

How to Unconfound the Directional and Orientational Information in Visual Neuron's Response

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Abstract. When drifting bars or gratings are used as visual stimuli, information about orientation specificity (which has a period of 180°) and direction specificity (which has a period of 360°) is inherently confounded in the response of visual cortical neurons, which have long been known to be selective for both the orientation of the stimulus and the direction of its movement. It is essential to "unconfound" or separate these two components of the response as they may respectively contribute to form and motion perception, two of the main streams of information processing in the mammalian brain. Wörgötter and Eysel (1987) recently proposed the Fourier transform technique as a method of unconfounding the two components, but their analysis was incomplete. Here we formally develop the mathematical tools for this method to calculate the peak angles, bandwidths, and relative strengths, the three most important elements of a tuning curve, of both the orientational and the directional components, based on the experimentally-recorded neuron's response polar-plot. It will be shown that, in the 1-D Fourier decomposition of the polar-plot along its angular dimension, 1) the odd harmonics contain only the directional component, while the even harmonics are contributed to by both the orientational and the directional components; 2) the phases and the amplitudes of all the harmonics are related, respectively, to the peak angle and the bandwidth of the individual component. The basic assumption used here is that the two components are linearly additive; this in turn is immediately testable by the method itself.

1 Introduction

Research in the past three decades has shown most convincingly that neurons in mammalian visual cortex respond to, among others, visual presentations of properly oriented stimulus since the pioneering work of Hubel and Wiesel in cat (Hubel and Wiesel 1959, 1962)

and monkey (Hubel and Wiesel 1968). A common method of quantifying this orientation selectivity is to drift the stimulus bar or grating across the receptive field of the neuron at varying orientations over a full cycle of 360° . The neuron's response to each of these presentations (measurable from the post-stimulus histogram) is recorded, and then plotted against the stimulus orientation. In most experiments, drifting stimuli (rather than stationary ones) are used for two technical reasons: 1) A stationary stimulus is usually not as effective in driving the cell as a drifting one; 2) Moreover, it is very difficult to align a stationary bar or grating exactly at the center of the receptive field, especially for non-optimal orientations. If, instead, patterns are drifted across the receptive field, no precise alignment is necessary. However, using moving stimuli creates a problem: the information on orientational selectivity and directional selectivity is confounded in the cell's overall response, i.e., the cell would respond to the directional aspect of the stimuli in addition to the orientational aspect. As a result, a bar or grating of a particular orientation moving at opposite directions might elicit responses of quite different amplitudes. In Fig. 1 is shown the single cell recording result from a typical striate cell, where the response amplitude is plotted radially against the stimulus angle, commonly known as the response "polar-plot". Indeed, most visual cortical cells show some degree of directional selectivity, and a number of different "directionality indices" have been used to quantify this selectivity (e.g. Schiller et al. 1976; Baker et al. 1981; De Valois et al. 1982; Maunsell and Van Essen 1983; Albright 1984; Mikami et al. 1986; Orban et al. 1986; Berman et al. 1987). However, since the orientational component and the directional component of the cell's response are confounded (not separated), these efforts can hardly be successful. In particular, it is generally impossible even to "read out" from the response polar-plot the optimal orientation and/or direction that the cell is tuned to, not to mention the bandwidths and strengths of these tuning functions.

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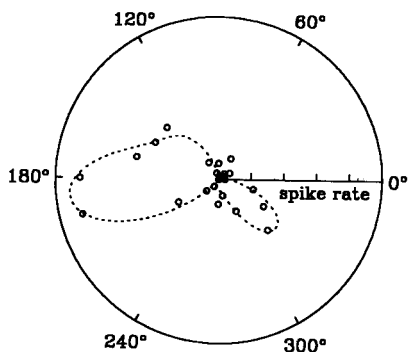


Fig. 1. The response polar plot of a typical visual cortical cell. The cell's response, in terms of firing rate (here with unspecified unit), is plotted radially against the polar angle which represents the moving (drifting) direction of the visual stimulus (either a bar or 1-D grating). Note that the response curve is not symmetric about either the origin or any axis passing the origin, suggesting that the cell is neither purely direction selective nor purely orientation selective

Recently, Wörgötter and Eysel (1987) proposed the Fourier transform technique to unconfound the directional and orientational components in the cell's response plot, taking advantage of the fact that they can be described as functions having periods of 360° and 180° respectively. However, they inaccurately identified the first harmonic in the Fourier expansion to be the directional component and the second harmonic to be the orientational component, and therefore unduly truncated the higher harmonics which are of equal, if not greater, importance (as shall be clarified in Methods and further mentioned in Discussion). Besides, they did not provide a technique for estimating the bandwidth of each component.

