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Axis of preferred motion is a function of bar length in visual cortical receptive fields

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Summary. The responses of 82 simple cells and 41 complex cells in area 17 of anesthetized and paralysed cats were examined with light bars of different length. For 84% of the simple cells and 66% of the complex cells the preferred axis of orientation of a *stationary flashing long bar* (orientational selectivity) and the preferred axis of movement of a small spot were parallel. As a consequence, the axis of maximal response to a *moving light spot* was mostly orthogonal to the optimal axis of a moving bar. Thus, a single cell responds to *two perpendicular axes of preferred movement* one for a long bar and one for a light spot, respectively. For both axes independent direction preferences could be distinguished. Additional preferred axes of movement between the two orthogonal extremes could be found with moving bars of intermediate lengths. This can be explained by the fact that cells with a pronounced response to a moving spot showed a strong tendency for intermediate bar length to elicit responses consisting of a superposition of both components. Therefore, decreasing bar length resulted in a gradual rotation of the preferred direction of movement from orthogonal to parallel with respect to the orientational axis, rather than to a mere widening of the tuning curve. Accordingly, the change in orientation selectivity with decreasing bar length is a regular transition from the orientation dependent response to a response type that depends only on the movement axis of the spot. Thus, in a simple model, the resulting response characteristic can be interpreted as an average of both components weighted according to the length of the stimulus.

Key words: Moving stimuli – Orientation specificity – Preferred axes – Spot-response-axis – Striate cortex – Cat

Introduction

Orientational tuning surely is one of the most extensively analysed features of visual cortical cells (Hubel and Wiesel 1962; Henry et al. 1974a, b; Rose and Blakemore 1974; Heggelund and Albus 1978; see also Orban 1984). Most of the studies have been performed using stationary flashing or moving elongated stimuli such as light bars. Less attention, however, has been focussed on the response characteristic elicited by moving light spots (Henry et al. 1974a, b; Rose 1977). In general the elongated axis of a light bar is used to define the cell's orientational axis. A small moving light spot, on the other hand, has no orientation but an axis of movement. Henry et al. (1974a) reported that the optimal axis of movement for a cell in response to a light spot is orthogonal to the orientational axis determined by a light bar (see also Orban 1984). This corresponds to a movement of the spot crossing the elongated receptive field in the shortest way possible. However, indirect indications exist that, at least for some cells, the strongest response obtained by a light spot could be evoked with movement parallel to the orientational axis (see Fig. 7C in Rose 1977). This would reflect movement of the spot along the elongated excitatory zone of the cell's receptive field.

These contradictory findings indicated that the types of response elicited by a moving spot could be subdivided in two different groups (orthogonal

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Offprint requests to: U.Th. Eysel (address see above) and parallel) with different underlying mechanisms. In particular, the question arises, as to whether there is a systematic relationship between the cell class (i.e. simple vs. complex) and the response characteristic of a cortical cell to a moving spot. The aim of the present study, therefore, was to quantify the response characteristic to moving spots of cells in cortical area 17 of the cat and compare this with either stationary flashing or moving bar stimuli of different length. Differences in a cell's response to a bar or a spot may indicate the involvement of different mechanisms, and provide some insight into the relationship between changing stimulus parameters and a cell's response characteristic.

