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Quantitative Determination of Orientational and Directional Components in the Response of Visual Cortical Cells to Moving Stimuli

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Abstract. The response characteristic of visual cortical cells to moving oriented stimuli consists mainly of directional (D) and orientational (O) components superimposed to a spontaneous activity (S). Commonly used polar plot diagrams reflect the maximal responses for different orientations and directions of stimulus movement with a periodicity of 360 degrees in the visual field. Fast Fourier analysis (FFT) is applied to polar plot data in order to determine the intermingled S, D, and O components. The zero order gain component of the spectrum corresponds to a (virtual) spontaneous activity. The first order component is interpreted as the strength of the direction selectivity and the second order component as the strength of the orientation specificity. The axes of the preferred direction and optimal orientation are represented by the respective phase values. Experimental data are well described with these parameters and relative changes of the shape of a polar plot can be detected with an accuracy better than 1%. The results are compatible with a model of converging excitatory and inhibitory inputs weighted according to the zero to second order components of the Fourier analysis. The easily performed quantitative determination of the S, D, and O components allows the study of pharmacologically induced changes in the dynamic response characteristics of single visual cortical cells.

1 Introduction

The static and dynamic receptive field properties of visual cortical cells have been analysed from different qualitative and quantitative viewpoints. The direction and orientation dependent response components to moving oriented stimuli have been first described by Hubel and Wiesel (1959, 1962). Later, attention has also been payed to quantitative models of response characteristics to static stimuli. In particular Fourier analysis has been used to determine the spatial frequency response characteristics of cortical cells (Maffei and Fiorentini 1973; Glezer and Cooperman 1977; Glezer et al. 1980) and to predict the spatial arrangement of the on- and off-subregions (Kulikowski and Bishop 1981), which could be verified by static receptive field plots. On the basis of a theoretical framework approximating simple cell receptive fields with Gabor elementary signals (Gabor 1946; Marcelja 1980) a model of the 2-dimensional spatial frequency and orientational tuning has been developed (Daugman 1980, 1984; Kulikowski et al. 1982).

The importance of directional tuning as an attribute of the dynamic characteristic of cortical cells, however, is underestimated by models based on static receptive field properties (Kulikowski and Bishop 1981), and often the dynamic properties cannot be predicted from static field plots (Palmer and Davis 1981). Especially interactions between directional and orientational tuning during stimulation with moving light bars are far from clear (Henry et al. 1974). We propose a method to quantitatively separate the direction dependent from the orientation dependent component of the responses to moving light bars. This approach appears useful to describe changes induced by microiontophoretical influences at the single cell level, and, in addition, might help to develop models of the underlying basic neuronal networks, which are most probably different for orientation specificity and direction selectivity (Hammond 1978).

2 Material and Methods

Adult cats (body weights between 2.5 and 4.5 kg) were used. During the experiments the animals were anaesthetized by artificial respiration with 0.2–0.5%

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halothane added to N_2O/O_2 (70:30). Relaxation was maintained by continuous intraarterial infusion with *d*-tubocurarine (0.3 mg/kg · h) and gallamine triethiodide (4.0 mg/kg · h) in a glucose and Ringer solution. Gamma-amino-butyric acid (GABA, 0.5 *M*, pH 3.0) was applied microiontophoretically from a four-barrel micropipette in the vincinity of the recording site for local cortical inactivation (Eysel and Wörgötter 1986). Recordings were made with glass coated tungsten electrodes and the impulse activities of cells in area 17 of cat visual cortex were studied. Cells with small receptive fields ($\leqq 1$ degree) with non-overlapping on- and off-subregions were classified as *S*-cells (Henry 1977; Kato et al. 1978). For visual stimulation light bars moving back and forth across the receptive field were presented on an oscilloscope and stimulus orientations were changed by multiples of 30 degrees using a pseudo random sequence. The dimensions of the bar as well as velocity and contrast were adjusted to obtain maximum responses in the preferred direction, and the orientation of the stimulus bar was always orthogonal to its direction of movement. Polar plots (Figs. 3–5) were derived from peristimulus time histograms (PSTHs) recorded for each stimulus orientation by plotting the maximal impulse rate as length and the direction of movements as angle of a vector in a polar coordinate system. Data analysis was performed with an LSI-11/23 laboratory computer with implemented fast Fourier analysis routines from Cambridge Electronic Design. Fast Fourier analysis (FFT) was applied to polar plot data (12 data points) expanded to a 1 kB data array by periodical repetition.