Here we formally develop the Fourier analysis technique to unconfound the orientation and direction components under one (but a major) assumption: that the two components are linearly additive. We shall see that, under this assumption, we are able to obtain from the response polar-plot the peak angles, bandwidths, and relative strengths of each of these components. We shall further demonstrate that the assumption of linear additivity of the orientational and directional components can be tested by the method itself in an extremely simple way, a unique feature of this method.

2 Method

We know that the response of a visual cortical neuron to oriented bars or gratings is a function of the stimulus angle, θ . More specifically, it is a function of θ through an orientational component $O(\theta)$ and a directional component $D(\theta)$, i.e.,

$$R(\theta) = R(O(\theta), D(\theta)), \quad (1)$$

where the orientation term and the direction term are defined respectively as

$$\begin{aligned} O(\theta) &= O(\theta + \pi), \\ D(\theta) &= D(\theta + 2\pi). \end{aligned} \quad (2)$$

We first deal with $D(\theta)$. Since it is a periodic function (with period 2π), we can expand it into Fourier series with fundamental frequency $f_0 = 1/2\pi$):

$$D(\theta) = a_0 + \sum_{k=1}^{\infty} a_k \cos k\theta + d_k \sin k\theta,$$

where the expansion coefficients are given by

$$\begin{aligned} a_0 &= \frac{1}{2\pi} \int_0^{2\pi} D(\theta) d\theta, \\ a_k &= \frac{1}{\pi} \int_0^{2\pi} D(\theta) \cos k\theta d\theta, \\ d_k &= \frac{1}{\pi} \int_0^{2\pi} D(\theta) \sin k\theta d\theta. \end{aligned} \quad (4)$$

Now let us take a closer look at a_k and d_k . Without loss of generality, we temporarily assume the peak angle of the directional tuning to be zero (by choosing the appropriate polar axis in the polar-plot). Further, we assume that the tuning function is symmetric about its peak, an intuitive consideration of parity equivalency:

$$D(\theta) = D(-\theta). \quad (5)$$

In cases of arbitrary tuning functions, the above assumption implies that we are considering the even-symmetric part of the tuning function only, and ignoring the odd-symmetric part to avoid unnecessary complications. From (2), (4) and (5)

$$\begin{aligned} d_k &= \frac{1}{\pi} \int_0^{2\pi} D(\theta) \sin k\theta d\theta \\ &= \frac{1}{\pi} \int_0^{2\pi} D(-\theta) \sin k\theta d\theta \\ &= \frac{1}{\pi} \int_0^{2\pi} D(2\pi - \theta) \sin k\theta d\theta \\ &= -\frac{1}{\pi} \int_0^{2\pi} D(2\pi - \theta) \sin k(2\pi - \theta) d\theta \\ &= -\frac{1}{\pi} \int_0^{2\pi} D(\theta) \sin k\theta d\theta \\ &= -d_k, \end{aligned}$$

or

$$d_k = 0. \quad (6)$$

So (3) becomes

$$D(\theta) = \sum_{k=0}^{\infty} a_k \cos k\theta. \quad (7)$$

In general, if the directional tuning $D(\theta)$ has a peak at θ_{dp} instead of zero, the expansion takes the form

$$D(\theta - \theta_{dp}) = \sum_{k=0}^{\infty} a_k \cos k(\theta - \theta_{dp}). \quad (8)$$

With the same mathematical operations, we can expand the orientational component $O(\theta)$ into its

Fourier series

$$O(\theta - \theta_{op}) = \sum_{k=0}^{\infty} b_k \cos k(\theta - \theta_{op}), \quad (9)$$

where θ_{op} is the peak of orientation tuning and

$$\begin{aligned} b_0 &= \frac{1}{2\pi} \int_0^{2\pi} O(\theta) d\theta, \\ b_k &= \frac{1}{\pi} \int_0^{2\pi} O(\theta) \cos k\theta d\theta. \end{aligned} \quad (10)$$