Methods

The experiments were performed on six adult cats anesthetized with a mixture of halothane (0.2–0.5%) and $N_2O:O_2$ (70:30). During the 3–4 day experiments the animals were paralysed with a continuous infusion of d-tubocurarine (0.3 mg/kg·h) and gallamine triethiodide (4.0 mg/kg·h) in a glucose and ringer solution; blood pressure, body temperature and end-expired CO_2 were monitored and kept within normal limits during the experiment. The eyes were covered with zero-power contact lenses and refraction was corrected by lenses for a viewing distance of 38 cm. Recordings were made with glass-coated tungsten electrodes (Wörgötter and Eysel 1988) and the impulse activity of cells in area 17 of the visual cortex was studied. Cells were classified as simple or complex cells according to the classification scheme of Henry (1977), intermediate classes A and B were not distinguished. The receptive field regions were determined using handheld stimuli and the major ON and OFF zones plotted in order to allow accurate placement of the computer controlled stimuli. For visual stimulation light bars were generated by an image generator ('Picasso', Innisfree, USA) and were presented on an oscilloscope 38 cm in front of the cat's eyes moving back and forth across the receptive field region (4–10°/s). Stimulus orientation was changed by multiples of 30° using a pseudo random sequence. Width and contrast of the bars were adjusted to obtain the best possible response and then remained constant for the cell studied, whereas the stimulus length was varied over a range of 0.1–15° within the visual field. As an additional stimulus light spots with diameter equal to the width of the bars were applied and a stationary long flashing bar was used to determine the orientational axis of the recorded cell. For each type of stimulus a minimum of five sweeps at each orientation were recorded and peristimulus time histograms (PSTH's, bin width 200 ms) computed. Polar plots were obtained by plotting vector length as a function of peak impulse rate per second versus the direction of stimulus movement. For moving stimuli, directions in the polar plots are defined with regard to the directions of stimulus movement, for the stationary flashing bar, whereas, they are defined with regard to the orientation of the bar. Responses to a flashing bar have a 180° periodicity, however, in our representation these polar plots have been completed over the full field (360°) by adding the mirror image of the response and appear as shaded polar-plots in the figures. For a more detailed description of the experimental procedures see Eysel et al. 1988.

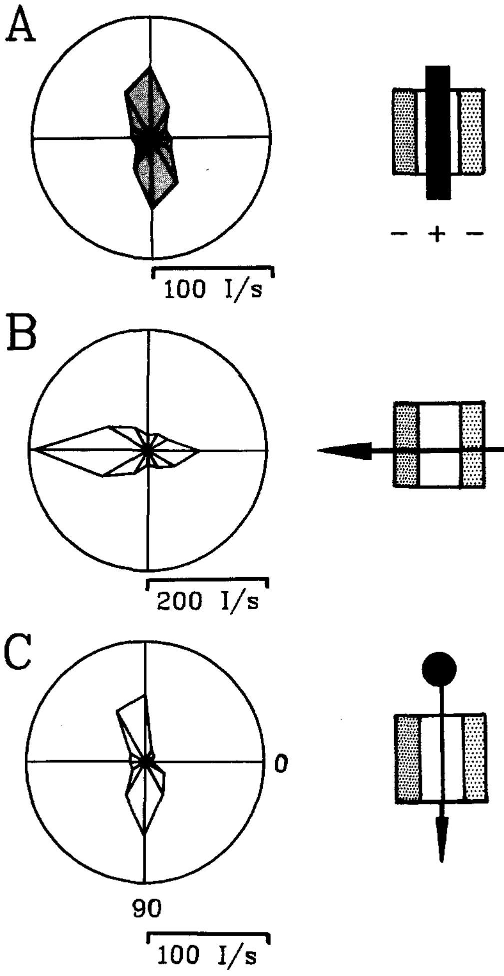

Fig. 1 A–C. Demonstration of the response components that can be elicited by different types of stimuli. A schematical plot of the optimal stimulus and the receptive field is shown to the right of the polar plots. **A** Response to a flashing bar (completed to 360° by adding the mirror image of the 180° periodical orientation-response) shows a clear preference for the 90° orientational axis. **B** Response to a long moving bar with preferred direction of 180°. **C** Response to a moving light spot with a preferred axis of 90°, which is the same as for the flashing bar. No direction preference for the moving spot can be detected

Results

Influence of different bar length on the axis of preferred motion

A total of 119 simple cells and 53 complex cells were recorded in layers II–VI of the striate cortex; of this sample 82 of the simple cells and 41 of the complex cells could be tested with different bar lengths to evaluate both spot and bar responses.

