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Quantification and Comparison of Cell Properties in Cat's Striate Cortex Determined by Different Types of Stimuli

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Abstract

Direction and orientation tuning elicited by moving bars, flashing bars and a moving noise field were compared in cells in area 17 of the cat. Fourier analysis of tuning curves (SDO-analysis) was applied to quantify the general sensitivity (S) to visual stimulation, tuning strength to direction(D) and orientation (O), as well as the preferred direction (PD) and orientation (PO). Results from SDO-analysis were compared with the commonly used direction index and half-width-at-half-height orientational tuning parameter and it is demonstrated that the commonly used parameters can be replaced and are superseded by the results from SDO-analysis. The comparison of the responses elicited by the different types of stimuli showed that a linear correlation between D (or O) components was mainly found in simple cells, while in most cases no correlation was obtained for complex cells. Since several of the simple cells also showed no linear relationship, a direct mutual prediction of the S, D and O components can only be achieved for ~50% of the cortical cells applying commonly used stimulus types. The general responsiveness (S) shows that flashing bar stimuli are at least as effective as moving bars, whereas moving noise stimulates cortical cells more weakly. A moving bar tends to increase the orientation tuning (O) in most cells and with a moving noise stimulus predominantly the directional tuning (D) of complex cells is strongly enhanced. In conclusion, Fourier analysis of tuning curves (SDO-analysis) provides a valuable and simple tool for the quantification of direction and orientation specificity. Motion enhances the cortical response specificity which indicates the involvement of facilitation or inhibition exclusively induced by movement.

Introduction

Bar stimuli are most often used for the investigation of direction and orientation tuning of visual cortical cells (Orban, 1984). However, with a moving bar stimulus directional (D) and orientational (O) components are mixed together and both might contribute to the response characteristic of a cell. For this reason, when careful treatment of the terminology for a moving bar stimulus is required, the terms directional and orientational tuning are avoided by some investigators (for a discussion see Orban, 1984) and the term axial selectivity is used instead. Commonly, orientation selectivity is thought to be reflected by the axial selectivity for nearly all cells. Thus, the term orientation (and direction) selectivity will be used throughout this study instead of axial selectivity. Since the aim of this study is the comparison of the different components elicited by different stimulus types, the terms will only be used together with the stimulus type by which they were elicited.

Flashing bars or moving noise field stimuli contain only the orientational or the directional component respectively, and have therefore been used for a comparison of the tuning strengths with those obtained by a moving bar (Henry *et al.*, 1973, 1974b; Hammond, 1978; Hammond and Reck, 1980; Duysens and Orban, 1981; Emerson and Coleman, 1981; Hammond and Smith, 1983). In previous studies the quantification of the tuning parameters has normally been performed by heuristic measures, such as the direction index or the half-width-at-half-height orientation tuning parameter (Orban, 1984). It has been suggested that Fourier analysis of tuning curves provides a more reliable description of cortical specificities (Batschelet, 1981; Thibos and Levick, 1985; Swindale *et al.*, 1987; Wörgötter and Eysel, 1987). The so-called SDO-analysis (Wörgötter and Eysel, 1987) interprets the first order Fourier harmonic as the directional (D) and the second order as the orientational (O) component, thereby directly reflecting the periodicities of a moving light bar in the visual field (see Fig. 2B). The zero order component describes the general sensitivity (S) of a

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cell to visual stimulation. Directional (D) and orientational (O) components are separated by SDO-analysis, but this separation may differ from the separation of direction and orientation as tested with different stimulus types. Thus, a comparison of D and O for different stimuli can provide insights into both the computational and the physiological separability of these components and reveal functional relationships.

In this study the tuning of cortical cells for direction and orientation is compared for different types of stimuli. In view of the numerous possible stimulus parameter combinations (e.g. contrast, velocity, width and length) we restricted this study to the comparison of 'optimal responses' in the sense that for each stimulus the parameters were adjusted so as to elicit the maximal response possible. For this particular situation, directional and orientational components elicited by moving noise and flashing bars were determined and compared with those elicited by a moving bar. We show that, mainly in simple cells, the directional and orientational components for the different stimulus types are directly related and that a separation of the components by SDO-analysis for these cells corresponds to the separation that is achieved by flashing bar and moving noise stimuli. In addition it will be demonstrated that for a large number of cells the tuning strengths, but not the general responsiveness, increase with a moving bar stimulus relative to a moving noise or flashing bar stimulus.

Materials and methods

Physiological recording procedures

Eight adult cats (2.5–6.0 kg) were used; initially the cats were anaesthetized with Ketanest (20–25 mg/kg i.m.). The femoral artery was cannulated for a continuous measurement of arterial blood pressure and heart rate. Anaesthesia was subsequently maintained by artificial respiration with N_2O:O_2 (70:30) and 0.2–0.5% Fluothane to ensure an adequate anaesthetic level. The blood pressure, heart rate and EEG were used to monitor the depth of the anaesthesia, which could be adjusted by the amount of added Fluothane. 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 and P6 and L0.5 and L3.5. A continuous infusion of *d*-tubocurarine (0.3 mg/kg/h) and gallamine triethiodide (4.0 mg/kg/h) in a glucose (1.25%) and Ringer solution was given throughout the 2–3 day experiment. The end-expired CO_2 was held at 3.8% and mean arterial blood pressure remained above 90 mm Hg at all times. Rectal temperature was kept constant at 38.5°C. Atropine sulphate (1%) and phenylephrine hydrochloride (5%) were applied to the eyes for mydriasis and for retraction of the nictitating membranes and eyelids respectively. The corneas were covered with zero power contact lenses

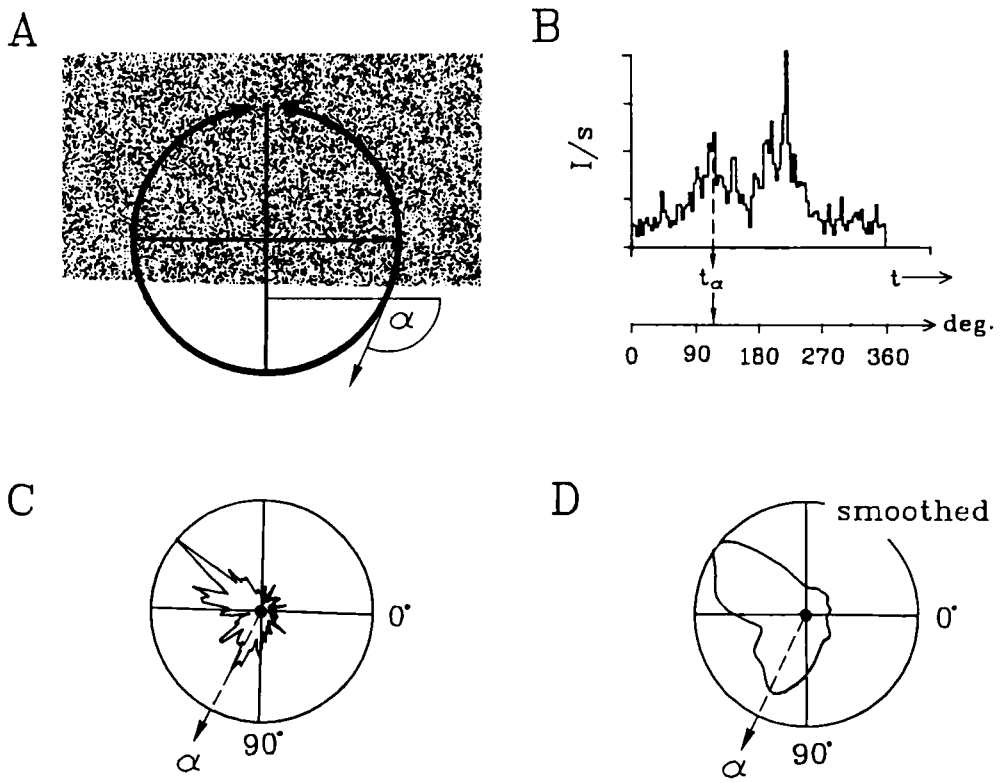

FIG. 1. Stimulation of visual cortical cells with a rotating noise field (A) and preliminary steps of data analysis (B–D). (A) Noise stimulation is performed by a clockwise rotating noise field with starting point t_0 as indicated by the dot. The actual direction of motion is always tangential to the circle on which the noise field rotates, i.e. at a given time, t_α, (B) the direction of motion is α. Thus, the directions of motion occur progressively and all directions (0–360°) in the visual field are covered as soon as the rotation is completed. The noise field is bigger than 30° of the visual field and the receptive field of the studied cell is located close to the centre of rotation (crossed bars). The angle α is depicted to demonstrate its position during the data analysis steps (B–D). (B) The neuronal response of a simple cell is recorded as a poststimulus time histogram (angular velocity 36°/s, bin size 20 ms, angular resolution 0.7°, 30 sweeps, linear velocity 4.7°/s). Each point on the temporal axis (e.g. t_α) corresponds to a point on the angular axis below. (C) A polar plot is constructed by plotting the histogram bins in a polar coordinate system corresponding to the angular axis in (B) starting at 0°. The maintained discharge is indicated as a circle (2.0 I/s). (D) Same polar plot after smoothing (eq. 1, see text). The two responses peaks are much better revealed than in the unsmoothed polar plot (C).

containing vertical slit pupils and the eyes were 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° from the projection of the area centralis were recorded in layers II–VI with glass coated tungsten microelectrodes (Wörgötter and Eysel, 1988).