Note that $O(\theta)$ has a period of π , as in (2),

$$\begin{aligned} b_k &= \frac{1}{\pi} \int_0^{\pi} O(\theta) \cos k\theta d\theta + \int_{\pi}^{2\pi} O(\theta) \cos k\theta d\theta \\ &= \frac{1}{\pi} \int_0^{\pi} O(\theta) (\cos k\theta + \cos k(\theta - \pi)) d\theta \\ &= \frac{1}{\pi} \int_0^{\pi} O(\theta) (1 + (-1)^k) \cos k\theta d\theta. \end{aligned} \quad (11)$$

Before going further, let us consider some general issues. We know that the cell's response $R(\theta)$ is a function of θ through some function $O(\theta)$ and $D(\theta)$, and $R(\theta)$ is all we measure experimentally as the response polar-plot. Yet we do not know a priori:

1) the functional dependence of $R(O, D)$ on O and D ;

2) the parametric dependence of $O(\theta)$ and $D(\theta)$ on θ .

Without specifying either of the two, the other can never be uniquely determined from only $R(\theta)$. Therefore, the issue of unconfounding the two components is, in general, an ill-posed problem that would yield infinite solutions. However, we can make some assumptions about either 1) or 2) to solve this problem, and then test the validity of our assumption with the neurophysiological data. This is what we are going to do next.

We assume that the functional dependence of $R(O, D)$ on $D(\theta)$ and $O(\theta)$ is such that these two components are linearly additive to give rise to the overall response $R(\theta)$:

$$R(D(\theta), O(\theta)) = D(\theta) + O(\theta). \quad (12)$$

Again we stress that there is no a priori reason for making this assumption, except that it is the simplest well-defined and testable (either verifiable or falsifiable) assumption. Under this condition and referring to (8) and (9),

$$\begin{aligned} R(\theta) &= \sum_{k=0}^{\infty} a_k \cos k(\theta - \theta_{dp}) + b_k \cos k(\theta - \theta_{op}) \\ &= (a_0 + b_0) + \sum_{k=1}^{\infty} (a_k \cos k\theta_{dp} + b_k \cos k\theta_{op}) \cos k\theta \\ &\quad + (a_k \sin k\theta_{dp} + b_k \sin k\theta_{op}) \sin k\theta. \end{aligned} \quad (13)$$

On the other hand, if we expand $R(\theta)$ directly (remembering $R(\theta)$ itself is a periodic function of period 2π),

$$R(\theta) = \eta_0 + \sum_{k=1}^{\infty} \eta_k \cos k\theta + \zeta_k \sin k\theta, \quad (14)$$

where

$$\begin{aligned} \eta_0 &= \frac{1}{2\pi} \int_0^{2\pi} R(\theta) d\theta, \\ \eta_k &= \frac{1}{\pi} \int_0^{2\pi} R(\theta) \cos k\theta d\theta, \\ \zeta_k &= \frac{1}{\pi} \int_0^{2\pi} R(\theta) \sin k\theta d\theta. \end{aligned} \quad (15)$$

Comparing (13) with (14), we immediately have

$$\begin{aligned} \eta_0 &= a_0 + b_0, \\ \eta_k &= a_k \cos k\theta_{dp} + b_k \cos k\theta_{op}, \\ \zeta_k &= a_k \sin k\theta_{dp} + b_k \sin k\theta_{op}. \end{aligned} \quad (16)$$

Because of the factor $1 + (-1)^k$ in (11), b_k is zero for odd k . Therefore, in the response polar-plot expansion, the odd harmonics contain only the directional contribution while the even harmonics contain both directional and orientational contributions (not just the orientation component, as Wörgötter and Eysel (1987) concluded).

2.1 Peak Angle

For odd harmonic terms, we have, according to (16):

$$\begin{aligned} \eta_k &= a_k \cos k\theta_{dp}, \\ \zeta_k &= a_k \sin k\theta_{dp}, \end{aligned} \quad (17)$$

or equivalently

$$\begin{aligned} \tan k\theta_{dp} &= \frac{\zeta_k}{\eta_k}, \\ a_k &= \pm \sqrt{\eta_k^2 + \zeta_k^2}, \quad (k = 1, 3, 5, \dots). \end{aligned} \quad (18)$$

Therefore, the peak angle of the directional component is related to, or computable from, the phases of the odd harmonics. Notice that the peak angle of the orientational component is *not* directly computable from the even harmonics; one needs first to subtract out the contamination from the directional component. We shall provide a method later.