In order to avoid confusion and to introduce an unambiguous nomenclature in the descriptions

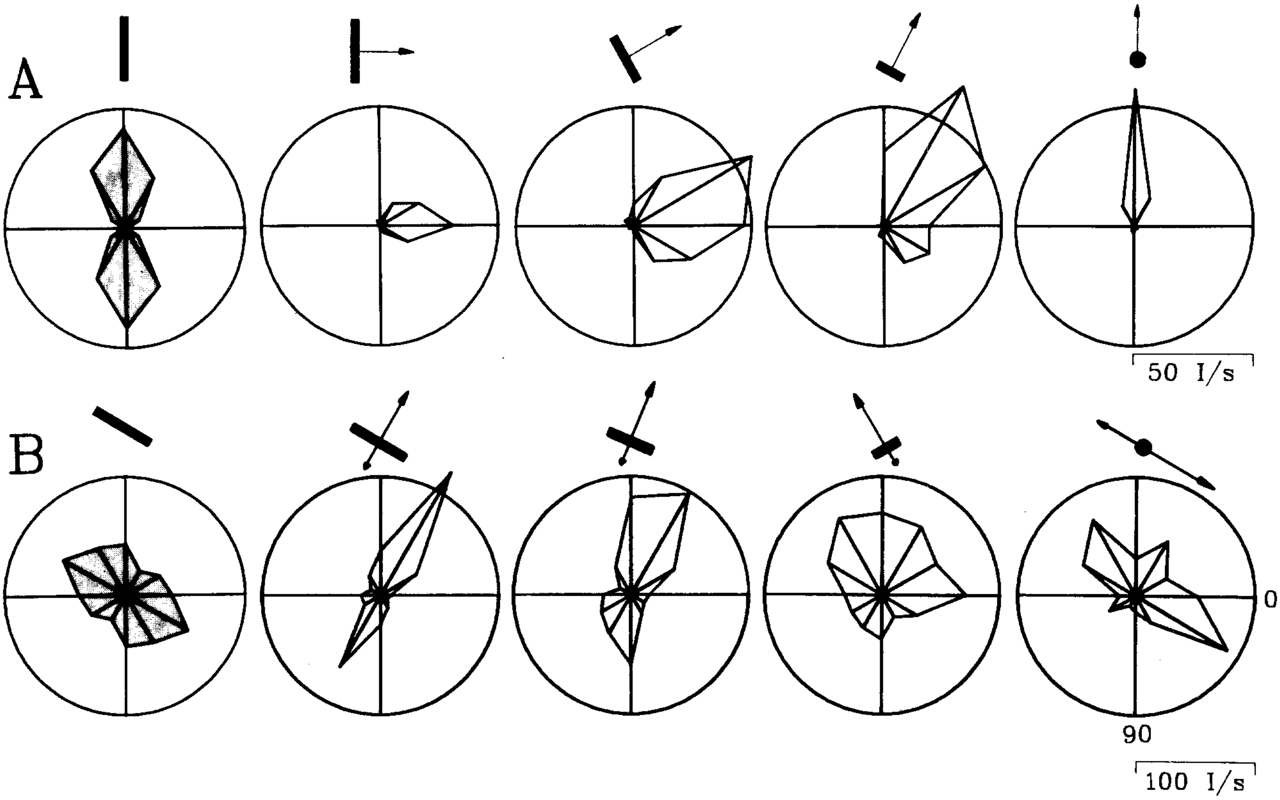

Fig. 2 A, B. Influence of stimulus length on the preferred direction of cortical cells. The bar length is indicated schematically above the polar-plots. The rightmost polar-plots show the responses of the cells to a moving light spot, the leftmost plots to a flashing bar. **A** End-stopped layer IV simple cell. Bar length: flashing bar 3.6°, moving stimuli (from left to right) 4.4°, 2.8°, 1.2°, 0.3°. **B** Layer V complex cell. Bar length: flashing bar: 9.8°, moving stimuli (from left to right) 9.8°, 2.4°, 1.2°, 0.15°. Both cells have a spot-response-axis parallel to the orientational axis, but the preferred direction gradually changes with decreasing bar length