3 Results

3.1 Interpretation of Direction and Orientation in the Fourier Domain

The response characteristic of a visual cortical cell to a moving stimulus of a certain orientation is difficult to interpret because it consists mainly of three parts: spontaneous activity, direction dependent response and orientation dependent response. A priori these response components cannot be separated quantitatively and this makes it impossible to distinguish between the contributions of possibly different neuronal networks responsible for the generation of the individual response characteristic. The principel difference, however, between the directional and the orientational components can be interpreted in terms of Fourier analysis realizing that the direction of motion of a stimulus bar has a periodicity over the full 360 degrees in the visual field (Fig. 1a), whereas orientation is repeated every 180 degrees (Fig. 1b).

Accordingly, direction is regarded as first order ($j=1$) and orientation as second order ($j=2$) Fourier component with the coefficients A_j and B_j, and an approximation of the impulse rate IR of a cortical cell is derived for all degrees α of the visual field:

$$\mathrm{IR}(\alpha)=A_0+\sum_{j=1}^{2}[A_j\cos(j\alpha)+B_j\sin(j\alpha)], \quad (1)$$

where A_0 represents the spontaneous activity (zero order component).

3.2 Simulation of the Dynamic Response Characteristics

In a first step a simplyfied version ($A_0=\mathrm{const}$; $B_j=0$, $j=1,2$) of the formula was used with different coefficients A_1, A_2 to generate polar plots.

The first polar plot (1) in Fig. 2 displays only "spontaneous" (orientation and direction insensitive) activity ($A_1=0$, $A_2=0$). For the other plots in the upper row of Fig. 2 (2, 3) the second order coefficient A_2 is increased ($A_1=0$) and the simulated polar plots resemble results from cortical cells without any directional tuning. The first column (4, 7) on the other hand displays pure directionality changes (A_1 increased, $A_2=0$) that – in this idealized form – are practically never observed in cortex because nearly all cells show at least some orientation sensitivity. The other simulated polar plots (5, 6, 8, 9) with all coefficients A_j not equal zero, however, show strong similarities to polar plots of real cells and can only be distinguished from them by their extraordinary symmetrical form that results from the exclusion of the sine components. Using merely cosine coefficients generates polar plots with preferred direction for zero degrees where the cosine-function reaches its maximum (Fig. 2).

3.3 Fourier Analysis of Polar Plots

Fast Fourier (FFT) analysis was applied to calculate gain and phase values from the polar plots in Fig. 2 and from several cortical cells (Figs. 3–5).

In the following the gain of the zero order component will be called spontaneous activity (S), whereas the first order gain represents the strength of the directional tuning (D) and the second order gain the strength of the orientational tuning (O). The gain values are defined in arbitrary units that, for convenience, will be referred to as "Impulses per second (I/s)". It is evident that the first order phase value describes the preferred direction (PD) in degrees, and the second order phase the optimal orientation ("preferred orientation", PO), which should be orthogonal to PD.

The polar plot no. 9 of Fig. 2 was generated with a spontaneous activity rate of S = 40 I/s and additional directional and orientational components of D = O = 30 I/s each. Fourier analysis yielded