2.2 Test of Linear Assumption

Equation (18) holds true for all odd integer numbers; we can calculate the peak angle θ_{dp} from any odd k . Realizing that this is a direct consequence of (12), our linear assumption, we may actually calculate θ_{dp} from all of these odd harmonics and examine their mutual compatibility to test the validity of our hypothesis. We know from the deduction that (18) is a necessary condition of (12); we further argue that it is also a sufficient condition, since any other combination of $O(\theta)$ and $D(\theta)$ would practically prevent the odd harmonics from being the sole contribution to $D(\theta)$. Therefore, by testing against this necessary and sufficient condition (18), we are establishing the validity of linear assumption (12). To relate this to the neurophysiological data, we actually examined 38 cells in monkey primary visual cortex (V1) which were recorded during early experiments (De Valois et al. 1982) and found that more than half of the cells follow the linearity assumption strikingly

well. The details of this work are only in preliminary form (Zhang and De Valois 1988) and shall be presented elsewhere (Zhang and De Valois, in preparation).

2.3 Bandwidth of the Tuning

Intuitively, we expect that the bandwidth of the tuning curve in the spatial domain would be inversely related to the “bandwidth” in the conjugate frequency domain, as a consequence of the well-established “uncertainty principle”, i.e. the narrower the tuning function is in the spatial domain, the more harmonics in the frequency domain that would contribute towards its composition, and vice versa. (The careful reader should not confuse this with the relationship between the orientation bandwidth and the 2-D spatial frequency bandwidth as given, say, by Daugman (1985)). We want to establish this relationship explicitly under certain approximations. The study of a_k is important not only because we want to get the bandwidth of the directional tuning, but also because we must subtract out the directional contamination in the case of even harmonics for our computation to proceed to the orientation term in (16).

Before going on, we first ask ourselves what is the operational definition of “bandwidth”? Researchers have used the distance (in angles) between the points where the response is 71% of the peak response (e.g. Schiller et al. 1976), or 50% of the peak response (e.g. Henry et al. 1973; Rose and Blakemore 1974; De Valois et al. 1982). This is quite arbitrary. We suggest here a more objective way, namely to use the distance between the points having the steepest slope in the cell’s tuning curve. At these points, the cell is most sensitive to differential stimuli, i.e. a slight change in the stimulus angle will result in a dramatic change in the cell’s response. These points reflect more appropriately the transition of the neuron from one state to another and can be regarded in this sense as “turning points” of the cell’s tuning curve. It turns out that this operational definition of “bandwidth” is also very convenient for mathematical manipulations.

From (4)

$$\begin{aligned} a_k &= \frac{1}{\pi} \int_0^{2\pi} D(\theta) \cos k\theta \, d\theta \\ &= \frac{1}{k\pi} \int_0^{2\pi} D(\theta) \, d(\sin k\theta) \\ &= -\frac{1}{k\pi} \int_0^{2\pi} \sin k\theta \frac{dD}{d\theta} \, d\theta. \end{aligned} \quad (19)$$

If the cell’s response with respect to the stimulus angle is smooth and bell-shaped, namely, when the stimulus angle deviates from the cell’s optimal tuning, it changes very slowly at first and then decreases abruptly to reach the ground level, then the derivative of $D(\theta)$ can be approximated by the delta impulse function (Fig. 2)

$$\frac{dD}{d\theta} = \lambda_d (\delta(\theta + \theta_{db}) - \delta(\theta - \theta_{db})), \quad (20)$$