Visual stimulation

Light and dark bar stimuli moving back and forth across the receptive field (r.f.) were generated by a cathode ray tube image generator ('Picasso', INNISFREE, Cambridge, MA) and presented on an oscilloscope (Tektronics 608, screen: 8×10 cm) 38 cm in front of the cat's eyes. Care was taken to use only bars that were long enough to completely cover the receptive field at the optimal orientation. Background illumination and dark bars had a luminance of 0.25 cd/m^2; luminances of light bars could be varied between 1.0 and 12.5 cd/m^2. Six different stimulus orientations were presented in a pseudorandom sequence (30° steps). The response of each cell was recorded for the optimal bar length (0.5–15°) and velocity. Contrast was individually adjusted for an optimal response. ON and OFF responses at different orientations were recorded by stationary flashing of the same bar.

Visual noise was used as an additional stimulus and a static noise field covering more than 30° of the visual field (average grain diameter: 0.05°) was rotated excentrically in a clockwise manner (Schoppmann and Hoffmann, 1976) at optimal velocity, thereby covering all directions of movement (Fig. 1A). The noise field was projected with a slide projector and care was taken to locate the receptive field of the studied cell well inside the projected area. The angular velocity range for the noise fields was 18–72°/s. The radius for the circular motion varied between 2.5 and 10.0 cm. Thus, at the viewing distance of 0.38 m, the range of linear velocities covered was 0.78–18.84°/s. Depending on the responsiveness of the studied cell, between 10 and 50 sweeps were measured. The bin size for sampling spikes was 10–100 ms. The angular resolution (depending on the angular velocity and the bin size) was always better than 2.0°.

As mentioned above, stimulus parameters for all types of stimuli were individually adjusted for length, width, contrast and velocity to elicit maximal response at the preferred direction of movement.

Classification of cells

Cells were classified as belonging to the simple group (S-cells) or complex group (C-cells) according to the classification schemes proposed by Henry (1977). Intermediate classes A and B (Henry, 1977; Orban, 1984) 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

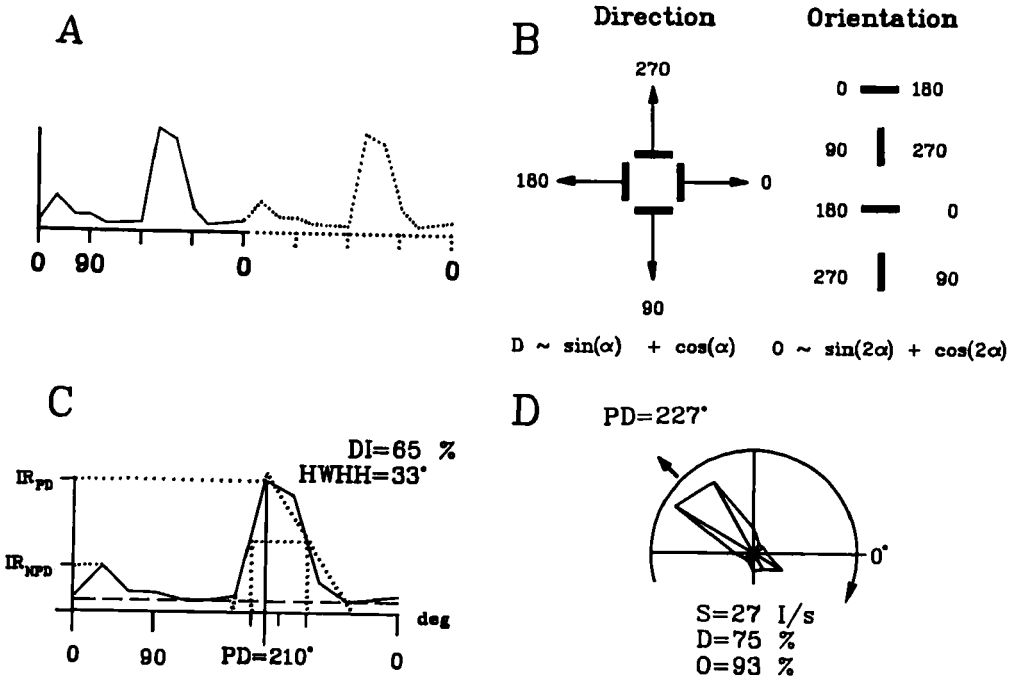

FIG. 2. Methods for the determination of directional and orientational tuning strength. (A) Tuning curve of a simple cell. Every orientation tuning curve can be regarded as a periodical function with a first harmonic of 360°. (B) The periodicity in the tuning curve corresponds to the periodicity of the direction of motion of a moving light bar (left). Orientation of the bar, however, has a periodicity of 180° in the visual field (right). Therefore, direction can be regarded as first order and orientation as second order component in the Fourier domain and Fourier analysis can be applied to polar plots (eq. 2, see text). The tuning strength of direction (D) and orientation (O) is given by the gain values (eq. 3, see text), the preferred direction (PD) and preferred orientation (PO) by the respective phase values (eq. 4, see text) of the phase-magnitude spectrum. The zero order component (not shown) is considered as sensitivity (S) of the cell to visual stimulation. This form of analysis, therefore, is called SDO-analysis. (C) Commonly used methods to determine directional and orientational tuning strength. The direction index (DI) is calculated applying eq. 5 (see text). The half-width-at-half-height (HWHH) orientational tuning parameter is defined as half width of the tuning curve (in degrees) at half of the peak height as given by the two regression lines on either side of the peak. Prior to the calculation of the direction index and the half-width-at-half-height the maintained discharge (dashed line) has to be subtracted. Direction index, preferred direction and the half-width-at-half-height orientation tuning of this simple cell are indicated in the diagram. The maintained discharge was 8.5 I/s (dashed line). (D) Polar plot diagram of the same tuning curve as above; the results from the SDO-analysis are indicated.

(PSTH) showing the discharge regions in response to moving light and dark bars. Since stimulation was only performed at optimal bar length, end-stopped cells were not treated separately.

Data analysis

Data representation

The initiation of the stimulus sweeps, data acquisition and preliminary data analysis was controlled on-line by a digital computer (LSI-11/23, Digital Equipment Corp., USA) via a laboratory interface (Model 502, Cambridge Electronic Design, Cambridge, UK); analysis was completed on an IBM AT Compatible (RMC, Oberhausen, FRG). Typically, five sweeps for each orientation (back and forth movement) of the bar were recorded. The bin width for the recording was 20 ms; for subsequent computations 5 or 10 bins were combined (100 or 200 ms). The peak impulse rates for each direction of bar movement were used to generate polar plots by plotting the impulse rate per second as vector length and the direction of stimulus movement as vector angle, in a polar coordinate system. For a flashing bar, ON and OFF responses were represented in separate polar plots of peak response against bar orientation. [Generally, the direction of movement of a stimulus bar is orthogonal to its orientation, therefore polar plots for a moving bar are orthogonal to their flashing bar counterparts (e.g. see Fig. 4). Responses to a flashing bar have a 180° periodicity. However, for display reasons their polar plots were completed over the full field (360°) by adding the mirror image of the response (shaded polar-plots in the figures).]

For the analysis of noise stimulation PSTHs were recorded (bin size 10−100 ms) where each bin represents a different direction of movement of the noise field (Fig. 1B), thus the complete histogram can be directly transformed to a polar plot (Fig. 1C).

Depending on the variability of the cell responses, polar plots recorded with noise stimuli often had a very jagged appearance (Fig. 1C). Therefore, a symmetrical exponential smoothing (eq. 1) was applied to the impulse rates IR_i for each histogram bin i (Fig. 1D):

$$\text{Smoothed } IR_i = \frac{\sum_{j=-w}^{+w} IR_{i+j}\exp[-(j\delta)^2]}{\sum_{j=-w}^{+w} \exp[-(j\delta)^2]} \quad (1)$$

where w represents the width of the smoothing window and δ defines the steepness of the exponential decay. At all data points, the smoothing operation can be regarded as a bilateral weighted mean with exponentially decaying weights. The decay is symmetrical around the centre point, thereby avoiding phase shifts. In addition, the bins at the beginning of the histogram were connected to those at the end so that smoothing was performed over the complete circle. Generally, a window of $w = 5$ was used and δ was adjusted so that a decay of −6 dB occurred between the center point ($j = 0$) and the adjacent points ($j = +1, j = -1$). The smoothing operation was performed on all polar plots measured with moving noise. Smoothing predominantly acts as a low pass filter, thus reducing the high frequency components in the signal. Since we were predominantly interested in low frequency components (D component, see next paragraph) the results are not significantly distorted by the smoothing but the visibility of the low frequency components is enhanced for the human observer. This has also been tested by comparing results from unsmoothed with those from smoothed polar plots in some cells.

