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Axial responses in visual cortical cells: Spatio-temporal mechanisms quantified by Fourier components of cortical tuning curves

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Summary. The responses of 81 cells from area 17 in paralysed and aneasthetized cats were studied with moving spots and moving bars of different lengths. Tuning curves were measured and plotted as polar-plots. The strongest response of visual cortical cells to a moving bar occurs when the stimulus trajectory crosses the long axis of the receptive field (Hubel and Wiesel 1962). The optimal orientation for a moving and a flashing bar are identical, so that this response-type has been called the *orientational component*. For a moving spot, however, in most cases the strongest response occurs for motion along the receptive field long axis *(axial component)*. Thus, the axial and orientational components are orthogonal (Wörgötter and Eysel 1989). It is shown that orientational and axial components can display direction selectivity and for short bar stimuli a superposition of the two orthogonal components is demonstrated. Such a superposition in general, resulted in a polar-plot with four peaks 90° apart from each other (four-symmetrical polar-plot). Polar-plots with three or two response peaks were also found; the actual number of response peaks depending on the direction selectivity of the components. In many cells pure axial responses could be elicited with a light spot which stimulates only motion dependent mechanisms. Thus, it was concluded that temporal facilitation is strongly involved in the generation of axial responses. Fourier analysis of polar-plots (SDO-analysis, Wörgötter and Eysel 1987; Wörgötter et al. 1990) was applied to determine the tuning strengths of the different components. In correspondence with the periodicities of a moving oriented stimulus in the visual field, the first harmonic represents directional selectivity, the second orientation selectivity and the fourth harmonic was used to quantify the four-symmetrical superposition effect. It was statistically shown that the strongest superposition (i.e. largest fourth harmonic) occurred for intermediate bar lengths (1–2°). For longer bars only the orientational and for shorter bars predominantly the axial component occurred. In monkey visual cortex (V1, V3) four-symmetrical polar-plots can be obtained even with long stimuli (De Valois et al. 1982; Felleman and Van Essen 1987). Consequentially, we show that a strong fourth order Fourier component occurs. This supports the importance of quantification of higher order symmetries in cortical tuning curves by higher order harmonics in SDO-analysis.

Key words: Moving stimuli – Orientational component – Axial component – Fourth harmonic – Cat – Monkey

Introduction

Responses of visual cortical cells have been described with respect to several parameters including direction and orientation specificity (Hubel and Wiesel 1962), spatial frequency tuning (Campbell et al. 1969), contrast sensitivity (Tolhurst and Movshon 1975), and various other aspects (see Orban 1984). Consequently, quantification of these specificities has been of major importance, without which a detailed analysis of cell behavior would be impossible. In spite of this, remarkably little is known about the basic principles which could be used to quantify cortical specificities and quantification so far has been mostly based on heuristic measures (e.g. direction index and half-width-at-half-height orientation tuning parameter; see Orban 1984).

Recently it has been shown (Thibos and Levick 1985; Swindale et al. 1987; Wörgötter and Eysel 1987) that direction and orientation tuning can be quantified by a method which reflects the inherent periodicities of direction (360°) and orientation (180°) in the visual field. The so called SDO-analysis (Wörgötter and Eysel 1987) performs Fourier analysis of tuning curves recorded with moving oriented stimuli resulting in an approximation of the tuning curve by Fourier coefficients up to the second order ($k = 2$, Eq. 1). This approximation is in good correspondence with the actual experimental data as exemplified by Fig. 1 where cortical tuning curves are shown

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Offprint requests to: F. Wörgötter (address see above) which mainly contain only one, the directional (Fig. 1A, MT-cell in macaque monkey[1]) or the orientational component (Fig. 1B, Area 17 simple cell in cat). The lower part of the Fig. (Fig. 1C, D) shows the strong similarity of tuning curves simulated applying Eq. 1 with components corresponding to their real data counterparts.

$$IR(\alpha) = A_0 + \sum_{i=1}^{k} [A_i \cos(i\alpha) + B_i \sin(i\alpha)] \quad (1)$$

$$G_i = \sqrt{A_i^2 + B_i^2} \quad (2)$$

$$P_i = \arctan \frac{B_i}{A_i} \quad (3)$$

(IR(α) = maximal Impulse rate at angle α.)

Quantification of cortical tuning curves by SDO-analysis is achieved by computing the gain-phase spectrum (Eq. 2, 3) from the Fourier coefficients. The first and second order gain values (G_i, Eq. 2) are interpreted as strength of direction (D) and orientation (O) tuning, respectively. The corresponding phase values (P_i, Eq. 3) define the axes of preferred direction (PD) and preferred orientation (PO). The zero order component A_0 reflects the mean activity in the tuning curve which can be regarded as the general sensitivity (S) of a cell to visual stimulation (Wörgötter and Eysel 1987; Wörgötter et al. 1990).