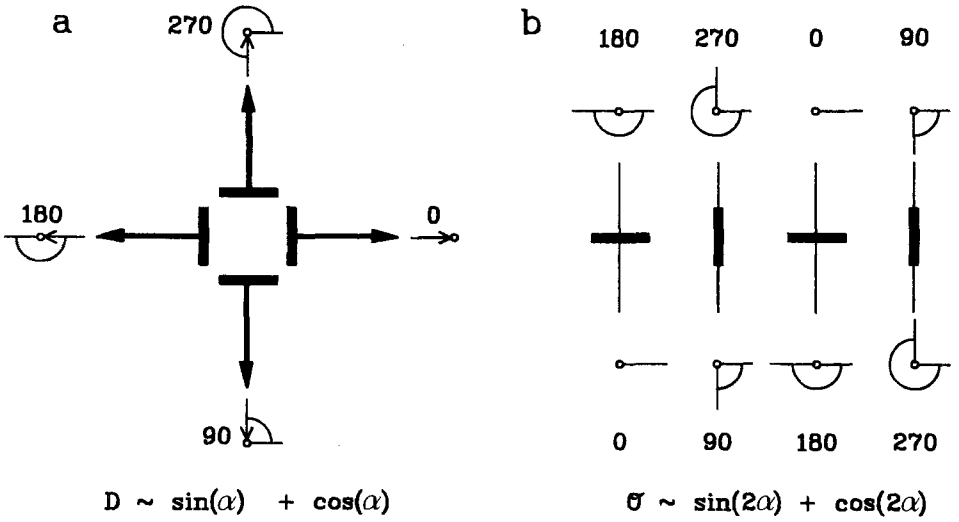

Fig. 1a and b. Interpretation of stimulus features in the Fourier domain. **a** Direction of movement of a stimulus light bar is regarded as first order component, and **b** its orientation as second order component

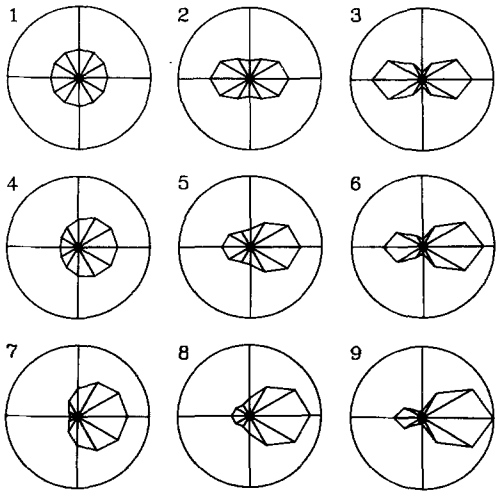

Fig. 2. Simulation of polar plots by zero, first and second order sinusoidal components applying formula (1). For all plots: Zero order coefficient $A_0 = 40$ I/s and all coefficients $B = 0$. Vertically: first order coefficient A_1 is increased with values of 0; 15 and 30 I/s, horizontally: second order coefficient A_2 is increased using the same values

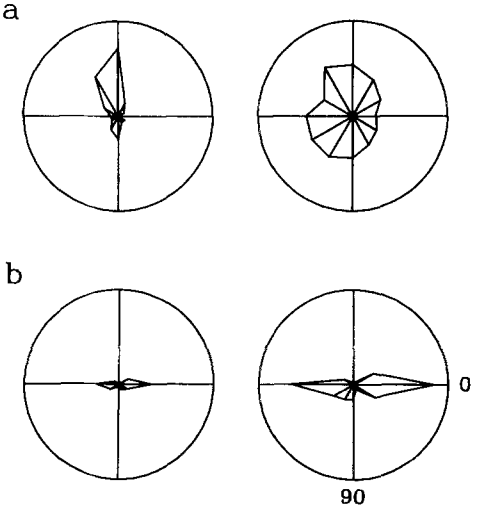

Fig. 3a and b. Examples of changed response characteristics of S-cells during GABA-microiontophoresis. **a** The right plot displays an increase in S combined with strong reduction of D and O. **b** Different cell. Here only the spontaneous activity S is increased but no specific changes in D and O occur (compare Table 1a)

S = 39.2 I/s and D = O = 31.2 I/s in good agreement with the original values. The small differences are explained by the fact that FFT-analysis requires a data set of 2^n data points. This introduced a slight inaccuracy when 12 polar plot values were periodically reiterated to fill a 1 kB data field, but due to the structure of our experimental methods it was unavoidable to take multiples of 12 data points as the basis of the calculations. Relative deviations of any of the components, however, are detected with an accuracy better than 1% for changes between different polar plots.

Phase values for the same plot were PD = 0.0 deg and PO = 90.0 deg as would be expected.

