tuning curves, plotted against the corresponding measurement of the half-width of the tuning curve at half-height, determined from the value of k according to (6a). Estimates of the errors in ν are shown for some of the points

width of the tuning curve, σ, was fixed at either $15°$, $25°$ or $45°$, and the peak response, A, was always $= 1$. Simulated, noisy orientation tuning functions, $R(\theta_i)$ were generated for sets of orientations, θ_i, spaced at either $10°$, $15°$, $22.5°$ or $45°$ intervals (i.e. $N = 18$, 12, 8 or 4, respectively), with $R(\theta_i) = G(\theta_i) + \xi$, where ξ is a random number drawn from a Gaussian distribution with a mean of zero and a standard deviation of 0, 0.025, 0.05, 0.075, 0.1, 0.15 or 0.2. These values are referred to as the noise-to-signal ratio. Estimates of preferred orientation, φ_{est}, were then calculated by a least-squares fit of a wrapped Gaussian function, and by vector averaging. The accuracy of the estimate was calculated as the rms value, $\varphi_{err} = \langle (\varphi_{est} - \varphi)^2 \rangle^{1/2}$ for sets of 50 different simulated tuning curves.

Figure 4 shows results from these calculations. It was found that (a) φ_{err} usually increases linearly with the noise-to-signal ratio for both methods, and (b) for well-sampled, narrow, orientation tuning functions, the curve-fitting method is about twice as accurate as the vector method. However, this difference disappears for broader tuning curves and for coarser sampling intervals: for conditions which resemble those of optical recording, with a sampling interval of $45°$, the vector method performs as well as the curve-fitting method, while, surprisingly, the vector method was better for narrow tuning curves sampled at $45°$ intervals and with noise-to-signal ratios between 0.075 and 0.2. Overall, the estimates for poorly sampled, noisy data seem surprisingly accurate: for example, the results show that preferences can be estimated with an accuracy of about $\pm 12°$ from only 4 samples at $45°$ intervals with a signal-to-noise ratio of 5:1.

5.5 Interpretation of vector magnitude

Vector averaging yields a magnitude, L, (1c) which, in optical recording experiments, is sometimes regarded as a measure of orientation tuning strength. Figure 5a shows how this measure varies as a function of tuning curve width. There is a non-monotonic relationship with tuning width: L has a maximum at a tuning width (σ) of about $29°$ and decreases

for smaller as well as larger tuning widths. It is clear from the definition (1c) that L will vary in proportion to the overall response magnitude. Small values of L may therefore imply a high degree of orientation selectivity, or poor selectivity and/or low responsiveness.

The interpretation of the normalised measure of L (1d) used by Wörgötter and Eysel (1987) and Bonhoeffer et al. (1995) is more straightforward. The measure is insensitive to overall responsiveness and decreases, approximately linearly, with increasing tuning width over a biologically probable range of tuning widths (Fig. 5b).

6 Discussion

6.1 Quantitative modelling of orientation tuning curves

The results presented above suggest that single-unit orientation tuning curves can be empirically well-described by a wrapped Gaussian (5) or a von Mises function (6), which each have three free parameters, or by two variants of a von Mises function (7, 8), described here for convenience as 'flat-topped' and 'skewed', respectively, which have four free parameters. The additional parameters allow in one case (7) for variation in the sharpness of the peak of the function, independently of its width at half-height or, in the other, for different slopes of the two flanks (8). Of these four, the skewed function gives the best overall fit to the data, whether assessed by statistical goodness-of-fit (Table 1) or by the overall closeness of the data points to the fitted functions (Table 2). This suggests that asymmetry makes a small, but significant contribution to shape variations in tuning curves. Such asymmetries have been described by other experimenters (e.g. Henry et al. 1974; Rose and Blakemore 1974). However, the advantage of this model over the other three in statistical terms is slight. For this reason, it may be simpler in many cases to use the von Mises function (6), which has one less free parameter and describes the data nearly as well. The wrapped Gaussian would seem to have no particular advantage over the von Mises function as a model, except perhaps for the greater familiarity of the Gaussian function.