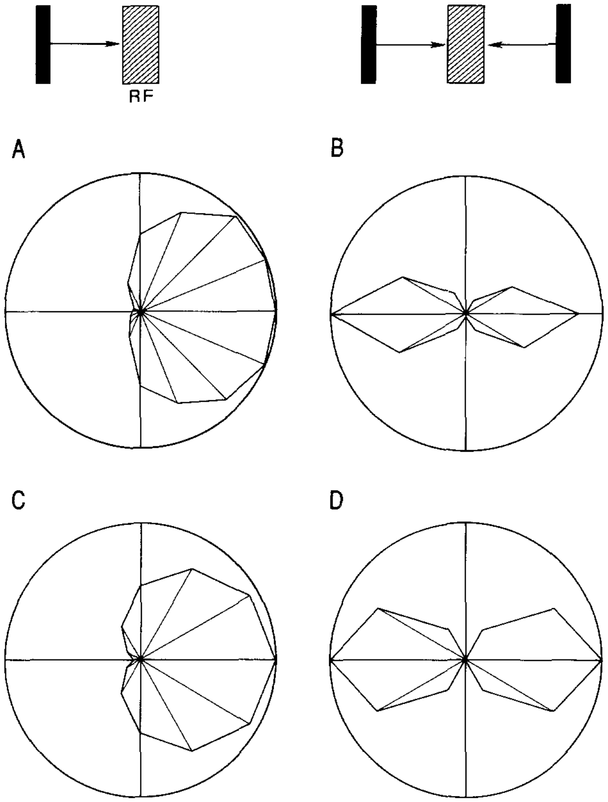

Fig. 1. A, B Examples of cortical tuning curves (polar-plots) obtained with moving bar stimuli plotting the peak response rates against the direction of stimulus motion. Below (**C, D**) polar-plots are shown simulated applying Eq. 1 (see text) with zero + first (**C**) or zero + second (**D**) order Fourier components. The high similarity between simulation and real data demonstrates that for some cortical cells this simple approximation is sufficient. Diagrams on top represent the optimal stimulus condition with respect to a schematic representation of the receptive field. **A** Purely direction selective cell response of an area MT cell stimulated with a long bar (modified from Albright 1984). **B** Area 17 simple cell of layer IV which displays only orientation selectivity while stimulated with an 3.6° long bar. **C** Simulation of a direction specific response. Coefficients for Eq. 1: $A_0 = 100$, $A_1 = 90$, all other coefficients = 0. **D** Simulation of an orientation specific response. Coefficients for Eq. 1: $A_0 = 100$, $A_2 = 100$, all other coefficients = 0

Recently it has been demonstrated that tuning curves obtained from cells in cat area 17 with *long bar stimuli* are approximated with high accuracy by a Fourier series only up to the second order ($k = 2$, Eq. 1; Wörgötter and Eysel 1987) and that the contribution of the higher order components can be disregarded in these cases.

Zhang (Zhang and De Valois 1988; Zhang 1990) claimed, however, that for a correct estimation of direction and orientation tuning the higher order components have to be included. In their approach all odd harmonics contribute to directionality whereas all odd *and* even harmonics shape the orientation tuning. This interpretation of cortical specificities is different from the classical view of direction and orientation tuning.

The most recent results (Wörgötter and Eysel 1989) from our laboratory showed that the strongest response to a moving long bar is most often orthogonal to the strongest response elicited by a moving light spot. In the present study it will be shown that a superposition of these two orthogonal, and probably independent, response components can be regularly elicited in cortical cells using *intermediate length bar stimuli* (e.g. 2° length). Such a superposition, however, results in "unusual" tuning curves with four symmetrically arranged response peaks. We will show that this higher order symmetry (i.e. fourth order) can be quantified by the fourth order Fourier component. This indicates that the fourth order Fourier component requires an independent interpretation and should not be included in the description of direction and orientation specificity. This will be further confirmed by discussing cell responses from other cortical areas which already display higher order symmetries when stimulated with long stimuli. In addition, a more detailed analysis of the spot response component or so called *axial component* will be provided and temporal mechanisms will be discussed.

Methods

Physiological recording procedures

The data for this study were obtained from eight adult cats (2.5–6.0 kg); initially the cats were anesthetized with Ketanest (20–25 mg/kg I.M.) and anesthesia was subsequently maintained by artificial respiration with $N_2O:O_2$ (70:30) and 0.2–0.5% halothane. The head was fixed in a stereotaxic headholder and xylocaine cream applied to all pressure points. The skull was opened to allow access to area 17 of the visual cortex in both hemispheres between Horsley-Clarke coordinates P0–P6 and L0.5–L3.5. The femoral artery was cannulated for a continuous measurement of arterial blood pressure and infusion of d-tubocurarine (0.3 mg/kgh) and gallamine tri-

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[1] Modified from Albright 1984

ethiodide (4.0 mg/kgh) in a glucose (1.25%) and Ringer solution throughout the 2–3 day experiments. The end-expired CO_2 was held at 3.8% and mean arterial blood-pressure remained above 90 mmHg at all times. Rectal temperature was kept constant at 38.5°. Atropine sulphate (1%) and phenylephrine hydrochloride (5%) was applied to the eyes for mydriasis and for retraction of the nictitating membranes and eyelids, respectively. The corneae were covered with zero-power contact lenses containing vertical slit pupils and the eyes then refracted with a refractoscope (Heine) and corrected with lenses for a viewing distance of 0.38 m. Cortical cells of the dominant eye within 5 degrees from the projection of the area centralis were recorded in layers II–VI with glass coated tungsten micro-electrodes (Wörgötter and Eysel 1988).

Classification of cells

Cells were classified as simple cells or complex cells according to the classification scheme proposed by Henry (1977, S- and C-cells). Intermediate classes A and B were not distinguished. Preliminary classification was performed by hand-held stimuli on a plotting board in front of the cat and confirmed by quantitative analysis of peristimulus time histograms (PSTH) showing the discharge regions in response to moving light and dark bars.

Visual stimulation

Prior to quantitative analysis, length and width of the receptive field regions were determined using hand-held stimuli and the major ON and OFF zones were plotted in order to allow accurate placement of the computer controlled stimuli. Stimuli moving back and forth across the receptive field were generated by a cathode ray tube image generator ("Picasso", INNISFREE, Cambridge, Mass., U.S.A.) and presented on an oscilloscope (Tektronics 608, screen: 8 × 10 cm) 38 cm in front of the cat's eyes. Bar and spot stimuli were used and special care was taken that the crossing point of all stimulus motion trajectories was located exactly in the center of the dominant excitatory zone of the receptive field (Wörgötter and Eysel 1989). Stimulus width was between 0.25° and 0.50°. Background illumination and dark bars had a luminance of 0.25 cd/m^2; luminances of light bars and background of dark bars could be varied between 1.0 and 12.5 cd/m^2. Six different stimulus orientations were presented in a pseudo-random sequence (30° steps). The response of each cell was recorded at optimal velocity and contrast.

Data analysis

Data representation and statistics. The initiation of the stimulus sweeps, data acquisition and preliminary data analysis were controlled on-line by a digital computer (LSI–11/23, Digital Equipment Corp., U.S.A.) via a laboratory interface (Cambridge Electronic Design, Cambridge, U.K.); analysis was completed on an IBM AT Compatible (RMC, Oberhausen, F.R.G.). Typically five sweeps for each orientation (back and forth movement) of the bar were recorded. Responses were analysed in the most common way computing PSTH histograms (bin size 10–200 ms) and polar-plots were generated by plotting peak impulse rates (maximum response) against the direction of bar movement. All polar-plots were normalized with respect to the maximum in the tuning curve to make them comparable with simulated results.