FFT-analysis applied to polar plots of cortical cells can be used to separate the S, D, and O components. By this the differential contributions of the different components to an experimentally induced modification of the response characteristic of a given cell can be determined (Figs. 3 and 4 and Table 1).

To enable a valid comparison all plots have been normalized to a full scale of 100 I/s. Figure 3 shows two examples of cortical cells displaying different modifications of their response characteristics when

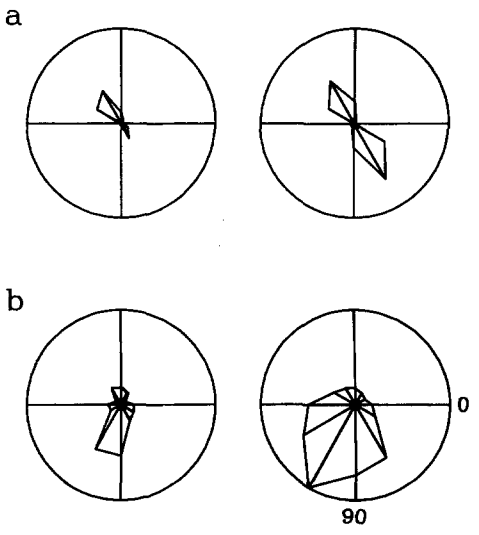

Fig. 4a and b. Changes in the directional tuning of S-cells induced by GABA-microiontophoresis. **a** Direction inversion accompanied by a strongly reduced direction selectivity. **b** Cell with increased directionality but reduced orientation specificity (compare Table 1b)

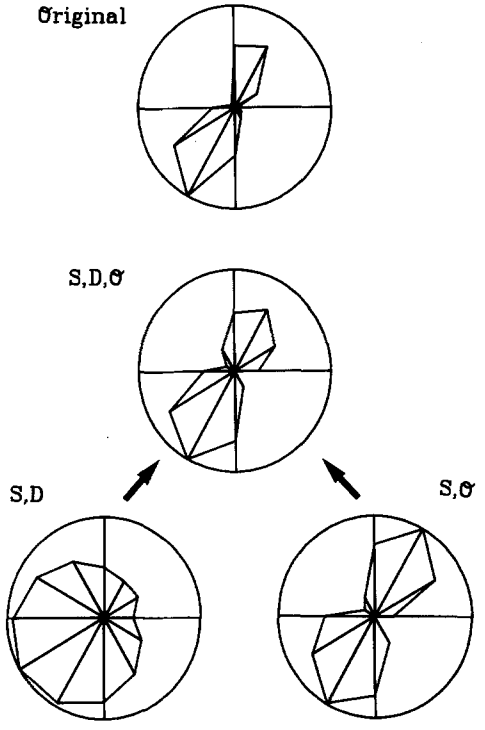

Fig. 5. Inverse Fourier transform of the S, D, and O components. Above: original response characteristic of an S-cell. Middle: Retransformation using the S, D, and O components as revealed by Fourier analysis. A slightly diminished orientational tuning in the retransformation indicates only small contributions of Fourier components above the second order. Below: Retransformation using only S and D components (left) or S and O components (right). Summation of the bottom plots weighted by their gain values (and subtracting one S-value) would yield the plot in the middle

subjected to GABA microiontophoresis at a distance lateral to the recorded cell (Eysel and Wörgötter 1986; Eysel et al. 1987). While the cell in Fig. 3 a clearly loses directionality as well as orientational tuning during GABA application it is hard to determine the differential effects on orientation and direction from the plots of the other cell (Fig. 3b) where an increased response is combined with possible changes of one of these components. Here FFT-analysis yields a percentage change for D of −4.5% and for O of −3.2% (Table 1a), that is no specific change at all consequently only an increased spontaneous activity can be detected in this case (+153.7%). For the cell shown in Fig. 3a, on the other hand, D changes by −70.0% and O by −81.1% in agreement with the obvious loss of both specifities that is seen in the right plot. The first order phase PD is not well defined for the cell of Fig. 3b, because its directional tuning is only weakly expressed, whereas PO = 89.2 deg agrees with the finding that the best responses are obtained with vertically oriented stimulus bars. PD and PO are well defined for the left plot of Fig. 3a, but again not for the right plot.