Fourier analysis of polar plots

Directional and orientational components of a response were extracted from polar plots by Fourier analysis of the peak impulse rates $IR(\alpha)$ (Wörgötter and Eysel, 1987). This is exemplified for a simple cell in Figure 2. In general, the orientation tuning curve can be interpreted as a periodical function with 360° periodicity (Fig. 2A); the first harmonic (A_1 and B_1; eq. 2) is then regarded as directional and the second harmonic (A_2 and B_2; eq. 2) as the orientational component (Batschelet, 1981). Thereby the periodicities in the visual field of direction (360°) and orientation (180°) of a moving bar (Fig. 2B) are directly reflected. The gain values (G_i; eq. 3) define the strength of the respective directional (D) and orientational (O) components,

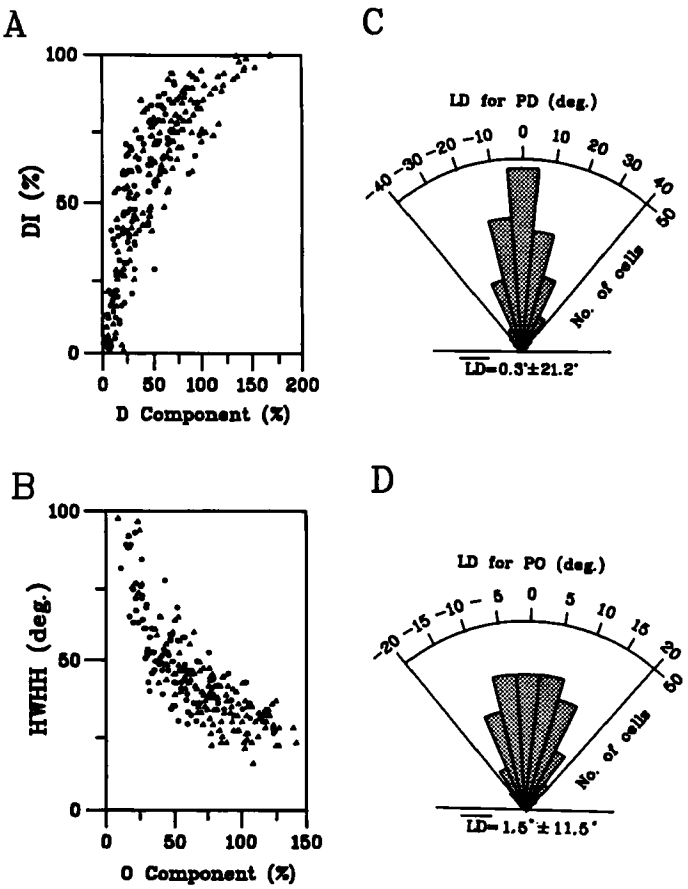

FIG. 3. D and O components from SDO-analysis are plotted against the direction index and the half-width-at-half-height orientation tuning parameter (A,B) respectively. The graphs include 143 simple cells (filled triangles) and 106 complex cells (open circles). (C,D) Comparison of the least differences between preferred direction (C) or preferred orientation (D) as determined by the strongest response in the polar plot and the respective PD or PO values computed by SDO-analysis. (A) Plot of DI versus D. (B) Plot of HWHH versus O. Both curves (A,B) are monotone; this demonstrates that the commonly used parameters can be replaced by the results from SDO-analysis. For complex cells, lower directional and orientational tuning predominates but no discrete separation between simple and complex cells can be observed. (C) Comparison of the least differences between preferred direction determined conventionally and the respective PD values computed by SDO-analysis. (D) Comparison of the least differences between the preferred orientation determined conventionally and PO from SDO-analysis. The mean least differences in both diagrams are close to zero, showing that the SDO-method, on average, leads to the same PD and PO values as obtained by prima vista analysis.

whereas the phase values (P_i; eq. 4) represent the preferred direction (PD) and preferred orientation (PO).

$$IR(\alpha) = A_0 + \sum_{i=1}^{k} [A_i\cos(i\alpha) + B_i\sin(i\alpha)] \quad (2)$$

$$G_i = \sqrt{(A_i^2 + B_i^2)} \quad (3)$$

$$P_i = \arctan \frac{B_i}{A_i} \quad (4)$$

The zero-order component A_0 describes the mean peak response rate for all directions of movement. Thus, it reflects the average sensitivity (S) of the cell to visual stimulation and can be used as a measure of the general excitability of a cell on which all specific directional and orientational modulations are superimposed. [In a previous description of the SDO-analysis (Wörgötter and Eysel, 1987) the S component has been associated with the 'spontaneous activity' of a cell—this is incorrect. According to the theory of discrete Fourier analysis the zero order component describes the mean value of the sampled data points (see eq. 3.2 in Oppenheim and Schafer, 1975). Thus, the S component reflects the mean peak height of all histograms, which can be interpreted as the average sensitivity (S) of the cell to a given visual stimulus.] S describes the mean peak response rate, which is different from the maintained discharge. Note that the maintained discharge rate cannot be directly obtained from SDO-analysis but requires an additional measurement without the presence of the stimulus. As for the determination of half-width-at-half-height (HWHH) and the direction index (DI), the maintained discharge has to be subtracted prior to SDO-analysis.

D and O components are normalized with respect to S, so that all D and O values can be interpreted as a percentage of the S value. This compensates for shrinkage or expansion of a polar plot, which is reflected in the S component allowing a valid comparison of D and O for different cells. Therefore, the non-normalized S component is defined in 'Impulses per second' (I/s), D and O in % of S, whereas PD and PO are given in degrees ($0° \leq PD < 360°$, $0° \leq PO < 180°$). As seen in eq. 2, D and O can reach values above 100% of S.

In a statistical analysis the relative contribution of the higher order components (third and above) was compared to the S, D and O (zero to second order) components. It was found that about 75% of the power contents in the spectrum are covered by the zero- to second-order Fourier components. This shows that a tuning curve can be approximated with good accuracy using only the S, D and O components.

Any determination of preferred directions or preferred orientations requires a sufficient tuning strength. Simulating tuning curves applying

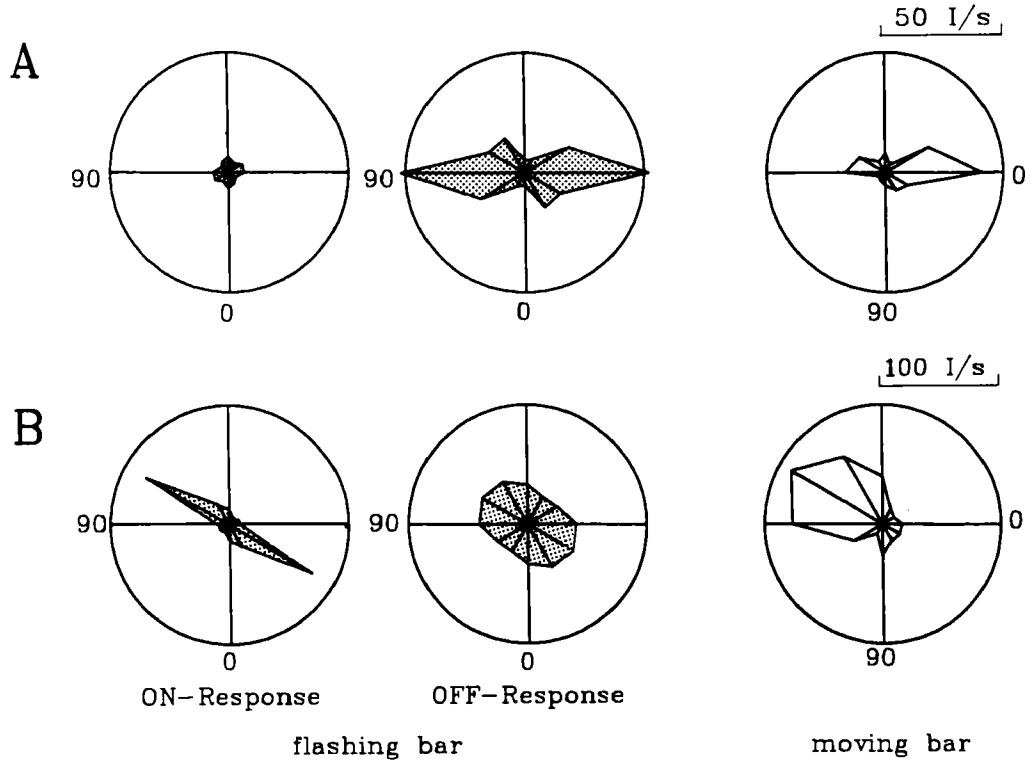

FIG. 4. Examples of simple cell responses to flashing and moving bars for cells where a functional relationship between the different O components was revealed. Polar plots resulting from flashing bar stimulation (shaded) are plotted with respect to the orientation angle and are, therefore, orthogonal to their moving bar counterparts. (A) Cell with predominant OFF response: maintained discharge 0.8 I/s, S = 20.1 I/s, D = 0.0 (irrelevant), O = 88.3%, PO = 92.4°; the results for the moving bar are: S = 11.6 I/s, D = 56.74%, O = 81.7%, PD = 345.5°, PO = 91.7°.O and PO values for flashing and moving bar stimulation are similar.(B) Cell with clear ON and OFF response: maintained discharge 3.2 I/s, S_{ON} = 25.0 I/S, S_{OFF} = 34.8 I/s, D_{ON} = D_{OFF} = 0.0% (irrelevant), O_{ON} = 101.6, O_{OFF} = 26.5%, PO_{ON} = 124.2°, PO_{OFF} = 123.3°. A moving bar yields: S = 33.3 I/s, D = 89.1%, O = 57.7%, PD = 209.2°, PO = 122.9°. For both stimulus types the PO values are nearly equal and the tuning strength of the response to a moving bar (O = 57.7%) can be regarded as average between both (O_{ON} = 101.6, O_{OFF} = 26.5%) tuning strengths resulting from flashing bar stimulation.

eq. 2 and adding random noise we observed that even at high noise levels (ratio of signal to noise approximately 0.75) PD and PO can be determined reliably for D and O values above 20 or 10% respectively. Therefore, in any statistical comparison of PD or PO values throughout this study, only those cells with D above 20% or O above 10% are included. The factor of two between these thresholds results from the fact that two data points define the response for each orientation, but only one point for each direction in the polar plot. Thus, for each orientation angle twice as many data points are used for the computation of O and PO than for D and PD and, therefore, the average accuracy of O and PO is twice that for D and PD. In general, the accuracy of determination of any component is parallel to the order of the component.