Fourier analysis of polar-plots. Directional and orientational components of the responses were extracted from polar-plots by Fourier analysis of the peak impulse rates IR(α) (Wörgötter and Eysel 1987) as described in the introduction. It is necessary to emphasize that the normalization process in this report is different from the previously used normalization procedure (Wörgötter and Eysel 1987; Wörgötter et al. 1990; see also Wörgötter et al. 1991 in this volume), namely: To determine the *relative* strength of the different contributions of the gain components up to the fourth order, the sum of the zero to fourth order gain components was regarded as 1.0 and, with this respect, all gain components are given as relative values[2]. *PD* and *PO* are given in degrees ($0° \leq PD < 360°$, $0° \leq PO < 180°$).

Note. Fourier analysis requires two data points per full period to retrieve the corresponding frequency component (Sampling theo-

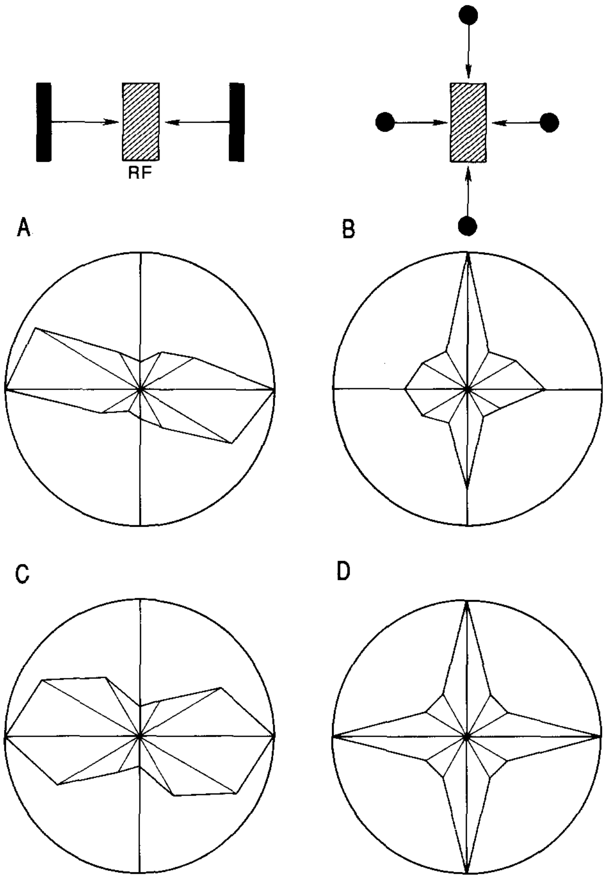

Fig. 2A–D. Layer VI simple cell of area 17 that displays only an orientational response during stimulation with a long bar (**A**), but a superposition of orientational and axial response when stimulated with a dot (**B**). Simulated polar-plots are shown applying only zero + second (**C**) or zero + fourth order Fourier components (**D**) in Eq. 1. Diagrams on top represent the optimal stimulus condition with respect to a schematic representation of the receptive field. **A** Bar length 4.1° The preferred orientation PO is 96.5°. No directional selectivity is obtained. **B** Dot size 0.6°. The orientational component is smaller than for the long bar stimulus but still very pronounced; an additional response occurred for motion along the receptive field long axis (axial response). **C** Simulation of the orientation specific response in (**A**). Coefficients for Eq. 1: $A_0 = 100$, $A_2 = 50$, $B_2 = 15$, all other coefficients $= 0$. **D** Simulation of the four-lobed response in **B**. Coefficients for Eq. 1: $A_0 = 100$, $A_4 = 75$, all other coefficients $= 0$

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[2] The central purpose of SDO-analysis is the comparison of direction and orientation tuning in different cells. Therefore, in the basic version of SDO-analysis and in the previous paper D and O are normalized with respect to S (Wörgötter and Eysel 1987, Wörgötter et al. 1990). The purpose of this study, however, is the determination of the relative contribution of the different gain components within each individual cell. Thus, the normalization described in the text had to be used

rem). 30° orientation steps correspond to 12 data points in 360° or six data points in 180° which is the periodicity of the orientation domain. Such a threefold oversampling should be entirely sufficient to retrieve the correct orientation tuning even of narrowly tuned simple cells (cf. Wörgötter et al. 1990). This justifies the use of the apparently coarse 30° sampling steps.

Histology

The electrode tracks were marked by two electrolytical lesions (1–2 μA, 10–15 s, tip negative) at the end of the recordings in the lower and upper layers of the cortex. At the end of the experiment all animals were fixed by intra-arterial vascular perfusion with 4% phosphate-buffered paraformaldehyde (pH 7.4) under deep halothane anaesthesia. Electrocoagulations were identified in frozen sections of 50 μm, counter-stained with Cresyl Violet and recording depths were determined from the reconstructed electrode tracks.

Results

Basic response types

A moving long bar in general elicits the strongest response in a cortical cell when crossing the long axis of the receptive field (Hubel and Wiesel 1962). In this case the moving bar optimally covers the receptive field at one position because the orientation of the bar is parallel to the orientation of the receptive field. Since this classical type of behavior can also be elicited by a flashing bar of the same orientation it has been called the *orientational response*. For a moving light spot, it has been reported that the strongest response most often occurs for movement *along* the axis of the elongated receptive field. Consequently, this axis is approximately orthogonal to that of the strongest response elicited by a long bar and has been referred to as the *axial response*[3] (Wörgötter and Eysel 1989). At least a weak axial response component has been found in about 70–80% of the cells in

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[3] It has to be emphasized that the term *axial response* in this and the previous study (Wörgötter and Eysel 1989) is used in a *completly different way* from the definition of "axial response" given by Henry et al. (1974). These investigators found that the "axial response" is *parallel* and not orthogonal to the orientational response and that no change in the axis of preferred motion occurs between long and short stimuli. The results from our laboratory disagree with this finding. A discussion of possible reasons for this discrepancy is given elsewhere (Wörgötter and Eysel 1989) and we believe that a redefinition of the term *axial response* is necessary