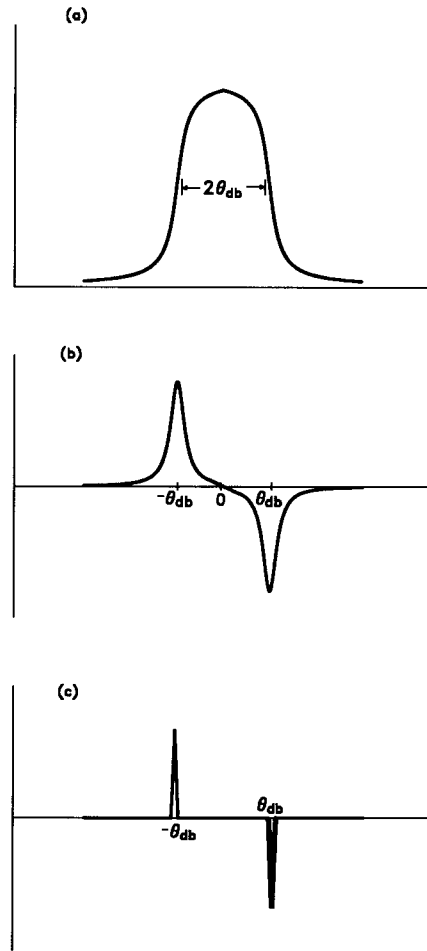


Fig. 2. **a** The tuning function of the directional component $D(\theta)$. Note that we made no assumption regarding what specific type of function $D(\theta)$ may be (e.g. Gaussian). Only the general shape is relevant in our computation, which is assumed to be symmetric about its peak (assumed to be 0 here for convenience), and decreasing first slowly and then abruptly at a distance θ_{db} from the peak, defined as the “half-bandwidth” of the tuning. **b** The derivative of $D(\theta)$ with respect to θ . Note the two peaks at $-\theta_{db}$ and θ_{db} , corresponding to the half-bandwidth in **a**. **c** The delta function $\delta(\theta + \theta_{db}) - \delta(\theta - \theta_{db})$, which can be viewed as an approximation to the derivative of $D(\theta)$ in **b**. Since the derivative of $D(\theta)$ only appeared inside an integral (19), this is indeed a good approximation

in which θ_{db} is the effective half-bandwidth, λ_d the peak response of the directional tuning and the delta impulse function is defined as

$$\delta(x) = \begin{cases} \infty, & \text{if } x = 0, \\ 0, & \text{otherwise,} \end{cases}$$

and that

$$\int_{-\infty}^{\infty} \delta(x) \, dx = 1, \quad \int_{-\infty}^{\infty} \delta(x - x_0) f(x) \, dx = f(x_0).$$

Therefore (19) becomes

$$\begin{aligned} a_k &= -\frac{1}{k\pi} \int_0^{2\pi} \lambda_d \sin k\theta (\delta(\theta + \theta_{db}) - \delta(\theta - \theta_{db})) \, d\theta \\ &= \frac{2\lambda_d}{\pi} \frac{\sin k\theta_{db}}{k}, \quad (k = 1, 3, 5, \dots). \end{aligned} \quad (21)$$

Combining (18) with (21), we have now related the peak response λ_d and the half-bandwidth θ_{db} of the directional component to the amplitudes of the odd expansion terms $\sqrt{\eta_k^2 + \zeta_k^2}$ for immediate calculation. Note again that (21) holds for all odd k , so there are obviously more equations than unknowns. Strictly speaking, this can also serve as the test for our previous linear assumption (12), though practically it is less convenient than using θ_{db} . In any case, we may solve for θ_{db} and λ_d (say, using a conventional regression method). Then we may want to substitute these values back into (16) for the expression of a_k for even k , so that they can be used in the future:

$$a_0 = \frac{2\lambda_d}{\pi} \theta_{db}, \quad (22)$$

$$a_k = \frac{2\lambda_d}{\pi} \frac{\sin k\theta_{db}}{k}, \quad (k = 2, 4, 6, \dots).$$

2.4. Calculating the Orientational Component

Once we get the directional component, we can deal with the orientational component. From (16) and (22) we have

$$b_k \cos k\theta_{op} = \eta_k - \frac{2\lambda_d}{\pi} \frac{\sin k\theta_{db}}{k} \cos k\theta_{dp}, \quad (23)$$

$$b_k \sin k\theta_{op} = \zeta_k - \frac{2\lambda_d}{\pi} \frac{\sin k\theta_{db}}{k} \sin k\theta_{dp}, \quad (24)$$

$(k = 2, 4, 6, \dots).$

The subsequent calculation for the orientation component is essentially the same as that for the directional component, only to note that in the case of the orientational peak response λ_o and half-bandwidth θ_{ob}

$$b_k = \frac{4\lambda_o}{\pi} \frac{\sin k\theta_{ob}}{k}. \quad (25)$$

So far, we have obtained all of the six parameters that completely characterize a cell's tuning, namely, the directional peak angle, the directional bandwidth, the directional peak response, the orientational peak angle, the orientational bandwidth, and the orientational peak response. The flow chart for the above procedure is outlined in Fig. 3, and the result of unconfounding the orientational and directional components of a typical cell using this method is schematically illustrated in Fig. 4.