Commonly used methods for the determination of tuning strengths

For a comparison of the results from SDO-analysis with the commonly used parameters for the strength of directional and orientational tuning the DI (eq. 5; see also Orban, 1984) and the HWHH parameter were computed (Fig. 2C). The maintained activity level is determined prior to stimulus onset and is subtracted before determining the parameters (dashed line in Fig. 2C).

$$DI[\%] = 100 \times \frac{(IR_{PD} - IR_{NPD})}{IR_{PD}} \quad (5)$$

IR_{PD} and IR_{NPD} are the impulse rates of the preferred direction and the non-preferred direction. IR_{PD} is determined conventionally (Orban, 1984) from the highest response peak without any fitting procedure of the complete tuning curve and IR_{NPD} is given by the response peak of the direction opposite to PD. The preferred orientation is by definition 90° apart from the preferred direction.

For the calculation of the HWHH orientation tuning parameter, as indicated in Fig. 2C, the data points forming the highest peak in the tuning curve were fitted by two regression lines; the tuning is then determined by calculating half the length of a line parallel to the abscissa which intersects the regression lines at half their peak height, thus defining HWHH in degrees (Orban, 1984).

In Figure 2C,D the results from the commonly used parameters and SDO-analysis can be compared. Several drawbacks of the commonly used methods are uncovered in this figure. The actual average comparability of the different methods will be described in the first paragraph of the Results section.

The directional and orientational tuning, as measured by the DI and the HWHH orientation tuning parameter, are both low. For the DI this is because the response in the non-preferred direction of the simple cell is larger than expected from extrapolation of the responses to adjacent directions. Thus, minor changes in the response to the non-preferred direction, which could be induced just by the response variability of cortical cells, strongly affect the DI but not the D

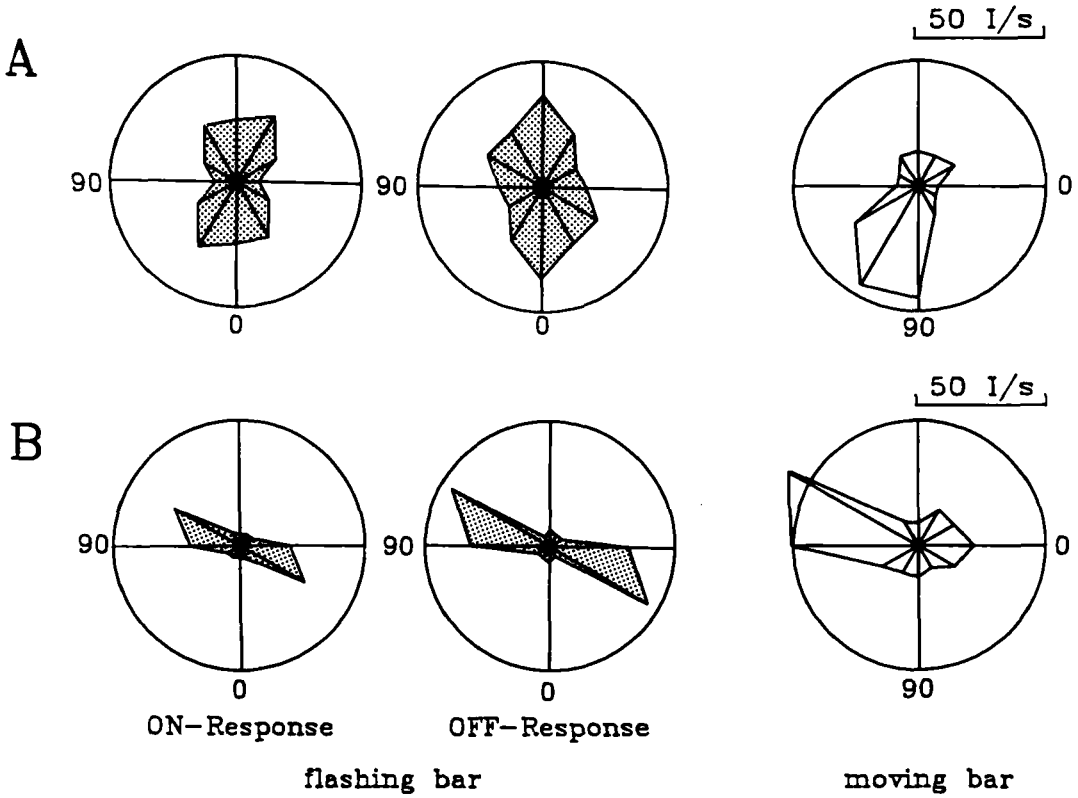

FIG. 5. Examples of cell responses to flashing and moving bars for cells without functional relationship between the different O components. (A) Simple cell with an O component from the moving bar stimulation that exceeds both O components (O_{ON} and O_{OFF} from the flashing bar stimulation. Maintained discharge 1.4 I/s. The results for the moving bar are: S = 18.3 I/s, D = 62.0%, O = 67.8%, PD = 113.9°, PO = 21.7°; for the flashing bar: S_{ON} = 19.8 I/s, S_{OFF} = 23.7 I/s, D_{ON} = D_{OFF} = 0.0% (irrelevant), O_{ON} = 46.6%, O_{OFF} = 34.5%, PO_{ON} = 6.6°, PO_{OFF} = 169.9°. (B) Complex cell. the moving bar O component is smaller than both flashing bar O components. Maintained discharge 3.6 I/s, a moving bar yields: S = 21.1 I/s, D = 55.1%, O = 68.7%, PD = 198.8°, PO = 101.3°. A flashing bar yields: S_{ON} = 11.7 I/s, S_{OFF} = 16.4 I/s, D_{ON} = D_{OFF} = 0.0% (irrelevant), O_{ON} = 95.8%, O_{OFF} = 112.6%, PO_{ON} = 109.1°, PO_{OFF} = 107.9°.

component from SDO-analysis because its calculation depends on all directions of movement.

The preferred direction is 210°, as determined by the strongest response (Fig. 2C). The response at 240° is nearly as strong as at the preferred direction and the results from SDO-analysis show that PD of this cell is greater than 210°. The PO value is 134° and thus is not exactly 90° apart from PD. This effect is even stronger for more lopsided tuning curves. Since the phase difference between PD and PO is not confined to 90°, this results in a sufficient approximation of lopsided curves by SDO-analysis.

The HWHH orientation tuning parameter is also affected by the similar responses for 210° and 240°, because the slope of the regression line on the right side of the peak is comparatively flat. Due to the coarse orientation steps used to record the polar plots, the stimulus orientation with maximum response could have been skipped. This leads to too flat a right regression line and consequently to an underestimate of the sharpness of the orientational tuning. Here, this resulted in a tuning of HWHH = 33° for the simple cell, which is high above the expected value for simple cells reported previously in literature (see Table 7/1 in Orban, 1984). However, SDO-analysis performs an averaging process over all data points in the polar plot and is less affected by this particular source of error.

In general, only two data points per period are sufficient to retrieve a frequency with Fourier analysis (Sampling Theorem). Sampling steps of 30° provide 12 (6) data points on the full period of the direction (orientation) domain, hence a rather large oversampling. Thus, the results from SDO-analysis are much more robust as compared to the commonly used methods and the interpolation effect achieved with SDO-analysis also justifies the use of the rather coarse 30° orientation steps during recording.

Determination of the least difference (LD) for PD or PO

PD and PO are defined in degrees and as an indication of the difference between values obtained by different methods the least difference within a circle can be calculated; for instance for PD values of $PD_1 = 350°$ and $PD_2 = 10°$ the least difference would be 20° rather than 340°.

Histological verification

Animals were fixed by intra-arterial vascular perfusion in deep anaesthesia at the end of each experiment with 4% phosphate-buffered paraformaldehyde (pH 7.4). Electrode tracks were determined from electrocoagulations in frozen sections of 50 μm counter-stained with Cresyl Violet.

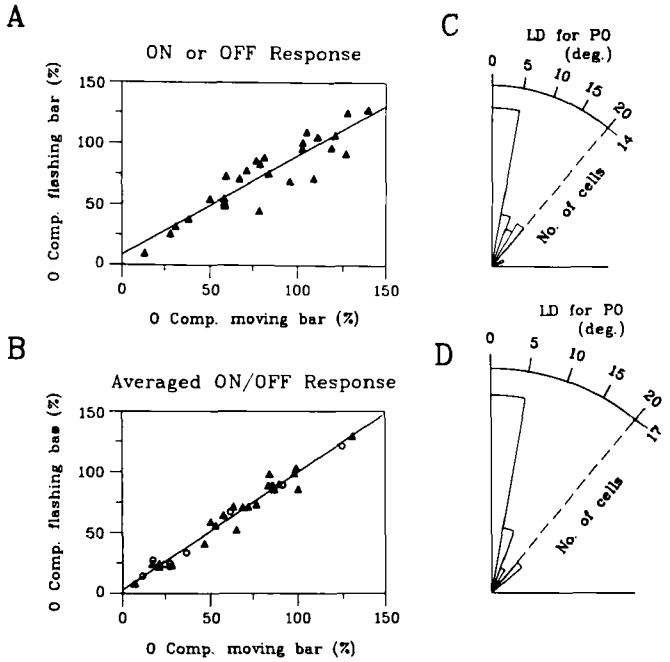

FIG. 6. (A and B) Correlation of the orientation tuning resulting from moving and flashing bar stimulation by plotting the respective O components for each stimulus against each other. Simple cells are indicated as filled triangles, complex cells as open circles. The border value for the calculation of linear regression lines between correlated and non-correlated has arbitrarily been set to $r = 0.5$. (C and D) Determination of the differences in the preferred orientations resulting from both stimuli calculating the absolute least differences (LD) for PO. Their distribution is shown only for orientated cells, i.e. for cells with O > 10% of S. (A) The graph shows 27 simple cells (no complex cells) with either ON or OFF response from which the respective O components (flashing bar) were plotted against O from the moving bar. Linear correlation: slope = 0.82, Y intercept = 7.13, $r = 0.91$. (B) Cells with ON and OFF responses: 23 simple, 9 complex cells. Included were all cells with an O component resulting from the moving bar stimulation which was intermediate to both O components from the flashing bar stimulation. The flashing bar ON and OFF O components were averaged and the result was plotted against the moving bar O component. Linear correlation: slope = 0.98, Y intercept = 1.55, $r = 0.98$. (C) Distribution of absolute least differences (LD) for PO for the cells in (A). The mean absolute LD is 8.4°. (D) Distribution of absolute least differences (LD) for PO for the cells in (B) with mean absolute LD of 7.2°.