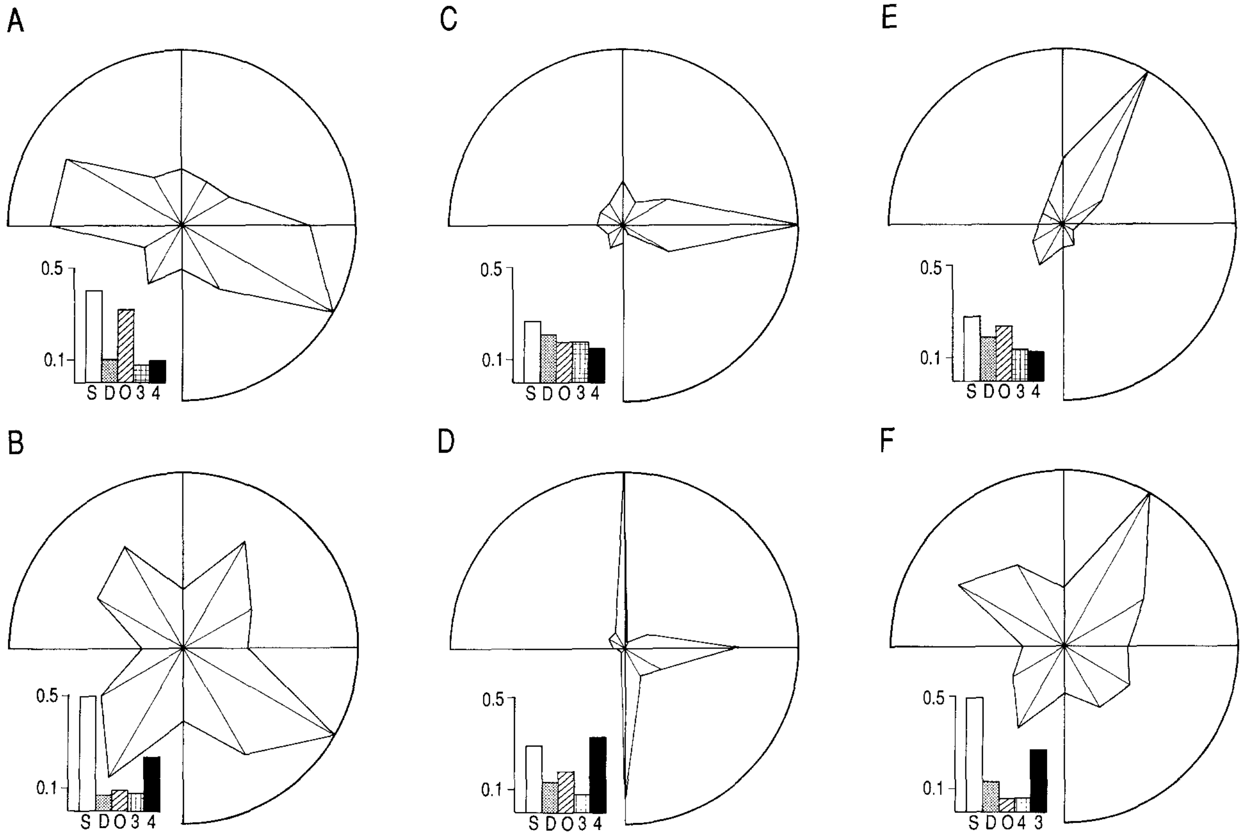

Fig. 3A–F. Characteristic examples of the basic response types found in area 17 during stimulation with long bars (**A, C, E**) or short stimuli (short bars or spots, **B, D, F**). The relative strengths of the different components as determined by SDO-analysis are shown in the insets. **A** Layer V complex cell. Bar length: 6.3° No significant directional selectivity can be detected. **B** Same cell as in **A**. Spot diameter 0.3° A four-lobed polar plot is produced. **C** Layer IV simple cell. Bar length: 5.7° This cell displays a strong directional specificity. **D** Same cell as in **C**. Bar length 0.8° The directional specificity is still reflected in the orientational component and a non-directional specific axial response is superimposed. **E** Direction specific Layer IV complex cell. Bar length: 9.8°. **F** Same cell as in **E**. Bar length: 3.2°. This cell shows a superposition between orientational and axial response component for relatively long bars. In addition, both components are directionally tuned area 17 (Wörgötter and Eysel 1989). Saito et al. (1988) use the criterion that cells respond equally well and strong to all directions of a moving dot to characterize them as "dot responsive". In area 17 they report 27% of the cells to belong to this group. A fair number of their cells, however, also seem to prefer the dot motion direction orthogonal to the preferred direction for a bar stimulus.

Nearly all cells showed a superposition of the two response components when stimulated with a bar of intermediate length and sometimes this superposition was still obtained for spot stimuli. Figure 2 shows a typical example of this behavior. When stimulated with a long bar this layer VI simple cell displayed no directional selectivity (Fig. 2A) and the preferred orientation was close to 90°. The tuning curve can be approximated applying Eq. 1 with only zero and second order Fourier coefficients (Fig. 2C). When stimulated with dot, the orientational response was still pronounced but now the axial response component was superimposed which resulted in a polar-plot with four peaks (Fig. 2B). A simulation utilizing only zero and fourth order Fourier coefficients in Eq. 1 ($k=4$) is similar to the real cell response (Fig. 2D). The asymmetry between the orientational and the axial response in Fig. 2B, however, indicates that for a valid approximation in this case the other Fourier components also would have to be included in the simulation.

In Fig. 3 different "basic response types" that are frequently observed with intermediate length bar stimuli (Fig. 3B, D, F) are compared with the corresponding polar-plots resulting from stimulation with a long bar (Fig. 3A, C, E).