For strongly orientation specific cells the sensitivity for a correct estimation of the first order phase PD is sharpened, so that inversion of directionality in a cell (Fig. 4a) is detected in spite of the reduction of its strength by −78.6% from $D = 36.9$ I/s to the low value of D = 7.9 I/s with an approximate change of PD by 180 degrees (Table 1b). Note that the orientational tuning remained unchanged O = 56.7 I/s.

Directionality as referred to by the relation between the response strength of the preferred direction versus non-preferred direction in general underestimates the contributions of the responses to directions adjacent to PD. The most often used direction index DI yields for Fig. 4b left DI = 76, right DI = 86 or a percentual change of +13.2%. With FFT-analysis the change of D equals +52.0% (Table 1b), which better reflects the directionality change that in this case is influenced by the increase in all directions in the interval between PD + 60 and PD − 60 degrees. This, of course, strongly depresses the orientational tuning (−51.9%).

3.4 Contributions of the Higher Order Fourier Components

It cannot a priori be expected that a polar plot is correctly recomposed from Fourier components of only up to the second order. Nevertheless, a polar plot generated by inverse Fourier transform (Fig. 5, middle) using only the first three components (S, D, O) obtained by FFT from the original cell response shown above,

[1] DI = 100 · (pd-npd)/pd (pd = response in the preferred direction, npd = response in the non-preferred direction)

Table 1. List of the three components S, D, O and their respective phase values PD and PO for the polar plots of Figs. 3 and 4. The percentual changes of S, D, and O during GABA application are indicated

a)

	(to Fig. 3a) S	D	O
Left			
Gain (I/s)	18.8	33.7	41.5
Phase (deg)	–	PD: 248.1	PO: 173.0
Right			
Gain (I/s)	44.7	10.1	7.8
Phase (deg)	–	PD: 201.2	PO: 10.7
Change			
Gain (%)	+137.8	− 70.0	− 81.1

	(to Fig. 3b) S	D	O
Left			
Gain (I/s)	9.5	14.1	47.4
Phase (deg)	–	PD: 39.1	PO: 89.2
Right			
Gain (I/s)	24.1	13.5	45.9
Phase (deg)	–	PD: 53.6	PO: 86.6
Change			
Gain (%)	+153.7	− 4.5	− 3.2

b)

	(to Fig. 4a) S	D	O
Left			
Gain (I/s)	19.2	36.9	56.7
Phase (deg)	–	PD: 236.4	PO: 142.5
Right			
Gain (I/s)	20.5	7.9	56.7
Phase (deg)	–	PD: 64.2	PO: 148.2
Change			
Gain (%)	+ 6.8	− 78.6	0.0

	(to Fig. 4b) S	D	O
Left			
Gain (I/s)	20.8	24.5	27.9
Phase (deg)	–	PD: 100.5	PO: 8.8
Right			
Gain (I/s)	39.6	37.2	13.4
Phase (deg)	–	PD: 117.3	PO: 19.1
Change			
Gain (%)	+90.4	+ 52.0	−51.9

displays a high degree of similarity to the original, indicating that the higher components contribute only little to the shape of the polar plot, mainly strengthening the orientational tuning. In principle the plot in the middle can be composed from the plots below which display the directional D = 25.1 I/s (left) or orientational O = 40.0 I/s (right) components respectively, each superimposed to the spontaneous activity with S = 25.4 I/s. All plots are normalized with respect to their maximal values to illustrate shape differences, therefore graphical addition is not possible. Compared to Fig. 2 the plots from retransformed data lack symmetry because sinusoidal as well as cosinusoidal elements are present.