Results

Comparison of D and O from SDO-analysis with the DI and the HWHH orientation tuning parameter

A moving bar stimulus was applied in 143 simple and 106 complex cells. To show the relationship between the commonly used parameters (DI and HWHH) and the results from SDO-analysis the results from both types of analysis are plotted against each other in Figure 3A,B. Both plots are monotone with a relatively small scatter. The scatter is probably introduced by the response variability of the cortical cells, which affects the measurement of the DI and HWHH orientation tuning parameters much more (see Discussion) than the parameters from SDO-analysis. Increasing D results in an increasing direction index, whereas with increasing O the orientation tuning measured by HWHH is reduced. In general, this shows that the commonly used parameters and the parameters from SDO-analysis are mutually predictable, and, therefore, can be replaced by each other.

The DI and HWHH orientation tuning parameter can be obtained from the SDO-parameters with the following empirical equations obtained by logarithmical regression:

$$DI = 60.9 \log_{10}(D) - 38.7 \quad (6)$$

$$HWHH = -63.1 \log_{10}(O) + 137.9 \quad (7)$$

In both cases the correlation, r, was found to be better than 0.88.

Directional and orientational tuning is stronger, on average, for simple cells than for complex cells (Henry *et al.*, 1973; Rose and Blakemore, 1974; Heggelund and Albus, 1978; Kato *et al.*, 1978; see also Orban, 1984) and a very strong direction and orientation specificity is found only in simple cells. With this exception, for both cell classes the whole range of directional and orientational tuning strength is covered. Several cells displayed very little orientation tuning (Fig. 3B, O component ≤ 20%) and most of them had complex receptive fields.

With standard methods the angle of stimulus presentation with the strongest response defines the preferred direction and the preferred orientation. Thus, for all cells, PD (and PO) values were determined by the strongest response and compared to PD (and PO) as computed by SDO-analysis. Only cells with D above 20% or O above 10% are considered as directed and oriented and are included in the histograms (see section on methods). Figure 3C and D shows the distribution of the least differences for PD (Fig. 3C) and for PO (Fig. 3D) determined by the two different approaches. The mean least differences are close to zero and, as expected, the standard deviation for the least difference for PD is twice that for PO. The low mean values indicate that the standard methods and SDO-analysis on average lead to the same results for PD and PO.

Responses to moving bars and stationary flashing bars

Comparison of the O and PO values

Sixty-six simple and 33 complex cells were tested with moving and flashing bars. The O components were determined for the ON and OFF response independently and compared to the O component in response to a moving bar. Three groups of response behaviour could be distinguished:

(i) In the first group all cells showed a pronounced difference between the ON and OFF response strength. For these cells the orientation tuning strength of the more prominent response as determined by the flashing bar was strongly correlated to the O component for the moving stimulus. The cell in Figure 4A, for instance, showed only an OFF response, with an O component of 88.3%; the O component as revealed by the moving bar (O = 81.7%) was nearly the same.

(ii) In the second cell group the orientation tuning strength elicited by a moving bar was similar to the average between both ON and OFF O components evoked by the flashing bar. This is demonstrated by the cell in Figure 4B, which had an O component of 101.6% for the ON response and of 26.5% for the OFF response. The O component for the moving bar was 57.7%, which is close to the arithmetic mean of both flashing bar orientation components.

(iii) The third group of cells showed clear ON and OFF responses to a flashing bar but the O component resulting from moving bar stimulation could not be directly predicted from the flashing bar O components (Fig. 5). The O components displayed by the cells from flashing bar stimulation were either smaller (Fig. 5A) or larger (Fig. 5B) than the moving bar O component.

The PO values for flashing and moving bar stimulation were nearly equal (Figs 4 and 5) and the axis of preferred movement of a long bar was approximately orthogonal to the orientational axis for all cells.

In Figures 6A,B and 7A,B, the O components elicited by flashing and moving bars are plotted against each other for cells of the groups described above. In Figures 6C,D and 7C,D, the distributions of the absolute least-differences are shown next to the graphs of the O components.

(i) For cells of the first group (Fig. 6A) the only existing O component (ON or OFF) was plotted against the moving bar O component and a good linear correlation is obtained ($r = 0.91$). Only simple cells were found in this group.

(ii) The second group of cells (Fig. 6B) included those with an O component elicited by the moving bar that fell in between both ON and OFF flashing bar O components. The arithmetic mean of the O components for the ON and OFF response was plotted against O resulting from the moving bar stimulus and the graph shows that the two measures are strongly correlated ($r = 0.98$). Simple cells also predominated in the second group and only a few complex cells were found (Fig. 6B, open circles).

(iii) Within the third group, the O components from moving or flashing stimuli showed no linear correlatoin ($r < 0.5$). Cells included in Figure 7A,B displayed ON and OFF O components in response to a flashing bar that were either greater or smaller than the respective O component evoked by a moving bar. Simple cells in this group usually had ON and OFF flashing bar O components that were lower than the O component resulting from a moving bar (mean O components for simple cells: $O_{movingbar} = 77.5\%$, $O_{flashingbar} = 44.0\%$, Fig. 7A). Thus, for these cells the orientation tuning is strengthened when stimulated with a moving, rather than a flashing, bar. This predominance is less pronounced for complex cells (Fig. 7B, mean O components: $O_{movingbar} = 48.1\%$, $O_{flashingbar} = 32.8\%$). For the cells shown in Figure 7, no clear difference in the PO values of ON and OFF responses could be detected and they are, therefore, averaged prior to the calculation of the least-difference.

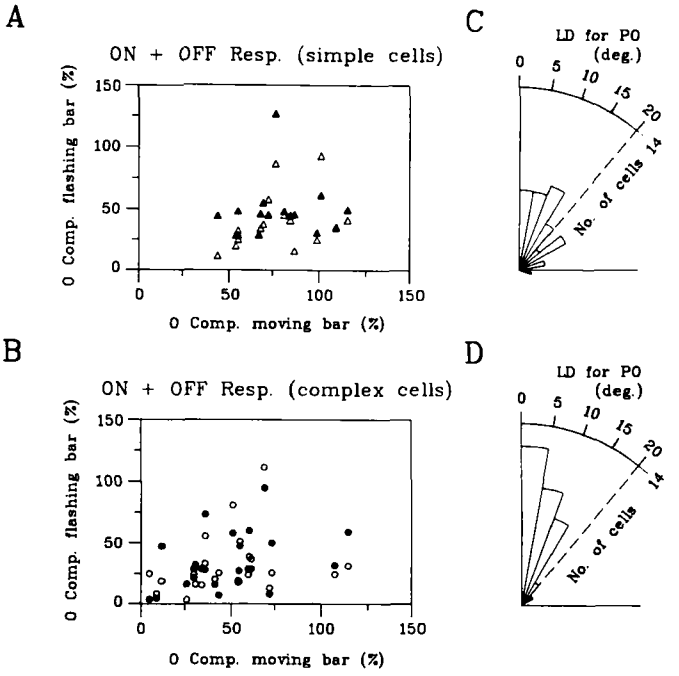

FIG. 7. Orientation tuning for flashing versus moving bar in 16 simple (A) and 24 complex (B) cells with values of both ON and OFF flashing bar O components either above or below that of the moving bar. Both ON (filled symbols) and OFF (open symbols) O components are plotted against the moving bar O component (A,B). However, no linear correlation ($r < 0.5$) is obtained for these cells, in contrast to those of Fig. 6. Absolute least differences for PO are shown in (C,D). (A) Simple cells. Orientation tuning is stronger for the moving than for the flashing bar. Mean O component for moving bars = 77.45±21.16%, mean O component for flashing bars = 44.03±23.42%. (B) Complex cells. No predominance for moving or flashing bar orientation tuning can be detected. Mean O component for moving bars = 48.05±27.95%, mean O component for flashing bars = 32.84±23.40%. (C) Distribution of absolute least differences (LD) for PO for the simple cells in (A) with mean absolute LD of 15.3°. (D) Distribution of absolute least differences (LD) for PO for the complex cells in (B) with mean absolute LD of 8.8°.

The histograms of the absolute least-differences (Figs 6C,D and 7C,D) show that the PO values obtained with a flashing and a moving bar are nearly identical for all cell groups.

Comparison of the S components

It has been often suggested that for visual cortical cells in general, and for complex cells in particular, a moving bar stimulus is more effective than a flashing bar (Bishop *et al.*, 1971; Henry *et al.*, 1974a; Hubel and Wiesel, 1962). To test this, the general sensitivities (S) for simple and complex cells were determined for both types of stimuli and plotted against each other (Fig. 8A,B). Subdividing the cells according to the groups described above did not show any clear differences between the groups and, therefore, only the distinction between simple and complex cells was made. The graphs show that for simple, as compared to complex, cells a preference for flashing bars exists. To eliminate the influence of general differences in the responsiveness of simple and complex cells, a flashing bar index is defined, by analogy with the 'dot index' used by Skottun *et al.* (1988), as the mean flashing bar S-component divided by the mean moving bar S-component. The index was approximately 1.40 for simple cells and 0.9 for complex cells, supporting the view that a flashing bar does not drive complex cells as efficiently as simple cells.