A second example of a four-lobed polar-plot ob-

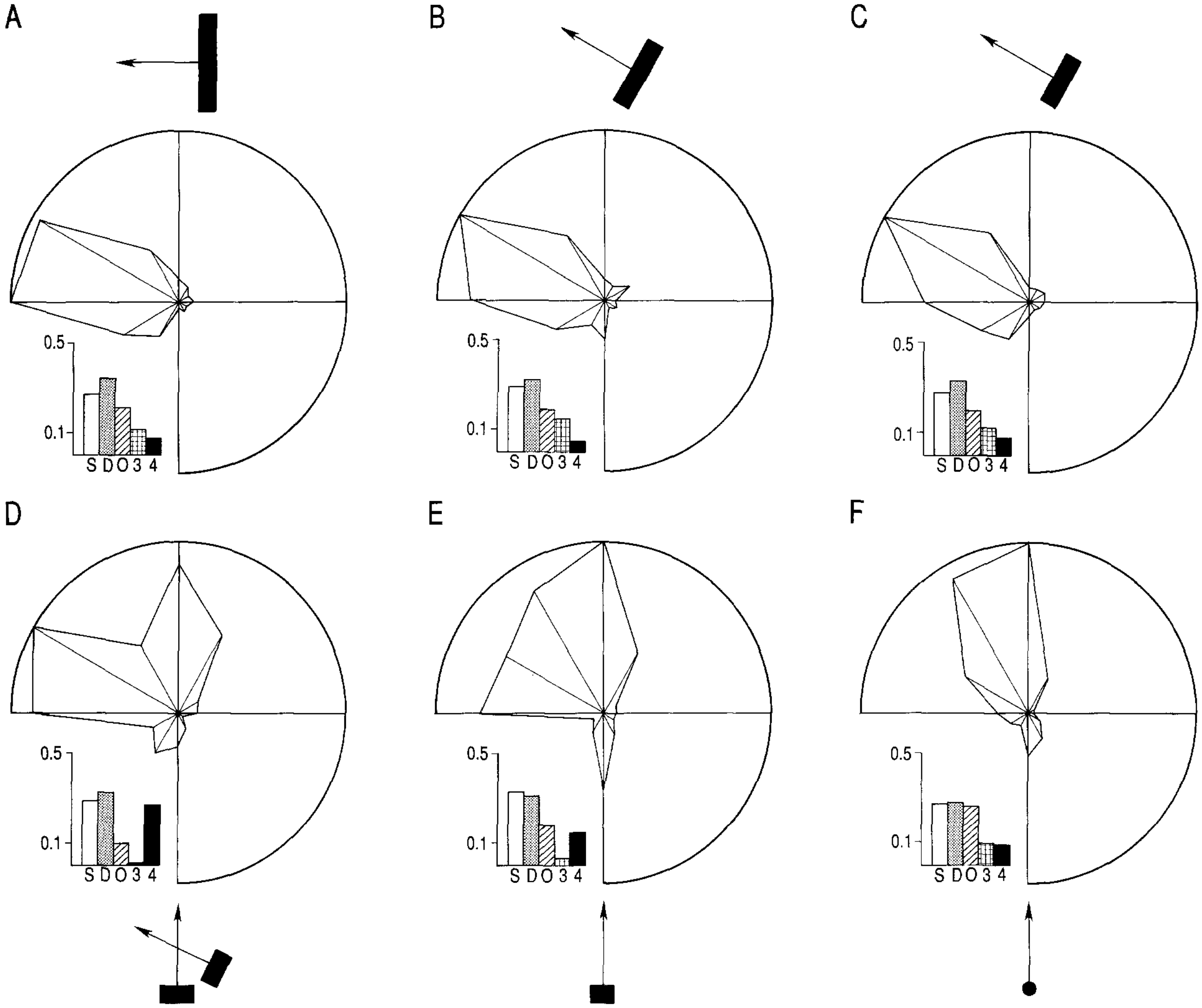

Fig. 4A–F. Continuous change from orientational to axial response with decreasing bar length in a layer III complex cell from area 17. The relative strengths of the different components as determined by SDO-analysis are shown in the insets. Optimal stimulus conditions are shown adjacent to the polar-plots. The strongest superposition (largest fourth order component) is obtained for an intermediate bar length. **A** Bar length: 13.0°. The cell shows a strong directional specificity. (*PD*=193.0°). **B** Bar length: 6.5°. (*PD*=195.0°). **C** Bar length: 4.8°. (*PD*=197.2°). **D** Bar length: 1.6°. The axial component is now superimposed on the orientational response. (*PD*=218.3°). **E** Bar length: 0.8° The axial and orientational components are still superimposed but the axial component predominates now and the preferred direction changed clearly. (*PD*=230.5°). **F** Spot diameter: 0.3° Only the axial component obtains for spot stimuli. (*PD*=249.7°)

tained with a light spot is given by the layer V complex cell in Fig. 3B. The results from Fourier-analysis show the strong predominance of the fourth order which occurs together with a very strong S component (zero order). As for the cell in Fig. 2 the polar-plot recorded during long bar stimulation showed virtually no directional tuning (Fig. 3A).

Four-lobed polar-plots, however, occurred only for a few cells in area 17; more often strong directional asymmetries were superimposed on either one or both of the response components. Such a response characteristic was observed in the layer IV simple cell in Fig. 3C, D. Here a strong direction specificity for the response component elicited with the long bar (Fig. 3C) was superimposed onto the non-direction specific axial response component. This resulted in a cut off of one lobe and, hence, in a tri-lobed polar-plot (Fig. 3D).

In the majority of cells the axial response component also displayed a directionally selective behavior. This can be seen in a layer IV complex cell in Fig. 3F. The polar-plot recorded during stimulation with an intermediate bar had only two lobes, although the response in the directions opposite to the lobes remained slightly stronger than in the other directions.

Applying short stimuli, only the fourth order gain was pronounced in all of the cells as can be seen in the insets in Fig. 3. The equally large (or even larger) increases in the S components are irrelevant for the specific tuning, because an increase in S only results in an expansion of the polar-plot.