of orientational, directional and spot responses refer to the responses of the simple cell shown in Fig. 1. The preferred stimulus orientation and/or axis of movement is shown to the right of the polar plots in relation to a schematic drawing of the receptive field which was derived from stationary receptive field plots. The *orientational axis* of a cell corresponds to that orientation of a *long stationary flashing bar* which evokes the strongest response; normally this corresponds to the long-axis of the elongated receptive field. The cell response shown in the shaded polar plot in Fig. 1 A, therefore, demonstrates a 90° orientational axis. The *preferred direction (PD)* of movement is defined by the strongest response to a *long moving light bar.* This simple cell, therefore, has a preferred direction of 180° (Fig. 1 B). The difference in the stippling of the sidebands in the figure schematically indicates a possible mechanism which would lead to the direction preference of 180°, however, whether inhibitory or facilitatory influences are responsible for directionality shall not be discussed in this paper. For a moving spot in principle a similar terminology can be applied. The *spot-response-axis* is given by that particular *axis of motion along which a light spot* elicits the strongest response. In the example (Fig. 1 C) a spot-response-axis of 90° is obvious; it is, therefore, parallel to the orientational axis (Fig. 1 A). Note: spot-response-axis and orientational axis are defined over 180° in the visual field. Finally, a *preferred spot direction* can be defined by the direction of a *moving light spot* with strongest response, however, in the example no directional tuning for a spot response can be detected (Fig. 1 C). The term *tuning* is used to denote the strength of the respective response property .

The effect of gradually decreasing bar length on the orientational tuning and the preferred direction of movement is shown for a simple and a complex cell in Fig. 2. The orientation of the preferred stimulus and the preferred axis of movement are indicated above the polar plots.

Both cells demonstrate an orientational axis in response to a flashing bar that corresponds to the

Table 1. Percentage of simple ($N=82$) and complex cells ($N=41$) with spot-response-axis aligned ($\leq 30°$ difference) or not aligned ($>30°$ difference) to the orientational axis. The numbers in parenthesis indicate the percentage of cells with 0° difference between both axis

	Simple cells ($N=82$)	Complex cells ($N=41$)
Aligned	84 (51)%	66 (37)%
Un-aligned	16 %	34 %

spot-response-axis. For the simple cell (Fig. 2A) the preferred direction for a moving long bar (0°) is orthogonal to the orientational axis (90°) as would be expected. For decreasing bar lengths, however, a gradual counter-clockwise rotation of the preferred direction can be observed until a spot is used and the preferred spot direction (270°) is attained. In addition, the simple cell also shows end-stopping, demonstrated by the decreasing responsiveness with increasing bar length. Both cells are directionally tuned for a long bar, the complex cell (Fig. 2B), however, shows no significant spot directionality in contrast to the simple cell which preferred spot direction of 270°.

Table 1 shows the distribution of cells with aligned or un-aligned orientational- and spot-response-axis. For many cells, however, the responsiveness to a spot was low and, therefore, only cells which clearly showed orientational- and spot-axis-alignment were included in the aligned sample shown in the table. All other cells including the cells that showed no spot response were regarded as un-aligned. The majority of the cells showed less than 30° difference between the orientational axis for a long bar and the spot-response-axis (Table 1). An exact alignment was mainly found in simple cells (Table 1, numbers in parenthesis). These small deviations suggest that orientational axis and spot-response-axis are parallel. The distributions of cells with and without aligned spot-response-axis in different cortical layers were also determined. However, no significant differences were found in the different layers and the only additional observation concerned the fact that spot responses seem to be stronger in cells with larger receptive fields.