4 Discussion

Fourier analysis is a powerful tool for investigation of the spatial frequency response characteristic of cortical cells (Maffei and Fiorentini 1973; Glezer et al. 1980; Movshon et al. 1978). Static field properties are predicted, and cortical S-cells can be compared by the distribution and dimensions of their on- and off-subregions. Difficulties arise if one tries to predict the response to moving stimuli from stationary field plots (Palmer and Davis 1981). Moreover, Kulikowski and Bishop (1981) reported that the fine structure of a receptive field is much better revealed by moving stimuli. This, in particular, causes the problem of superimposed direction and orientation dependent components in the dynamic response of cortical cells that normally are sensitive to both components at the same time. Therefore, the direction and orientation dependent parts of the response have to be separated to be able to compare the different components in different cells. Fourier analysis applied to polar plots performs this separation by yielding the spontaneous activity component (S) together with the strength of the

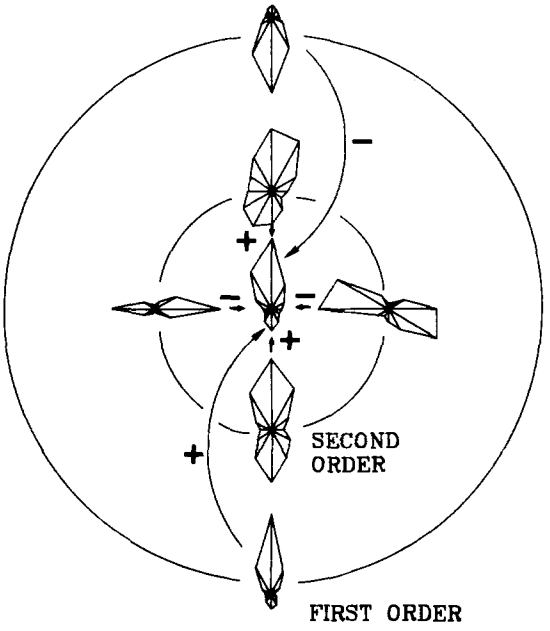

Fig. 6. Qualitative model describing the dynamic response characteristic of a cell (center) by converging intracortical inputs arranged and weighted according to Fourier components. First (D) and second (O) order inputs are added to the S component (not shown) generating approximately the response characteristic of the regarded cell

directional (D) and orientational tuning (O) and their angular values PD and PO. In this way the dynamic response characteristic of a cell is described by only three parameters, which without arbitrary assumptions, are equivalent to the stimulus parameters (Fig. 1). With FFT-analysis routines calculation is easily performed and a database of only 12 datapoints even would allow to implement simple user programmed routines for the calculation of the zero to second order components on small computers. The results reflect and supercede prima vista analysis of the polar plots for S-cells (Figs. 3 and 4) and the method is also applicable to C-cells, that, for simplicity, have been omitted from this study. The contributions of higher Fourier components above the second order seem mainly to affect the orientational tuning and can be disregarded without significant alterations of the result (Fig. 5). However, it is necessary to adjust the number of stimulus sweeps or other stimulus parameters in a way providing at least a single spike response for every orientation to avoid errors that are introduced by zero impulse rate values. For most of the cortical cells this is achieved for each direction with less than 5 stimulus sweeps so that data aquisition for a complete analysis of direction and orientation can be performed within a few minutes. This enables investigation of slow, transient changes of cell properties, for example during microiontophoretic application of pharmacological substances.

Negative values of the Fourier components occurring for the non-preferred direction and non-optimal orientation, could be interpreted in terms of inhibition that is opposed by excitation in response to the preferred stimulus parameters. This "inhibitory influence", in particular, accounts for the depression of the S-component, that is usually calculated much higher than any spontaneous activity observed in cortical S-cells. The S-component can be understood as "virtual spontaneous activity" an activity without any *specific* excitatory or inhibitory response. In terms of excitatory and inhibitory convergence as suggested by the positive and negative values of the Fourier components, polar plot response characteristics could be explained by a first order input provided by cells with a directionality axis aligned to the one of the recorded cell, contributing excitation in the preferred direction and inhibition in the non-preferred direction (Fig. 6). In addition a second order component of excitatory converging cells with receptive fields again aligned like the first order cells can be assumed to affect the optimal orientation (in both directions). This orientation dependent excitation is opposed by inhibition from cells with orthogonally oriented receptive fields that are mainly activated by stimuli of the non-optimal orientation. This interpretation, though speculative to a certain degree, is supported by physiological and anatomical findings (Sillito 1979; Matsubara et al. 1985). In our model both – first and second order – inputs are assumed to be added to the S component that is not indicated in Fig. 6.

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