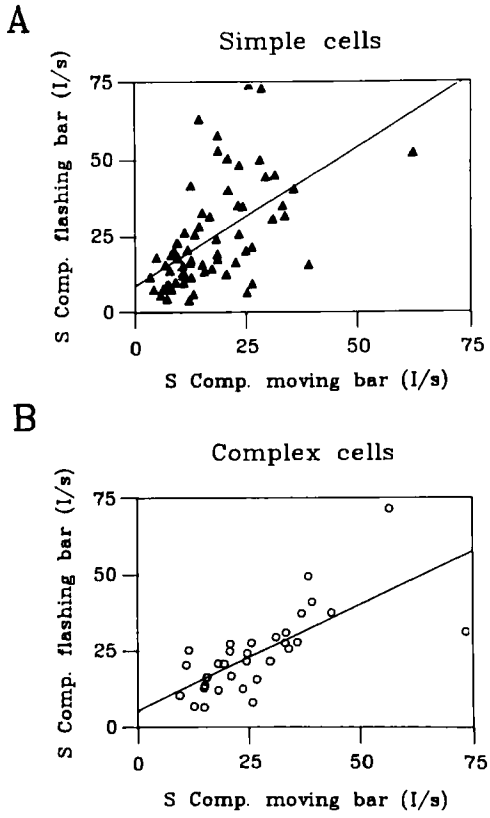

FIG. 8. Comparison of the S components from moving and flashing bar stimulation for 66 simple (A) and 33 complex cells (B). The correlation between the S components is weak in both cases. (A) Simple cells. Average S components for flashing bar: S = 24.2 ± 17.5 I/s; for moving bar: S = 17.3 ± 10.5 I/s. Ratio: $\frac{S_{flashingbar}}{S_{movingbar}}$ = 1.40; linear corelation: slope = 0.91, Y intercept = 8.40, r = 0.55. (B) Complex cells. Average S components for flashing bar: S = 24.2 ± 13.1 I/s; for moving bar: S = 26.7 ± 19.3 I/s. Ratio: $\frac{S_{flashingbar}}{S_{movingbar}}$ = 0.90; linear correlation: slope = 0.69, Y intercept = 5.30, r = 0.72.

Responses to moving bars and rotating noise fields

Response types

A comparison of the responses to moving bars and rotating noise fields was performed in 33 simple cells and 26 complex cells. Figure 9 shows

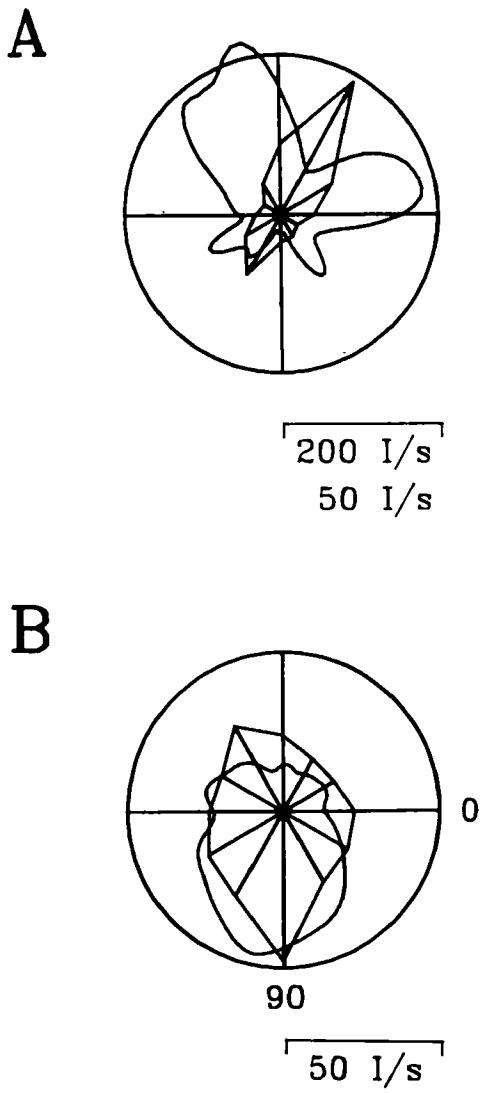

FIG. 9. Polar plots of a simple (A) and a complex cell (B) subjected to noise (smooth plot) and bar stimulation (other plot). (A) Simple cell. Noise stimulation renders a bimodal polar plot (angular velocity 72°/s, bin size 10 ms, 40 sweeps, angular resolution 0.7°, linear velocity 3.12°/s) with maintained discharge 3.8 I/s, S = 24.4 I/s, D = 57.7%, PD = 278.4°. The peak of the polar plot for the bar stimulation (S = 61.1 I/s, O = 76.3%, D = 49.6%, PD = 295.4%) is centred between both peaks in the bimodal polar plot. Similar D and PD values occur for the responses to bar stimulation as for the noise stimulation. (B) Complex cell. Noise stimulation leads to a unimodal polar plot (angular velocity 36°/s, bin size 50 ms, 20 sweeps, angular resolution 1.8°, linear velocity 9.4°/s) with maintained discharge 10.4 I/s, S = 36.9 I/s, D = 70.1% and PD = 110.5°. Bar stimulation results in S = 26.5 I/s, O = 27.1%, D = 24.3% and PD = 115.1°. The orientational component from the noise stimulation can be ignored. Thus, only the PD value is similar to PD from bar stimulation, whereas a large difference between the D components is observed.

examples of the two response types that could be distinguished. Rotation of a noise field leads to a polar plot with two major response peaks of nearly equal height for the simple cell in Figure 9A (smooth curve) so that its polar plot appears bimodal. By contrast, the polar plot obtained with the moving bar has only a single major response peak centred between the two peaks of the noise response curve. For this cell, the sensitivity to a moving bar (S = 61.1 I/s) was approximately three times that of the noise field (S = 24.4 I/s). By visual inspection of the polar plots it is obvious that the preferred directions for moving bar and rotating noise are quite different. However, the PD values calculated by SDO-analysis were 295.4° and 278.4° respectively. The surprising similarity of both PD values can be explained by the integrative properties of SDO-analysis, which uses the full set of measured cell responses to determine the directional preference. In the calculation of PD for the noise response, this integrative process is predominated by the major response peaks, thus PD is approximately equal to the vectorial average of the directions of both peaks. Visual inspection of the polar plot shows that this 'average preferred direction' corresponds to the PD obtained with the moving bar.

The generally accepted definition of the term 'preferred direction' refers to the particular direction of stimulus movement that elicits the strongest response. Thus, for bimodal cells, PD from SDO-analysis of a noise response is not directly related to the commonly defined preferred direction, but describes the average preferred direction resulting from both response peaks. A central result from this observation is that the PD value obtained by moving bar stimulation can be quantitatively predicted by SDO-analysis from the rotating noise response, which otherwise would not be possible.

There is also no clear difference for this cell (Fig. 9A) between the strength of the directional tuning (D) elicited by noise (D = 57.7%) and bar (D = 49.6%).

For the complex cell in Figure 9B, the polar plots for rotating noise and a moving bar have a single major response peak and a unimodal appearance. The sensitivities for noise (S = 36.9 I/s) and bar (S = 26.5 I/s) are nearly equal, as are the PD values (115.1° for the rotating noise and 110.6° for the moving bar). However, the D components are quite different (noise: D = 70.1%, bar: D = 24.0%).

Bimodal responses were normally generated by higher velocities of the rotating noise field, while unimodal responses were obtained with lower velocities (Hammond and Smith, 1983). In many cases, the response types (bi- or unimodal) could be changed with the stimulus velocity. For further analysis all cells were classified as either bimodal

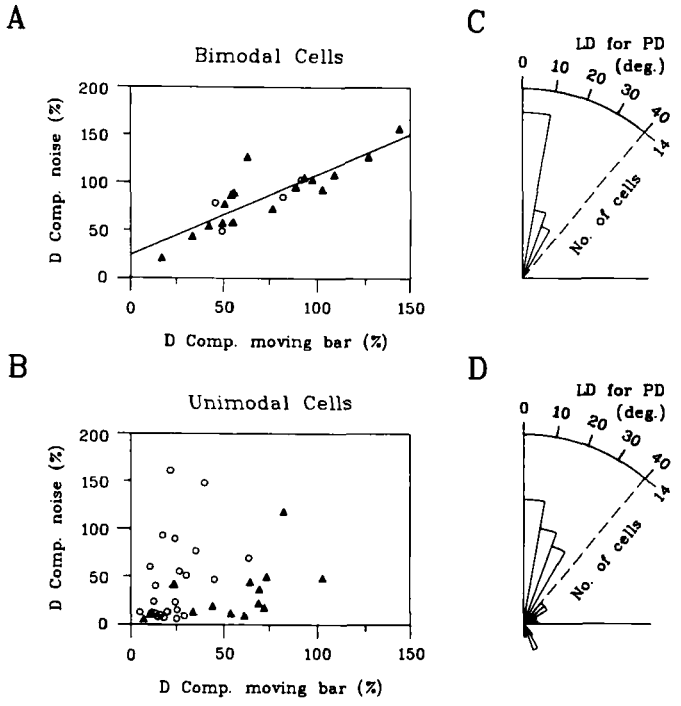

FIG. 10. A comparison of the D components resulting from moving bar and rotating noise stimulation for bimodal (A) and unimodal cells (B) is shown. Filled traingles = simple cells; open circles = complex cells. Determination of the differences in the preferred directions resulting from both stimuli calculating the absolute least differences (LD) for PD is shown in C and D. Their distribution is shown only for directed cells, i.e. for cells with D > 20% of S. (A) Bimodal cells. A linear correlation between both D components with Y intercept = 23.9, slope = 0.85 and r = 0.86 is obtained. (B) Unimodal cells. No linear relationship can be detected. Complex cells on average show a higher tuning strength for noise stimuli, simple cells for bar stimuli. (C) Distribution of absolute least differences (LD) for PD for the bimodal cells in (A) with mean absolute LD of 10.7°. (D) Distribution of absolute least differences (LD) for PD for the unimodal cells in (B) with mean absolute LD of 39.7°.