2.5 Some Technical Considerations

There are several noteworthy technical points which, though not conceptually important, may become appreciated in order to apply this method successfully.

First, from (17) or (18), we know that a_k and θ_{dp} are calculable from η_k and ζ_k . There are two things to take care about:

1) There is a potential problem in specifying θ_{dp} by taking the arctangent, due to the periodic nature of trigonometric functions. To avoid this $\pm\pi$ ambiguity, the following method is highly recommended: *a*) First, calculate the $\theta_{dp}^{(1)}$ using only the first harmonic ($k = 1$);

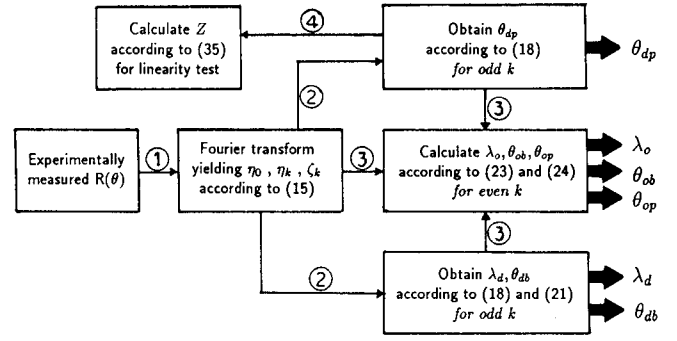


Fig. 3. Flow chart outlining the procedures for separating the orientational component and directional component using the present method. *Step 1.* Experimentally measured response curve $R(\theta)$ is converted, via Fourier transform, into its frequency composition of all harmonics. *Step 2.* Odd harmonics are used to calculate the directional component $D(\theta)$: its peak tuning θ_{dp} , peak strength λ_d and half-bandwidth θ_{db} . *Step 3.* Subtract out the directional contamination and then use the even harmonics to calculate the orientational component $O(\theta)$: its peak angle θ_{op} , peak strength λ_o and half-bandwidth θ_{ob} . *Step 4.* Calculate Z , the linearity index

since A_1 is always positive as indicated by (21), there should be no problem of specifying $\theta_{dp}^{(1)}$ within the range of 360° ; *b*) Then, rotate the polar axis to $\theta_{dp}^{(1)}$ and recalculate η_k and ζ_k , according to (15); *c*) Use the new η_k and ζ_k to do the linearity test and regression. Hopefully, the actual values of $k\theta_{dp}$ should be around zero now and should pose no serious problem in taking the arctangent.

2) The sign of a_k is also difficult to decide solely based on (17), since the unknown angle $k\theta$ can differ by multiples of π and hence flip the sign of a_k . However, with the new η_k and ζ_k obtained as described above, it is very easy to determine the sign of a_k . Since $\cos k\theta_{dp}$ is constantly positive for θ_{dp} in the vicinity of zero (no matter slightly greater or smaller), a_k is always positive (negative) if the new η_k is positive (negative).

Secondly, to get θ_{dp} and λ_d from a_k , the conventional regression method is always possible. Here, however, we refer to (21) and present another quick and simple way of getting these two parameters. The following equalities are employed (see standard references on the subject of trigonometric Fourier series, such as Gradshteyn and Ryzhik 1980):

$$\sum_{k=1,3,\dots} \frac{\sin kx}{k} = \frac{\pi}{4}, \quad (26)$$

$$\sum_{k=1,3,\dots} (-1)^{(k-1)/2} \frac{\sin kx}{k} = \frac{1}{2} \ln \tan\left(\frac{\pi}{4} + \frac{x}{2}\right), \quad (27)$$

$$\sum_{k=1,3,\dots} (-1)^{(k-1)/2} \frac{1}{k} \left(\frac{\sin kx}{k}\right) = \frac{\pi}{4} x, \quad (28)$$

$$\sum_{k=1,3,\dots} \frac{1}{k^2} \left(\frac{\sin kx}{k}\right) = \frac{\pi}{8} x(\pi - x), \quad (29)$$

$$\sum_{k=1,3,\dots} \left(\frac{\sin kx}{k}\right)^2 = \frac{\pi}{4} x, \quad (30)$$

$$\sum_{k=1,3,\dots} \frac{1}{k^2} \left(\frac{\sin kx}{k}\right)^2 = \frac{\pi}{2} x^2 \left(\frac{\pi}{4} - \frac{x}{3}\right). \quad (31)$$