Given the vagaries of neurophysiological responses, the statistical goodness-of-fit of the data to the best of the models – the skewed von Mises function (Table 1) – seems surprisingly good. In 52 of 58 cases, the model description was statistically acceptable. However, it should be remembered that the larger the estimated errors in the data, the more likely it is that any particular model will fit the data acceptably. More reliable data, obtained with a larger number of stimulus presentations, would almost certainly result in a much less good fit of all of the models in purely statistical terms (an inevitable consequence of more accurate data). Table 2 provides a different indication of how well the models describe the data. It shows by how much the fitted curves deviate from the data, expressed as a percentage of the maximum response. By this criterion, only the cosine function (4) performs unacceptably: the other functions, including the linear function, all deviate, on average, by no more than about 6%–7% on this scale. The lower performance of the linear model in statistical terms may perhaps be due to the fact
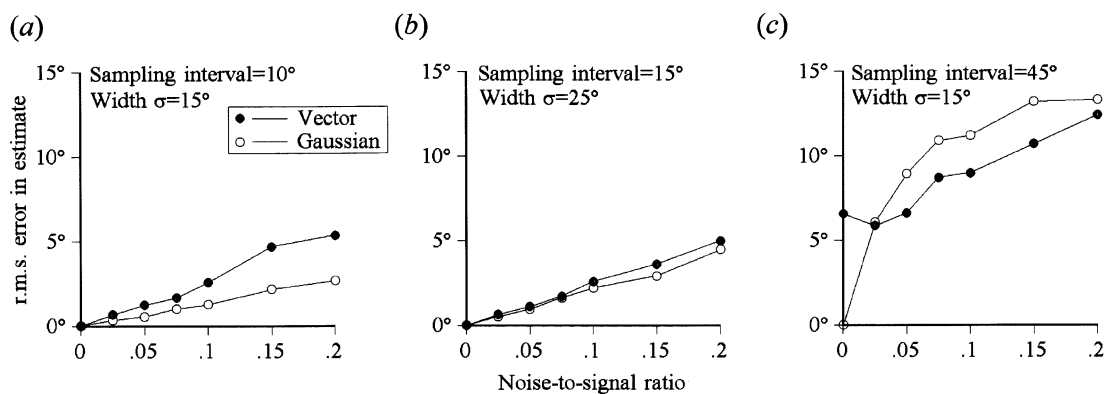
Fig. 4a–c. Calculations of the errors in measurements of preferred orientation, as a function of the noise-to-signal ratio, sampling interval and the width of the underlying orientation tuning function. *Solid circles* show the rms errors in the estimates made using the vector averaging method, and *open circles* are the errors made by fitting the correct model function (in this case a wrapped Gaussian) to modelled (i.e. simulated) orientation tuning data

that this model tends to fit the flanks of the tuning curves less well, where the measured error values tend also to be small. A relatively small difference between measured and predicted firing rate in these regions can have a large effect on the overall statistical goodness-of-fit.

6.2 Error-weighted vs unweighted fits

The procedures described above can be applied with, or without, weighting by the estimated error in the measurement of the response at each orientation. In principle, error-weighting should lead to more reliable estimates of parameter values, and it also allows one to make a statistical estimate of the goodness-of-fit between the data and the model. In practice, the estimates of preferred orientation obtained with unweighted fits did not differ much from those obtained with weighted fits (the rms difference was 1.0° for both wrapped Gaussian and von Mises fits), despite the fact that the error values usually vary substantially within individual tuning curves, increasing in size as the response increases. One problem with doing error-weighted fits is that occasionally a cell gives exactly the same response (typically zero spikes or a single spike) to all presentations of a particular orientation, leading to an error of zero. The resulting division by zero (3) means that an error-weighted fit cannot be performed. Cells in which this happened were excluded from the error-weighted fits done here. A solution to this problem would be to add noise of ±0.5 spikes to all responses: otherwise, it is not clear how to deal in statistical terms with an estimate of a response (zero) that is ostensibly certain.