Continuous transition from orientational to axial response

As mentioned above, the superposition of orientational and axial response was most often observed during stimulation with a bar of intermediate length. A long bar exclusively elicited an orientational response, whereas a moving spot resulted in an undisturbed axial component for most cells. The layer III complex cell shown in Fig. 4 retained its orientational response with decreasing bar length over several steps (Fig. 4A–C) until a superposition with the axial component occurred. The strongest effect was observed at 1.6° bar length (Fig. 4D). A further decrease of the bar length resulted in a fading of the orientational component (Fig. 4E) until, for a spot stimulus, only the axial response occurred (Fig. 4F). As expected, the largest fourth order gain component occurred for the strongest superposition effect which is seen in Fig. 4D, for all other plots a predominance of D and O components was observed.

The second most frequently observed situation included cells which showed the strongest superposition even for the shortest stimuli (i.e. spots). The layer IV simple cell shown in Fig. 5 displays a strong orientational component during stimulation with a long bar (Fig. 5A). In Fig. 5B it might be inferred that the small response peak in the lower left quadrant is already due to the rising axial response (compare also Fig. 3A). A clear superposition, however, was only obtained for a spot stimulus (Fig. 5C). As a consequence, cells with this behavior never express an axial component of their own and the fourth order gain component is strongest for spot stimulation.

Note that in a remaining percentage of about 20–30% of all cells no axial response could be observed (Wörgötter and Eysel 1989). In these cells the axial component is either completely absent or too small to be detected in the much stronger orientational response. Thus, the fourth order Fourier component does not exhibit any significance in these cells and, therefore, no example will be shown in the context of this study.

Statistical analysis

A statistical analysis was performed on the contribution of the different gain components with changing stimulus

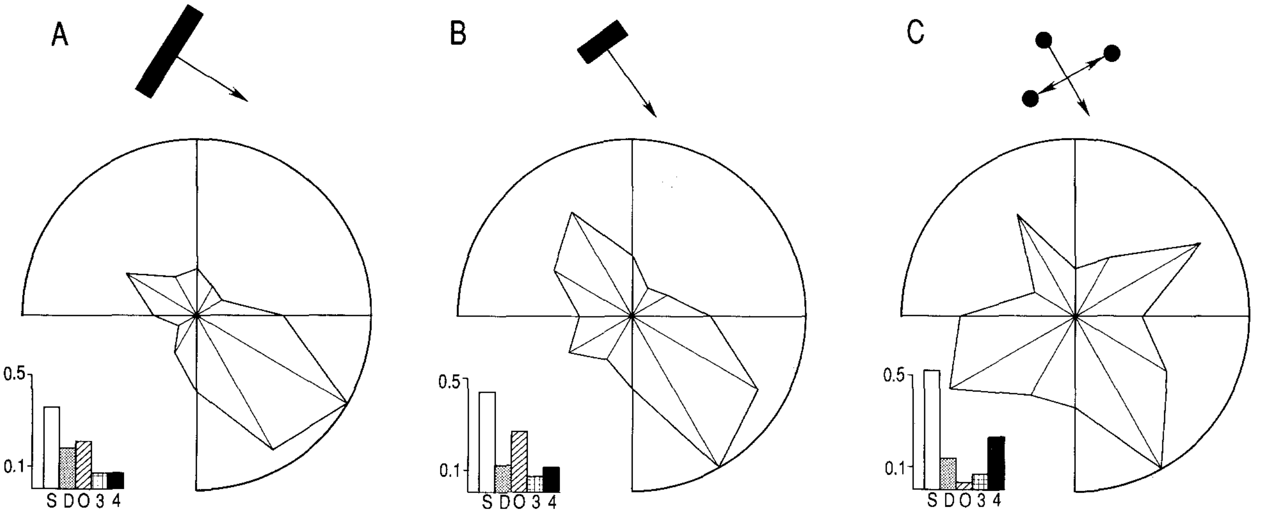

Fig. 5A–C. Continuous change from orientational to axial response with decreasing bar length in a layer IV simple cell from area 17. The relative strengths of the different components as determined by SDO-analysis are shown in the insets. Optimal stimulus conditions are shown on top of the polar-plots. Superposition between the components is only obtained for a spot stimulus. **A** For a bar length of 3.3° only the orientational component and a pronounced direction specificity was observed. **B** Bar length: 1.6° The directional tuning is reduced. **C** Spot diameter: 0.3°. A superposition between axial and orientational response occurs

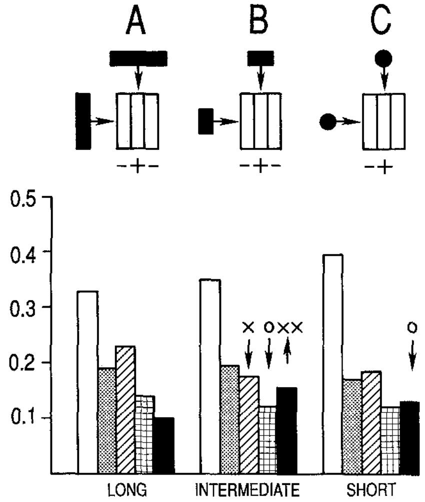

Fig. 6A–C. Distributions of the S, D, O, 3rd- and 4th-order gain components for different relations between stimulus length and receptive field dimensions as indicated above. Significance was tested (t-test) for the comparison of *long* to *intermediate* and *intermediate* to *short*. The arrows indicate the direction of the change (increase vs. decrease). Symbols: o:$p<0.05$, x:$p<0.001$, xx:$p<0.00001$. **A** Stimulus longer than the receptive field length. D and O predominate. **B** Stimulus shorter than receptive field length but longer than the width of the receptive field. A decrease in O and the third order component is accompanied by an increase in the fourth order gain component. **C** Stimulus shorter than receptive field width. A decrease in the fourth order component can be observed, which, however, is still larger than in **A**

length. Only cells ($n=61$) which showed at least a weak axial response were included. Due to the different receptive field diameters only three cases were distinguished:

Long: Stimulus longer than the receptive field length (Fig. 6A).
Intermediate: Stimulus shorter than the receptive field length but longer than the width of the central (ON- or OFF-) zone (usually between 1 and 2°, Fig. 6B).
Short: Stimulus shorter than the width of the central zone (Fig. 6C).