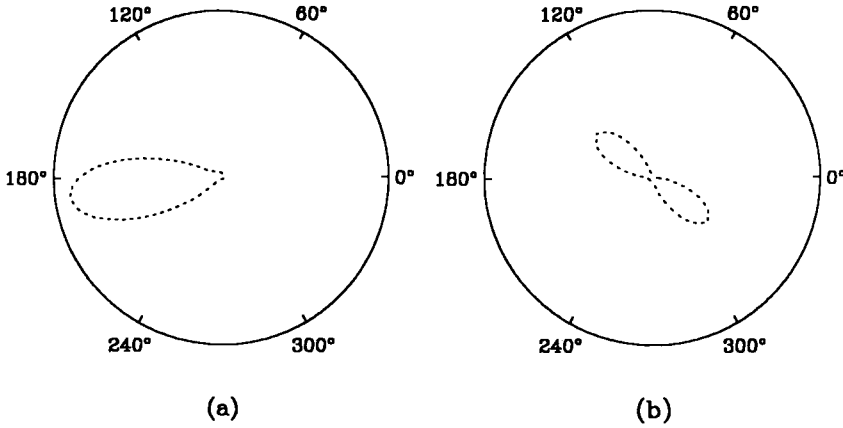


Fig 4. The directional component (a) and the orientational component (b) of the cell shown in Fig. 1, as separated by this method. These two components add up to become the overall response shown as dotted curve there

The above identities are true for $0 < x < \pi/2$. It suffices to solve θ_{db} and λ_d by any two of the equations. For instance, (26) and (30) yield:

$$\lambda_d = 2 \sum_{k=1,3,\dots} a_k,$$

$$\theta_{db} = \frac{\pi}{4} \left(\frac{\sum_{k=1,3,\dots} a_k^2}{\left(\sum_{k=1,3,\dots} a_k \right)^2} \right).$$

Obviously $1/k^2$ converges faster than $1/k$, $1/k^3$ faster than $1/k^2$, and so forth. In order to approximate the infinite summation over k with finite terms, it is necessary to determine which equations to use. The choice depends mainly on how many non-identical Fourier expansion terms are available in the response polarplot, which in turn is dependent upon how small an increment of stimulus angle is used during the experiment. On the other hand, the chosen series should not converge so fast as only to admit contributions from the first few harmonics because they may, due to the experimental noise, be inappropriately over represented. In general, identities (26) through (31) work fairly well when approximations for infinite summation include terms up to as small as $k = 9$ (corresponding to the experimental condition of 20° step increment in angles of the stimulus presentations).

The same technique may be applied to the calculation of orientational component. The following corresponding formulas are given only to complete the entire list of prescription:

$$\sum_{k=2,4,\dots} \frac{\sin kx}{k} = \frac{1}{2} \left(\frac{\pi}{2} - x \right), \quad (32)$$

$$\sum_{k=2,4,\dots} \frac{1}{k^2} \left(\frac{\sin kx}{k} \right) = \frac{x}{12} (\pi - x) \left(\frac{\pi}{2} - x \right), \quad (33)$$

$$\sum_{k=2,4,\dots} \left(\frac{\sin kx}{k} \right)^2 = \frac{x}{2} \left(\frac{\pi}{2} - x \right), \quad (34)$$

$$\sum_{k=2,4,\dots} \frac{1}{k^2} \left(\frac{\sin kx}{k} \right)^2 = \frac{x^2}{6} \left(\frac{\pi}{2} - x \right)^2. \quad (35)$$

Lastly, we would like to say a word or two about

the test of linear assumption. Suppose we have obtained a collection of θ_{dp} values from (18). Denoting $\theta_{dp}^{(k)}$ to be the peak angle calculated from the k -th harmonic, we construct the following expression:

$$Z^2 = \sum_{j \neq k} (\theta_{dp}^{(j)} - \theta_{dp}^{(k)})^2$$

$$= (\theta_{dp}^{(1)} - \theta_{dp}^{(3)})^2 + (\theta_{dp}^{(1)} - \theta_{dp}^{(5)})^2 + (\theta_{dp}^{(3)} - \theta_{dp}^{(5)})^2 + \dots \quad (36)$$

If the linear assumption does not hold, then the angles calculated from (18) would not follow any obvious rules and would practically be random. Therefore Z would be much larger than when the linear assumption holds. Elaborated statistical tests can be performed to distinguish reliably the two situations.