6.3 What factors determine the shapes of orientation tuning curves?

Although the mathematical models discussed here describe orientation tuning curves to a reasonable degree of accuracy, it is probably naive to suppose that any simple model is likely to be correct. The physiological processes that combine to determine the orientation tuning of single neurons

are certain to be many and varied, and even if they were not, it is not obvious that they would yield mathematically simple orientation tuning functions. The Gabor model of receptive field organization (Marcelja 1980; Kulikowski et al. 1982; Daugman 1985) is one of the simplest models which is likely to be applicable to the prediction of orientation tuning. However, it is doubtful whether this model will yield simple orientation tuning functions. I calculated orientation tuning curves from it by computer simulation (using the implementation of the model described in Swindale 1995) and found that they were only approximately described by Gaussian or von Mises functions: rms values of residuals were found to be in the range of 1.3%–2.5%, using the same criteria for goodness-of-fit used in Table 2. Atick and Redlich (1990) analysed a model of simple cell receptive fields mathematically, using a difference-of-Gaussians model for the LGN inputs, and derived an expression for the orientation tuning curve for a static bar. They also showed that the receptive field profile of their model could be closely approximated by the Gabor model. Their mathematical model for orientation tuning was not tested in the present study, partly because of its complexity and partly because it requires a knowledge of parameters such as receptive field length and width for its evaluation, and these were not available for most of the cells.

More general approaches to predicting the shapes of orientation tuning curves may be worthwhile. The central limit theorem shows that the probability distribution of an outcome to which a large number of different processes contribute will tend to be Gaussian. For circular distributions, the equivalent outcome is likely to be a von Mises distribution. Although it may seem tempting to suppose that the central limit theorem might apply straightforwardly, this is probably a mistake: the theorem applies to probability distributions, and a physiological tuning curve cannot be regarded as a probability distribution, even if it is the outcome of many probabilistic events. The reasoning used to prove the theorem might be applied, if it were the case that individual orientation tuning curves could be expressed as the convolution of a larger number of approximately Gaussian functions (or circular equivalents), and if the input-output relations of

(a)

(b)
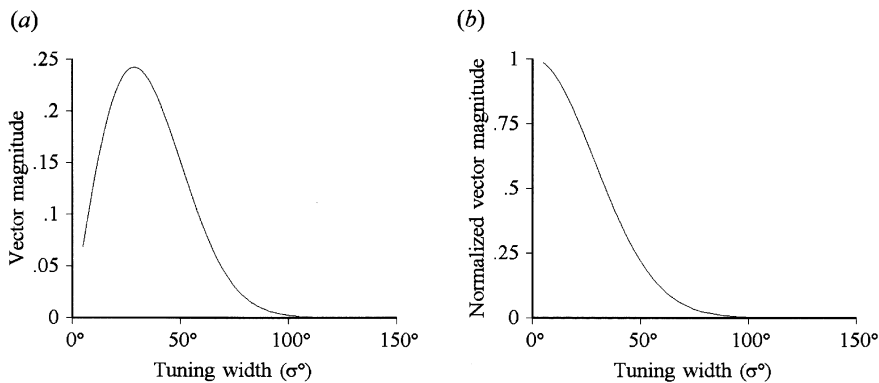
Fig. 5. a Variation in the vector magnitude (1c) with orientation tuning width, calculated for wrapped Gaussian tuning curves. Vector magnitude is largest for an orientation tuning width of about $29°$. **b** Variation in the normalised vector magnitude (1d) with orientation tuning width

individual neurons were linear. Such a result seems plausible, but remains to be demonstrated.

Information theory might be used to predict the shape of orientation tuning curves, and such predictions might be mathematically simple functions. It is an attractive possibility that evolution has selected mechanisms that tend to make orientation tuning curves conform, on average, to some ideal shape. So far, however, such predictions do not seem to have been made.

6.4 Estimation of preferred orientation

The present results show that the vector averaging (Blasdel and Salama 1986; Blasdel 1992) and Fourier transform (Wörgötter and Eysel 1987) methods are (a) equivalent to each other and (b) equivalent to finding a least-squares fit of an angle-doubled cosine function to the data. The results also show that the latter function provides a relatively poor description of single-unit orientation tuning data. For this reason, the vector averaging/Fourier transform methods may not necessarily be the most accurate way of estimating preferred orientation. Simulations showed that a least-squares fit of the 'ideal' (i.e. correct) model function was about twice as accurate as the vector method, when applied to well sampled, relatively narrow, orientation tuning functions i.e. data likely to be obtained in extracellular single-unit recordings. However, for model data that resembled those likely to be obtained in optical recording experiments, i.e. coarsely sampled, broad orientation tuning curves, the vector method was either as good, or in some cases, better. While this result suggests that vector averaging is a good way to estimate preferred orientation in optical recording data, it might be helpful to analyse optical recording data in the same way as has been attempted here for single-unit data. This means first finding a model function that accurately describes optical responses as a function of orientation, and then to use this to estimate preferred orientation.