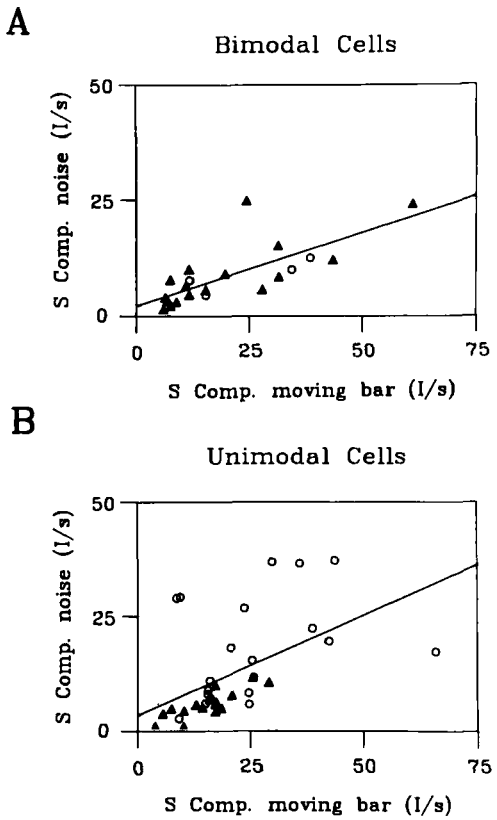

FIG. 11. Comparison of the S components from moving bar and rotating noise stimulation for bimodal (A) and unimodal cells (B). Filled triangles = simple cells; open circles = complex cells. A weak linear correlation is obtained in both cases. (A) Includes 17 simple and 4 complex bimodal cells. Linear correlation: slope = 0.32, Y intercept = 2.13, r = 0.74. (B) Unimodal cell group consisting of 16 simple and 22 complex cells. Linear correlation: slope = 0.44, Y intercept = 3.39, r = 0.52.

or unimodal according to their response characteristic to visual noise at optimal velocity. In this sense the percentage of unimodal cells (64.4%) was nearly twice that of the bimodal cells (35.6%). The bimodal sample contained mostly simple cells (81.0% simple cells, 19% complex cells) while the unimodal sample was more equally divided (42.1% simple cells, 57.9% complex cells).

Comparison of the D and PD values

The D components elicited by the noise field are plotted against those evoked by the moving bar for bimodal (Fig. 10A) and unimodal (Fig. 10B) cells. A linear correlation can be seen only for the bimodal cells (Fig. 10A, $r = 0.86$). The unimodal group showed no correlation between noise and bar D components for either simple or complex cells and by inspection of the average D components it is obvious that simple cells displayed a stronger tuning when stimulated with a moving bar (average $D_{movingbar} = 50.1\%$) rather than with rotating noise (average $D_{noise} = 32.0\%$). However, the reverse is true for complex cells, with an average D of 47.3% for noise and 23.9% for bar stimuli.

A comparison of the PD values that occur for the moving bar and the rotating noise field is shown in Figure 10C,D. From the absolute least differences for PD in bimodal (Fig. 10C) and unimodal (Fig. 10D) cells it is evident that both PD values display a high degree of similarity within each group. For the unimodal cells, the large value of the mean absolute least difference (39.7%) is mainly due to a small population of cells with large differences between both PD values; for the bimodal cells a very low mean absolute least difference of 10.7° is obtained.

Comparison of the S components

To estimate the general sensitivity of the cells to stimulation with moving noise or bar, the S component from SDO-analysis of the polar plots was determined. For bimodal and unimodal cells in Figure 11 the S components elicited by a rotating noise field is plotted against the S components from the moving bar stimulus. Within both cell groups a weak linear correlation between the two S components can be detected (Fig. 11A,B, $r = 0.74$, $r = 0.52$). The correlation coefficient in Figure 11B is substantially lowered by the scattered distribution of the complex cells.

It has been reported (Hammond, 1978) that simple cells cannot be driven by moving noise stimuli. To test this hypothesis, the average sensitivity S to moving bars and rotating noise was computed for simple and complex cells. The average sensitivity (S) to bars for simple cells was 18.5 I/s and thus was twice as high as the average sensitivity to the noise stimulus (9.6 I/s). In principle the same relationship between noise and bar S components was found for complex cells but the sensitivity for both types of stimuli was generally higher averaging 25.3 I/s for bar and 16.3 I/s for noise stimuli. The ratio between the mean noise and moving bar S components averaged 0.52 for simple cells and 0.64 for complex cells. This demonstrates that the higher sensitivity of complex cells reflects the difference in the general responsiveness of both cell groups rather than an enhancement of responses to noise.

Table 1 summarizes the results of the previous sections.

Discussion

Direction and orientation tuning of visual cortical cells were conventionally assessed with moving bars or edges (Hubel and Wiesel, 1962; Pettigrew *et al.*, 1968). However, the responses elicited by these stimuli confound direction- and orientation-dependent responses. To

TABLE 1. Comparison of cell numbers for simple and complex cells that show either linear correlation or no correlation between the tuning strengths elicited by different stimuli

		Flashing versus moving bar stimulus		
A)	correlated	$\frac{averageO_{flashingbar}}{averageO_{movingbar}}$	non-correlated	$\frac{averageO_{flashingbar}}{averageO_{movingbar}}$
Simple cells	50 (75.8)	0.90	16 (24.2)	0.57
Complex cells	9 (27.3)	0.97	24 (72.7)	0.68
Total	59 (59.6)		40 (40.4)	
B)		$\frac{averageS_{flashingbar}}{averageS_{movingbar}}$		
Simple cells		1.40		
Complex cells		0.90		
		Rotating noise versus moving bar stimulus		
C)	correlated	$\frac{averageD_{noise}}{averageD_{movingbar}}$	non-correlated	$\frac{averageD_{noise}}{averageD_{movingbar}}$
Simple cells	17 (51.5)	1.08	16 (48.5)	0.64
Complex cells	4 (15.4)	1.22	22 (84.6)	1.98
Total	21 (35.6)		38 (64.4)	
D)		$\frac{averageS_{noise}}{averageS_{movingbar}}$		
Simple cells		0.52		
Complex cells		0.64		

The numbers in brackets give the percentage values. Relative tuning strengths normalized with respect to the component elicited by a moving bar are also indicated. The central results are: (i) linear correlation occurs predominantly in simple cells. (ii) The S components for simple and complex cells are similar except for stimulation with a flashing bar. (iii) The orientation tuning for 'non-correlated' cells is significantly higher when stimulated with a moving bar. (iv) The directional tuning of 'non-correlated' complex cells is twice as strong with a moving noise field than with a moving bar.

separate these components, cells were tested with stimuli designed to elicit either the directional or the orientational component (Hammond and MacKay, 1975, 1977; Emerson and Gerstein, 1977; Hammond, 1978; Duysens and Orban, 1981; Emerson and Coleman, 1981; Kulikowski *et al.*, 1981; Heggelund and Moors, 1983; Camarda *et al.*, 1985a,b). Quantitative testing of simple and complex cells with moving versus flashing bars demonstrated that the response strength for both types of stimuli was similar (Duysens and Orban, 1981). It was also shown, at least for the preferred direction of movement, that the response to a moving bar could be linearly predicted from the responses to flashing bars in different receptive field regions (Emerson and Coleman, 1981). However, discrepancies between the number of subfields revealed by flashing or moving bars have been reported by other investigators (Camarda *et al.*, 1985a,b; Kulikowski *et al.*, 1981) and responses along the non-preferred direction seem to involve non-linear mechanisms (Emerson and Coleman, 1981). In view of this, the predictability of the response characteristic of cortical cells using different types of stimuli is still far from clear. In addition, only a few quantitative studies on direction (Hammond, 1978; Hoffman *et al.*, 1980) and orientation (Henry *et al.*, 1974a,b; Peterhans *et al.*, 1985) that compare the tuning strength revealed by different types of stimuli have been performed, and none of these were based on SDO-analysis (Wörgötter and Eysel, 1987).

Comparing SDO-analysis with the commonly used methods DI and HWHH

Over a wide range an approximately logarithmical relationship between the commonly used parameters and those from SDO-analysis was found with only a small range of scatter (Fig. 3A,B; eqs. 6 and 7). The deviations from a linear behaviour that occur for the graph of DI versus D (Fig. 3A) can be explained by the non-linear behaviour of the DI (eq. 5). In the comparison of the HWHH tuning parameter with O (Fig. 3B) deviations from linearity could be observed mainly for cells with low orientation tuning. For these cells the tuning curve has only one broad response peak. However, a reliable calculation of the HWHH parameter generally requires two peaks, one centred at the preferred direction and the other at the non-preferred direction, because of the 180° periodicity of oriented light bars. Therefore, the regression lines fitted onto the data points forming only a single response peak extend into regions of the tuning curve where the second peak would normally be expected. As a result, this parameter is overestimated in comparison to the O component from SDO-analysis, which probably leads to the steep non-linear descent of the curve in Fig. 3B at low orientation tuning. Finally, to explain non-linear behaviour, D and O are limited to a certain range (i.e. D, O < 170% of S, see Fig. 3A and B) so that no negative impulse rate values occur. The results from the comparison of PD or PO with the values of preferred direction or preferred orientation respectively, as determined conventionally from the strongest response, also show a high similarity (Fig. 3C,D).