When stimulated with a moving light spot most of the cells showed a superposition of responses elicited by movement along and orthogonal to the spot-response-axis, where the orthogonal response corresponded to the axis of preferred movement of a long bar. Thus, for short bars the response contained two components such that the total response could be interpreted as a weighted average between the responses for a spot and a bar. This resulted in *a gradually changing direction preference* with decreasing bar length and was observed for nearly all cells that showed a pronounced responsiveness for light spots. However, the range of different bar lengths over which the cells switched from orientational to spot responses in most cases was fairly small.

Two simple receptive field models (Fig. 3B, D) can be used to explain the response characteristic of the simple and complex cell shown in Fig. 3A, C. For the sake of simplicity ON and OFF zones are regarded as identical to excitatory and inhibitory zones.

The simple cell (Fig. 3A) had a spot-response-axis aligned to the orientational axis and the spot response was extremely pronounced. The directional tuning of the cell for a long bar was strong for approximately 0° and remained unaffected by the bar length. However, in contrast to the cell in Fig. 2A this cell showed no directional tuning along the spot response axis. A scheme with separate excitatory and inhibitory receptive field regions (Fig. 3B) could account for this response characteristic. For the cell in Fig. 2A, however, such a scheme would need to be extended by an additional inhibitory zone in the upper part of the visual field which would prevent a spot response in the 90° direction and, therefore, induce the strong spot-directional selectivity for 270°. For several cells similar to that in Fig. 3A we observed, that the maximal response for a moving spot was stronger than any response obtained with bar stimuli, however, in these cases the term "end-stopping" cannot be applied because "end-stopping" is used only in relation to the orientational axis of a cell which is optimally determined by a stationary stimulus.

For the complex cell (Fig. 3C) the spot-response-axis and the orientational axis were also aligned. The cell showed nearly no directional tuning with only a slight preference for oblique upward movement that is indicated in the model (Fig. 3D) by a small asymmetry in the inhibitory zones. ON and OFF zones, however, were highly overlapping as indicated by the stippling. The directional tuning of the complex cell in response to a spot could also be neglected. Both, simple and complex cell, when stimulated with a light spot, however, displayed a strongly superimposed response which contained both response components along and orthogonal to the orientational axis.