Schematic drawings that illustrate the grouping are shown for a simple cell with symmetrically arranged subfields in the top portion of Fig. 6. The average relative contributions of the gain components for these three cases are plotted on the bottom.

Changes in zero (S) and first (D) order gain component are insignificant, whereas the fourth order gain shows a highly significant increase from *long* (Fig. 6A) to *intermediate* (Fig. 6B). From *intermediate* to *short* (Fig. 6C) a significant decrease occurs which is in correspondence with the qualitative observations. The relative change of the fourth order component is accompanied by an anti-correlated and also significant change of the second (O) and third order component. The decrease in O corresponds to the observations of Henry et al. (1974) who reported a decrease in orientation tuning with decreasing stimulus length. The strong contribution of the fourth order gain component at intermediate stimulus length corresponds to the strongest superposition effects as shown above in Figs.3–5.

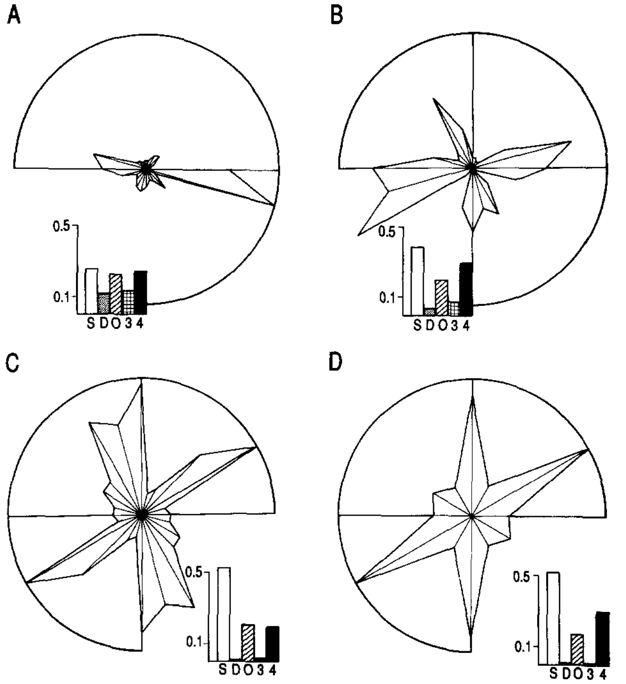

Fig. 7A–D. Examples of four-lobed tuning curves from V1 (**A, B**; modified from De Valois et al. 1982) and V3 (**C, D**; modified from Felleman and Van Essen 1987) in monkey. Note that these tuning curves were recorded with *long stimuli*. The tuning curves in (**A, B**) were recorded with a moving grating those in **C, D** with a flashing stimulus. Consequentially (**C, D**) are artificially completed over 360°. The relative strengths of the different components as determined by SDO-analysis are shown in the insets and a strong fourth order component can be observed in all cells

Examples of fourth order components in cell responses in monkey V1 and V3

The cell responses shown in Fig. 7A[4] and B[5] demonstrate that different and approximately orthogonal response components can be elicited even with long stimuli in different cortical areas of macaque monkey. The cells in Fig. 7A were recorded with drifting gratings, whereas in Fig. 7B stationary flashing long bars were applied. For flashing stimuli, as expected, the D component drops to zero. It is remarkable that four-lobed polar-plots were obtained despite of the use of quite different stimuli. Thus, the fourth (and second) order gain component predominate in these examples and the cell responses are at least phenomenologically similar to the superposition of orientational and axial components observed in cat's area 17. More examples of cells showing similar behavior can be found in the original reports of these investigators (De Valois et al. 1982; Felleman and Van Essen 1987).

Discussion

Axial responses so far have mostly not been included in the description of cortical cell behavior and numerous

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[4] Modified from De Valois et al. 1982

[5] Modified from Felleman and Van Essen 1987

studies were confined to the different aspects of direction and orientation tuning (for a review see Orban 1984). This study has tried to describe axial responses in a more generalized way as well as to provide a method of quantification. From this approach two major points of discussion arise, namely: (1) Are axial responses of any importance for models of cortical cell behavior, and: (2) What is the significance of higher order Fourier components in the response of cortical cells?

The importance of axial responses

Responses of cortical cells in general can be subdivided into responses elicited by moving or stationary stimuli. This subdivision is more or less parallel to the subdivision of responses predominantly due to temporal or spatial mechanisms. Since the first reports on visual cortical cell behavior (Hubel and Wiesel 1962), research has been strongly focussed on spatial effects. In particular, the elongated shape of simple cell receptive fields has been explained by predominance of spatial summation within the excitatory regions which can be elicited by a stationary flashing bar. Most cortical cells only respond weakly to a stationary flashing spot, whereas responses to a moving spot can be very pronounced and in several cells even excede the response strength to a flashing bar of optimal length (Rose 1977; Saito et al. 1988; Wörgötter and Eysel 1989). Thus, spatial mechanisms only play a minor role in spot responses; these responses seem to be mostly due to motion and, consequently, strongly involve temporal mechanisms. The strongest responses to moving spots were nearly always obtained for motion along the receptive field axis (axial component). This, however, suggests that not only spatial but also some kind of temporal summation contributes to the elongated shape of simple receptive fields. It was further shown that axial responses can be elicited independently from orientational responses which supports the view that the temporal and spatial mechanisms involved are independent. The importance of temporal mechanisms for the response characteristic of at least some cells can be judged from the sometimes remarkable strength of the axial component (Saito et al. 1988; Wörgötter and Eysel 1989). Furthermore, it can be speculated that the axial response component is the basis for the explanation of "unusual" cortical responses like the tuning curves obtained with a moving noise field which often also display multiple response peaks (Hammond 1978). Thus, a complete description of cortical cell behavior should include the axial component and models of cortical cells in general should implement temporal interactions (Wörgötter and Holt 1991) which so far have often been disregarded in modeling. This demand is strongly supported by the finding that tuning curves with multiple (four) response peaks are much more commonly obtained, even with long stimuli, in several cortical areas of monkey. In addition, superposition of axial and orientational responses is probably the most common case for a single cell subjected to a real visual scene so that "mixed" responses should predominate for all cells and in virtually all realistic situations.