It can be concluded that the DI and the HWHH orientation tuning parameter can be completely replaced by the results of the SDO-analysis without loss of information. Since SDO-analysis uses the full data set of the tuning curve for the computations, it is much more reliable and robust against either the use of coarse orientation steps while recording a tuning curve and/or the response variability of cortical cells. This can already be judged from the example cell shown in Figure 2.

Response types to moving and flashing bars

Using SDO-analysis our results support the finding (Duysens and Orban, 1981; Emerson and Coleman, 1981) that the general responsiveness (S) of cortical cells is similar when stimulated with flashing or moving bars (Fig. 8A and B). However, as judged by the ratio of the averaged S components there is a tendency for simple cells to respond more vigorously to a flashing bar than complex cells. Complex cells also respond quite phasically to flashed stimuli (Movshon *et al.*, 1978a). Together, these results may account for the earlier statements that complex cells can hardly be driven by flashing stimuli (Hubel and Wiesel, 1962; Bishop *et al.*, 1971; Henry *et al.*, 1974a). For the majority of simple cells (Fig. 6A,B) the tuning strengths for flashing and moving bars are linearly related and can, therefore, be mutually predicted. This behaviour is clearly seen in those cells for which the moving bar induces a process like an averaging of the tuning strength from the different ON and OFF subfields (Fig. 4B). However, tuning strength for orientation in response to a moving bar cannot always be directly predicted from the results of flashing bar stimulation. For several simple cells (Fig. 7A) and for the majority of complex cells (Fig. 7B) no direct correlation between the O components from moving or flashing bars could be obtained. The number of simple cells showing this type of behaviour was 22% of the sample and this group might be contained within the 32% of 'non-linear' simple cells observed by Movshon *et al.* (1978b). In our results, cells with no linear correlation showed a more pronounced orientation tuning when subjected to a moving bar than when subjected to a flashing bar. Stimulus motion is normally regarded to be essential only for the directional tuning of a cell. In this case, however, movement of the bar seems to amplify the mechanisms responsible for the orientation tuning. This could be due to a symmetrical influence induced by motion that enhances the responses in both the preferred and the non-preferred direction, resulting in an enhanced orientation tuning rather than in a changed directionality. Thus, a valid separation between direction and orientation by the use of different types of stimuli is not possible for cells showing this behaviour. For complex cells (Fig. 7B) the situation is more complicated and no qualitative prediction of the O components is possible. However, a minority of complex cells (28%) appeared to perform the 'averaging process' between ON and OFF O components (Fig. 6B) described above. These cells may belong to the group of complex cells that showed linear spatial summation within their receptive fields. Palmer and Davis (1981) reported that about 50% of complex cells have this property.

For all cells we found a fairly good correspondence between the preferred orientations determined by a moving or a flashing bar (Henry *et al.*, 1974a,b; Heggelund and Albus, 1978).

Response types to moving bars and rotating noise fields

Noise stimuli were used to determine the motion-dependent component in the response of cortical cells (Hammond and MacKay, 1975; Orban, 1975) and were first applied in a systematic way by Hammond and MacKay (1977). We used a rotating noise field to stimulate the cells. According to Schoppmann and Hoffmann (1976) this method does not result in significantly different tuning curves than those obtained with a noise field moving linearly in different directions across the receptive field. Similar to the results of Hammond and MacKay (Hammond and MacKay, 1977; Hammond, 1978), we have demonstrated bimodal and unimodal response types (Fig. 9). Additionally, it had been reported that simple cells cannot be driven effectively by noise stimuli (Hammond and MacKay, 1977). However, the noise indices we computed, which reflect the ratio of the S components for noise relative to bar responses, show a high degree of similarity for simple and complex cells (0.52 and 0.64 respectively). This agrees well with the

results of Skottun *et al.* (1988) who compared the responses to random dots and drifting gratings and found a 'dot index' of 0.43 for simple cells and of 0.55 for complex cells. The high degree of similarity between the indices of both cell classes indicates that the difference between the S components of simple and complex cells can largely be explained by a difference in the general responsiveness of cells in both classes rather than by a specific difference in sensitivity to noise stimulation.

A grouping between 'linearly correlated' and 'non-correlated' cells was revealed when comparing the D components in response to a moving bar or rotating noise stimuli (Fig. 10A,B). A linear correlation between the corresponding D components (Fig. 10A) occurred only in the cell group with a bimodal response characteristic. This group consisted mainly of simple cells. However, no clear predominance in directional tuning strength was found for either noise or bar stimuli for these cells. Nearly all complex cells showed a larger D component when stimulated with rotating noise than when stimulated with the moving bar; for simple cells belonging to the unimodal group the reverse is true. Thus, while for both cell classes the general sensitivity (S) for the bar is higher than for the noise stimulus, complex cells are more strongly tuned for the rotating noise field and only a subpopulation of simple cells is more strongly tuned for the moving bar.

The statement that simple cells cannot be driven efficiently by noise stimuli should thus be modified. The sensitivity, S, of both cell classes to rotating noise shows differences which are probably due to the different general responsiveness of the cells. Judged by the D components, for 50% of the simple cells moving noise is as specific a stimulus as a moving bar. The remaining 50% of simple cells were the only cells that showed a predominance in tuning strength for the bar stimulus.

The differences between our study and those of Hammond and MacKay (Hammond and MacKay, 1975, 1977; Hammond, 1978) could be due to differing cell classification schemes. Several cells were classified as belonging to the simple group using the modified ABCS scheme (Henry, 1977) which might otherwise have been regarded as complex cells by Hammond and co-workers (Hammond and MacKay, 1977; Hammond and Reck, 1980; Hammond and Smith, 1983). In addition, the difference in grain size of the noise stimulus between our studies and those of Hammond and co-workers, and the use of different anaesthetics, probably also contributes to the differences in the results.

A bimodal response characteristic to rotating noise was seen in about one-third of the cells at optimal stimulus velocity and the occurrence of a bi- or unimodal response characteristic in many cases could be changed with the velocity of the noise field (Hammond and Reck, 1980; Hammond and Smith, 1983). It has been reported that unimodal responses elicited at lower velocities are centred between the two peaks of a bimodal response evoked in the same cell at a higher speed. We found a similar relation between bar and noise stimuli; the response peak for a moving bar normally lies in between the two response peaks demonstrated with rotating noise (Fig. 9A).

It has recently been shown (Wörgötter and Eysel, 1989) that a moving dot elicits the strongest response along the receptive field long axis and, hence, orthogonal to the strongest response to a moving bar. Thus, two response components can be elicited in cortical cells when using appropriate stimuli (e.g. short bars) which can also result in a bimodal response characteristic (Wörgötter and Eysel, 1989). The different response components in a cortical receptive field may be driven depending on the stimulus type, but independently from each other. The response to a moving stimulus may, thus, result from an averaging process which involves both response components with different weights depending on the stimulus type. This effect could also underlie the generation of a bimodal response characteristic to noise.

SDO-analysis performs an 'averaging process' of the data points in the tuning curve, 'weighted' according to their direction vector. Thus, D and PD values computed from a bimodal response to noise and a bar response were strongly related and the bar response can be quantitatively predicted from the noise response applying SDO-analysis.

Concluding remarks

The majority of simple cells showed a linear correlation with a slope of about 1.0 between the respective S, D or O components, whereas for nearly all complex cells no linear correlation could be detected (Table 1). This shows that a subsequent presentation of stimuli apparently containing only one—the directional or orientational—component does not, in every case, lead to a functional separation of these components.

It should be noticed that for some cells the response characteristic to a moving stimulus can be reconstructed from the exact assessment of the responses within different zones in the receptive field (e.g. Kulikowski and Bishop, 1981). The aim of this study, however, was confined to simple stimulus types to gain an impression of the restrictions introduced by the most frequently used tests for cortical cells, rather than to demonstrate the limits of response predictability from every kind of possible stimulus.

It is generally agreed that different mechanisms underlie direction and orientation selectivity (Sillito, 1979, 1984; Hammond, 1978). However, for the cells that displayed no separation of direction and orientation by different stimulus types, a coupling of the mechanisms could exist, which would lead to a mutual enhancement of the D and/or O components when stimulated with a moving bar. This result is not entirely in agreement with previous findings that stimulus movement is not of particular importance for visual cortical cells (Duysens and Orban, 1981; Emerson and Coleman, 1981). Instead, we were able to show that stimulus movement may influence not the general sensitivity but rather the tuning strength in some simple cells.

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Abbreviations

D	directional tuning strength. First order gain component determined by Fourier analysis of tuning curves (eqs 2 and 3)
DI	direction index (eq. 5)
HWHH	Half-width-at-half-height orientation tuning parameter (see Fig. 2)
I/s	impulses per second
IR	impulse rate
LD	least difference between two angular values
NPD	non-preferred direction. Defined as the direction which is exactly opposite to the preferred direction (PD)
O	orientation tuning strength. Second order gain component determined by Fourier analysis of tuning curves (eqs 2 and 3)
PD	preferred direction. First order phase component determined by Fourier analysis of tuning curves (eqs 2 and 4)
PO	preferred orientation. Second order phase component determined by Fourier analysis of tuning curves (eqs. 2 and 4)
r	correlation coefficient.

S	General sensitivity to visual stimulation. Zero order gain component determined by Fourier analysis of tuning curves (eqs. 2 and 3)
SDO-analysis	analysis of direction and orientation based on Fourier analysis of tuning curves (eqs. 2–4)

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