6.5 Estimation of responsiveness and selectivity

The vector magnitude (1c) is a very uninformative measure when applied to orientation tuning data: a low value may imply either a high degree of selectivity or a poor degree of selectivity, as well as poor overall responsiveness (Fig. 5a).

Although it is recognized that regions of low vector magnitude in optical recording data may equally well be regions of poor responsiveness or poor selectivity, or both (e.g. Bonhoeffer and Grinvald 1991; Blasdel 1992; Bonhoeffer et al. 1995), it is perhaps less obvious that such regions might, at least in theory, have high selectivity: this could occur for tuning curves with half-widths (at half-height) of less than about $30°$. This is broad tuning by single-unit standards: the majority of cells in the present sample and those in the comparable study of Maldonado and Grey (1996) had tuning widths narrower than this. A decrease in selectivity in these cells could lead to a larger, rather than a smaller, vector magnitude. Because optical recordings average the responses of large numbers of neurons, the tuning curves from each region of cortex will be broader than single-unit responses, although it might be unwise to assume that the half-widths will always be greater than $30°$. The normalised measure of vector magnitude (1d) used by Wörgötter and Eysel (1987) and Bonhoeffer et al. (1995) avoids this problem, since it is insensitive to overall responsiveness and decreases nearly linearly with increasing tuning width (Fig. 5b). Although it is computationally intensive, the approach suggested above, namely least-squares fitting of an appropriate model response function to the data, should nevertheless provide the most accurate estimates of preferred orientation, peak responsiveness and selectivity.

6.6 Estimation of direction preference

Vector averaging can be applied to directional tuning data to estimate preferred direction (Malonek et al. 1994; Weliky et al. 1996), although, as with orientation tuning data, it is not *a priori* certain that the resultant angle is the best estimate of preference that could be obtained from the data. The interpretation of the vector magnitude is also subject to the uncertainties discussed above for orientation. As with orientation tuning, the best approach is probably to first measure direction tuning curves as accurately as possible in single-unit and/or optical recording experiments, and then to find a model function that describes the data well. A minimal requirement for this model function is that it should have two peaks, with independently variable heights, and possibly widths. Least-squares fits of this function to the data could then be used to estimate model parameters such as preference and selectivity. To my knowledge, the simple cosine

implied by the Fourier method is the only model function that has yet been applied to directional tuning data.

6.7 Physiological mechanisms

Although there are many ways in which to study the physiological mechanisms that generate orientation selectivity, it might be interesting to extend the approach undertaken here, by attempting to obtain more extensive and reliable data: e.g. tuning curves from larger numbers of stimulus presentation than (typically) 4–16 presentations of each condition. It is likely that relatively simple model functions will fit such data less well: systematic discrepancies would suggest the existence of better model functions, which could be used to constrain more detailed, physiologically based, models, while idiosyncratic discrepancies might, if they proved to be stable over time, also give clues. The discrete mosaic of retinal ganglion cell receptive fields, from which cortical fields are derived, is likely to have an impact on tuning curve shapes, especially since cortical neurons receive inputs from relatively small numbers of ganglion cells. Correlates of this mosaic have yet to be demonstrated directly in experiments on visual cortical neurons.

7 Appendix: Calculation of preferred orientation from the phase angle of the best-fitting, angle-doubled cosine function

Let the function to be fit to the data be

$$y = A \cos 2(x - \varphi) \tag{A1}$$

where A is the value of y at the preferred orientation φ. If there are N data values, y_i, obtained for a set of orientations x_i with measurement errors σ_i, then the goodness-of-fit of the data is given by

$$\chi^2 = \sum_{i=1}^{N} \frac{1}{\sigma_i^2} \{ y_i - A \cos 2(x_i - \varphi) \}^2 \tag{A2}$$