The significance of higher order Fourier components

Since often stimulus types are used which confound different cortical specificities (e.g. when using moving bars) the question how to quantify the responses has been of major importance in the investigation of cortical physiology. Fourier analysis of polar-plots (SDO-analysis) has been suggested for the separation of direction and orientation in cortical responses (Wörgötter and Eysel 1987; see also Thibos and Levick 1985; Swindale et al. 1987). A major advantage of SDO-analysis is that its results remain comparable to the results of the commonly used methods[6] (Wörgötter et al. 1990). In addition, the separation of direction and orientation by their periodicities in the visual field provides a more solid conceptional background than the heuristic assumptions which underlie other methods.

In the approach of Zhang (Zhang and De Valois 1988; Zhang 1990) the higher order Fourier components are included in the description of direction and orientation. This is correct from a mathematical point of view, however, an independent interpretation of the higher order components is prevented in this way. The present study strongly suggests that the superposition of axial and orientational response components is reflected in the fourth order Fourier component. This indicates that at least this component has an independent interpretation.

It has to be noted that several cells exist that never exhibit an axial component without the superposition of the orientational component. In addition, results from pharmacological manipulation of cell responses indicate that an induced change of orientation selectivity can occur predominantly as an increase of the axial response (Eysel et al. 1990). This also resulted in four-lobed polar-plots and the strength of the pharmacological effect can be estimated by the increase of the fourth order gain component. Finally, responses in monkey cortex (De Valois et al. 1982; Felleman and Van Essen 1987) directly show that the fourth order gain component can provide valuable information about possible different response components which can be elicited even with commonly used stimuli (i.e. long bars or gratings). The different conditions under which four-symmetrical polar-plots can be observed, thus, support the view that the fourth order Fourier component should not be included in the description of direction and orientation tuning (Zhang and De Valois 1988; Zhang 1990) but independently interpreted. In addition, the above examples show that the superposition of orthogonal response components is rather common so that its quantification is desirable.

Concerning other Fourier components (third, fifth, sixth and higher), it remains unclear if a neuronal mechanism exists which could result in the corresponding periodicity or if these components only contribute to direction, orientation and the fourth order component in the way Zhang (Zhang and De Valois 1988; Zhang 1990) suggested.

In conclusion, the fourth order gain component can provide additional information about the behavior of

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[6] Commonly used are the direction index DI and the half-width-at-half-height orientation tuning parameter (see Orban 1984)

cortical cells. In particular, it can be used to quantify the superposition of axial and orientational responses. This can help interpret temporal mechanisms which are probably involved in the generation of axial responses. The inclusion of the temporal domain in models of cortical cells should, therefore, lead to a better understanding of cell responses. More complex cell behavior (i.e. in higher areas) may also find partial explanation in models more strongly focusing on temporal mechanisms (Wörgötter and Holt 1991).

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References

Albright TD (1984) Direction and orientation selectivity of neurons in visual area MT of the macaque. J. Neurophysiol. 52:1106–1130

Campbell FW, Cooper GF, Enroth-Cugell D (1969) The spatial selectivity of the visual cells of the cat. J Physiol 203:223–235

De Valois RL, Yund EW, Hepler N (1982) The orientation and direction selectivity of cells in macaque visual cortex. Vision Res 22:531–544

Eysel UT, Crook J, Machemer (1990) GABA-induced remote inactivation reveals cross-orientation inhibition in the cat striate cortex. Exp Brain Res 80:626–630

Felleman D, Van Essen DC (1987) Receptive field properties of neurons in area V3 of monkey extrastriate cortex. J Neurophysiol 57:889–920

Hammond P (1978) Directional tuning of complex cells in area 17 of the feline visual cortex. J Physiol 285:479–491

Henry GH (1977) Receptive field classes of cells in the striate cortex of the cat. Brain Res 133: 1–28

Henry GH, Bishop PO, Dreher B (1974) Orientation, axis and direction as stimulus parameters for striate cells. Vision Res 14:767–777

Hubel DH, Wiesel TN (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J Physiol 160:106–154

Orban GA (1984) Neuronal operations in the visual cortex. Springer, Berlin

Rose, D (1977) Responses of single units in cat visual cortex to moving bars of light as a function of bar length J Physiol (Lond) 271:1–23

Saito H, Tanaka K, Fukada Y, Oyamada H, (1988) Analysis of discontinuity in visual contours in area 19 of the cat. J Neurosci 8:1131–1143

Swindale NV, Matsubara JA, Cynader MS (1987) Surface organization of orientation and direction selectivity in cat area 18. J Neurosci 7:1414–1427

Thibos LN, Levick WR (1985) Orientation bias of brisk transient Y-cells of the cat retina tor drifting and alternating grating. Exp Brain Res 58:1–10

Tolhurst DJ, Movshon JA (1975) Spatial and temporal contrast sensitivity of striate cortical neurones. Nature 257:674–675

Wörgötter F, Eysel UT (1987) Quantitative determination of orientational and directional components in the response of visual cortical cells to moving stimuli. Biol Cybern 57:349–355

Wörgötter F, Eysel UT (1988) A simple glass-coated, fire-polished tungsten electrode with conductance adjustment using hydrofluoric acid. J Neurosci Meth 25:135–138

Wörgötter F, Eysel UT (1989) Axis of preferred motion is a function of bar length in visual cortical receptive fields. Exp Brain Res 76:307–314.

Wörgötter F, Holt G (1991) Spatio-temporal mechanisms in receptive fields of simple cells: a model. J Neurophysiol (in press)

Wörgötter F, Gründel O, Eysel UT (1990) Quantification and comparison of cell properties in cat's striate cortex determined by different types of stimuli. Eur J Neurosci 2:928–941

Wörgötter F, Muche T, Eysel UT (1991) Correlations between directional and orientational tuning of cells in cat striate cortex. Exp Brain Res 83:665–669

Zhang J (1990) How to unconfound directional and orientational information in visual neuron's response. Biol Cybern 63:135–142

Zhang J, De Valois RL (1988) Unconfounding orientation and direction components in the visual neuron's response. Soc Neurosci Abstr 14/1:187.4