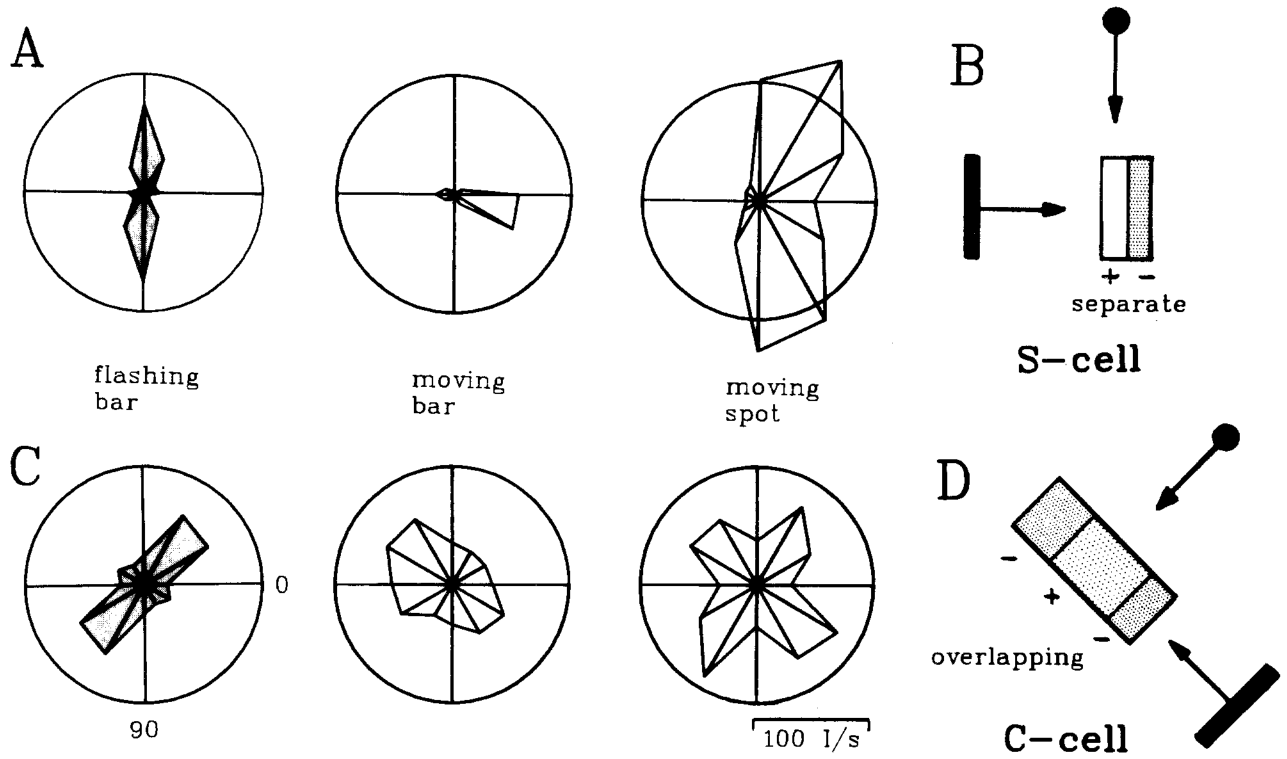

Fig. 3A–D. Schematical diagrams of the arrangement of excitatory and inhibitory receptive field regions (**B**, **D**) for the cells in **A** and **C**. The stimulus type is indicated between the polar plots. **A** Layer VI simple cell with a pronounced directional tuning which is maintained in the response to the light spot. **B** Separate receptive field regions in simple cells can account for a strong axial and orientational response. **C** Layer V complex cell with very little directional tuning as indicated by the small asymmetry of the inhibitory zones in **D**. **D** Partly overlapping receptive field regions with a separation of excitatory and inhibitory centers sufficient to elicit axial and orientational responses a in complex cell. Both cells show a strong and non-directed response to motion along the spot-response-axis and a pronounced superposition of axial and orientational responses

Influence of stimulus displacement on the axis of preferred motion

In the previous section it has been demonstrated that the spot-response-axis is mostly parallel to the orientational axis and that the optimal movement of a spot can be regarded as a movement along the long axis of the receptive field. Figure 4 shows the influence of the displacement of the moving spot with respect to the receptive field of a layer VI simple cell. As long as the stimulus was adjusted so that its movement for one orientation followed the long axis of the receptive field (Fig. 4B) as determined by hand-plotting a spot-response-axis was revealed which was parallel to the orientational axis (Fig. 4A). A slight displacement of approximately 0.3°, however, led to a completely different result and the spot-response-axis seemed to be rotated (Fig. 4C). With an even greater displacement (0.6°, Fig. 4D), the spot-response-axis appeared to be parallel to the axis of preferred movement for the long bar (Fig. 4E); the orientational tuning, however, seemed to be reduced. Such a behaviour may roughly be explained by the relation between the movement trajectory of the spot and the receptive field center as indicated schematically above the polar-plots. Such a displacement of the stimulus can lead to completely different estimates of the spot-response-axis because the elongated central part of the receptive field is missed by the trajectory of the moving spot. Thus, for a valid determination of the spot-response-axis the stimulus must be accurately placed. In view of the situation that subfields of cortical cells are not homogeneous, the optimal adjustment of the center for stimulus rotation would be that particular point in the visual field which has the maximum sensitivity to stimulation. Even slight displacements can result in rather strong changes in the response characteristic as shown. This is also demonstrated by the responses to spot stimulation in the direction of 60° which are similar for Fig. 4C, D but smaller than expected in Fig. 4B. This effect might