Values of A and φ for which χ^2 is a minimum can be found by setting the partial derivatives of χ^2 with respect to A and φ equal to zero. From (A2) we have

$$\left(\frac{\partial \chi^2}{\partial A} \right)_\varphi = 2 \sum_{i=1}^{N} \frac{1}{\sigma_i^2} \left\{ A \cos^2 2(x_i - \varphi) - y_i \cos 2(x_i - \varphi) \right\} \tag{A3}$$

and

$$\left(\frac{\partial \chi^2}{\partial \varphi} \right)_A = 4A \sum_{i=1}^{N} \frac{1}{\sigma_i^2} \{ A \sin 2(x_i - \varphi) \cos 2(x_i - \varphi)$$
$$- y_i \sin 2(x_i - \varphi) \} \tag{A4}$$

Setting $\left(\frac{\partial \chi^2}{\partial A} \right)_\varphi = 0$, and $\left(\frac{\partial \chi^2}{\partial \varphi} \right)_A = 0$, gives

$$A \sum_{i=1}^{N} \frac{1}{\sigma_1^2} \cos^2 2(x_i - \varphi) = \sum_{i=1}^{N} \frac{y_i}{\sigma_i^2} \cos 2(x_i - \varphi) \tag{A5}$$

and

$$A \sum_{i=1}^{N} \frac{1}{\sigma_i^2} \sin 2(x_i - \varphi) \cos 2(x_i - \varphi)$$
$$= \sum_{i=1}^{N} \frac{y_i}{\sigma_i^2} \sin 2(x_i - \varphi) \tag{A6}$$

A can be eliminated by dividing (5) by (6), and the resulting equation can be solved for φ after expanding the sine and cosine functions to obtain separate terms in x_i and φ. After defining the following five constants which can be calculated from the data values:

$$M = \sum_{i=1}^{N} \frac{1}{\sigma_i^2}$$

$$s = \sum_{i=1}^{N} \frac{y_i}{\sigma_i^2} \sin 2x_i \quad c = \sum_{i=1}^{N} \frac{y_i}{\sigma_i^2} \cos 2x_i \tag{A7}$$

$$g = \frac{1}{M} \sum_{i=1}^{N} \frac{\sin 4x_i}{\sigma_i^2} \quad h = \frac{1}{M} \sum_{i=1}^{N} \frac{\cos 4x_i}{\sigma_i^2}$$

the preferred orientation φ is given by

$$\varphi = 0.5 \left(\arctan \frac{s + sh - cg}{c - ch - sg} \right) \quad \text{if} \quad c - ch - sg > 0$$

or

$$\varphi = \pi + 0.5 \arctan \left(\frac{s + sh - cg}{c - ch - sg} \right)$$
$$\text{if} \quad c - ch - sg < 0 \tag{A8}$$

Once φ has been calculated, A, can be calculated from (A5) as

$$A = \left(\frac{2}{M} \right) \frac{c \cos \varphi + s \sin \varphi}{1 + g \sin 4\varphi + h \cos 4\varphi} \tag{A9}$$

Equation (A8) provides a way of estimating preferred orientation from a set of data values (x_i, y_i) defined in terms of an error-weighted least-squares fit of the cosine function defined in (A1), without having to resort to iterative curve fitting procedures. If the variances of the data values are equal, and if the x_i are uniformly distributed over the range $0 - \pi/2$, then $g = 0$ and $h = 0$, and (A8) reduces to

$$\varphi = 0.5 \arctan \frac{\sum y_i \sin 2x_i}{\sum y_i \cos 2x_i} \tag{A10}$$

which is the formula for vector averaging given in (1a). It seems reasonable therefore to regard (A8) as a generalization of the vector sum method to the problem of estimating the mean of a circular distribution from a set of estimates of the value of the distribution, made at an arbitrarily spaced set of measurement points. This is not the same problem as that of estimating the mean of a distribution from a set of values x_i obtained by randomly sampling from a probability distribution $P(x)$. In this case, the mean estimated from vector averaging can be shown to be the same as the maximum likelihood estimate of the mean under the assumption that the data are drawn from a von Mises distribution (Batschelet 1981).

Equations (A7–A9) can be generalized to the estimation of Fourier coefficients from non-uniformly sampled data series. A similar approach, created by N.R. Lomb, is described by Press et al. (1994).

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