3 Discussion

Without first separating the orientational component from the directional component, it is impossible to specify the cell's peak tuning for either component. The conventional way of identifying the maximum response angle as the peak angle of orientational tuning and/or directional tuning is in most cases problematic. Wörgötter and Eysel (1987), in their original study, correctly identified the directional and orientational components as being periodic functions of 2π and π respectively, and with genuine intuition, proposed the use of the Fourier transform technique to unconfound the two components. Unfortunately, they misinterpreted "the first order component" as the strength of the directional selectivity and the second order component as the strength of the orientational component". It is clear from our mathematical analysis that the second harmonic ("the second order component" in their terminology) receives contributions from both orientational and directional components, and that one needs to subtract out the directional contamination in order to calculate orientation selectivity. Also, Wörgötter and Eysel truncated the Fourier expansion series at the

second harmonic. This truncation is valid only when both the orientational and directional tuning curves are sinusoidally varying, which we know cannot be true. In fact, the higher harmonics are essential in verifying the linearity assumption about the cell's dependence on the two components, in subtracting out the directional contamination for calculation of the orientational component, and in estimating the bandwidths and relative strengths of both components.

We wish to stress once more that whether this method is successful or not depends on whether a cell responds to the orientational and directional aspects of a visual stimulus in a linearly separable fashion. We cannot assume this a priori. It is only after the linearity test as prescribed in Sect. 2.2 can we reach any conclusion. In fact, most of the cells in macaque striate cortex that we tested seem to pass this linearity test to various degrees, which is statistically significant (Zhang and De Valois, in preparation). If this is true for data collected in other laboratories and in other species, then a number of interesting questions emerge: 1) What is the origin of the orientation selectivity and direction selectivity? Do they have the same generating mechanism, or perhaps different mechanisms, one involving the LGN and the other involving the cortex? Do cells have the same peak angle for directional tuning and orientational tuning? Are there morphological differences between cells which are primarily orientation tuned and those which are primarily direction tuned? Are there functional differences in this respect between simple and complex cell types? 2) Are there laminar differences in cells' responses to either of the two components? Do "orientation columns" in V1 reflect the columnar organization of the orientational component or the directional component, or both? How about the fine structure of this columnar structure ("minicolumn")? All these interesting questions that result from a successful separation of the orientational and directional components await to be answered.

Also, this method provides a more sensible way of defining the "bandwidth" of a tuning function as being the distance between the points of the steepest slope (fastest change). This operational definition is both intuitive and directly calculable from the Fourier expansion coefficients of the response polar-plot. Therefore we believe that it is a good definition. Finally, our method gives a quantitative assessment of the relative strengths of the orientational component and directional component, and could answer questions like "whether the cell is mainly directional or orientational" in a non-ambiguous way.

List of Symbols and Notations

notation	is defined as	in Eq.
$\delta(x)$	delta impulse function	(20)
η_0, η_k	coefficients of Fourier expansion of response polar-plot	(15)

ζ_k	coefficients of Fourier expansion of response polar-plot	(15)
λ_d	peak strength of the directional component	(20)
λ_o	peak strength of the orientational component	(25)
θ_{db}	half-bandwidth of the directional component	(20)
θ_{dp}	peak angle of the directional component	(8)
$\theta_{dp}^{(k)}$	value of θ_{dp} computed from the k -th harmonic	(36)
θ_{ob}	half-bandwidth of the orientational component	(25)
θ_{op}	peak angle of the orientational component	(9)
a_0, a_k	coefficients of Fourier expansion of directional component	(4)
d_k	coefficients of Fourier expansion of directional component	(4)
b_0, b_k	coefficients of Fourier expansion of orientational component	(10)
$D(\theta)$	directional component of the cell's response	(2)
$O(\theta)$	orientational component of the cell's response	(2)
$R(\theta)$	the cell's overall visual response	(1)
$R(O, D)$	same as $R(\theta)$, merely denoting the fact that $R(\theta)$ is composed of $O(\theta)$ and $D(\theta)$	(1)
Z	index of linear additivity of the two components	(35)

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