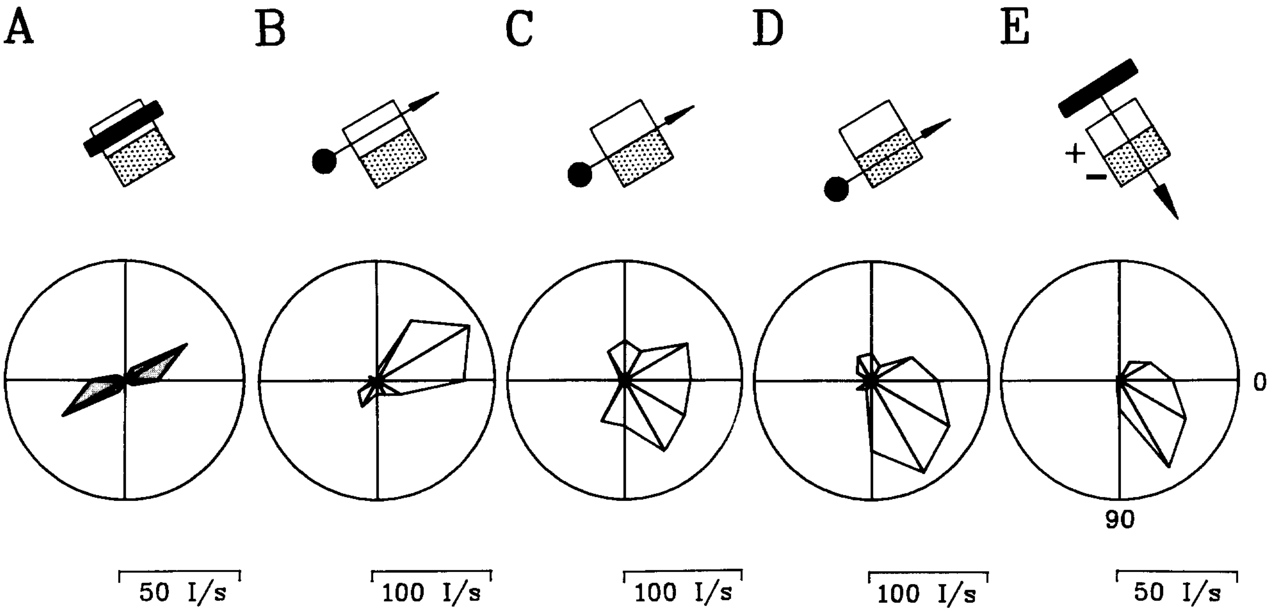

Fig. 4A–E. Influence of stimulus displacement on the estimate of the spot response axis in a layer VI simple cell. A schematic representation of the receptive field, the stimulus type and it's positioning is indicated above the polar-plots. **A** A 150° orientational axis is revealed by a flashing bar of 9° length. **B** Accurate placement of the moving spot (diameter = 0.15°) results in a spot-response-axis of also 150°. **C** Displacement of the spot by 0.3° leads to a virtual rotation of the spot-response-axis. **D** With larger displacement (0.6°) a spot-response-axis of 60° is obtained which is parallel to the axis of preferred motion of the long bar (length 9°) shown in **E**

be due to a displacement not only along the 60–240° axis but also orthogonally (150–330° axis).

Discussion

For visual cortical cells it is generally accepted that the preferred direction of a long moving bar is orthogonal to the cell's orientational axis (Bishop et al. 1971). Thus, for the preferred direction the axis of movement crosses the elongated receptive field in the shortest way possible and for one position the travelling light bar optimally covers the receptive field center (Fig. 1B). Previous investigations (Henry et al. 1974a) of the response characteristic of visual cortical cells to moving light spots reported that the cells mainly responded to spot movement which was also orthogonal to the orientational axis of the receptive field. Thus, these authors claimed that the optimal axis of movement of a light spot was identical to the optimal axis of movement of a light bar *for all cells* and they called this phenomenon *axis specificity* (see also Orban 1984). However, some findings indirectly indicated the possibility that strong spot responses could be elicited along the orientational axis (Rose 1977). Our results support this view and, moreover, demonstrate that the spot-response-axis was aligned with the orientational axis in 84% of the simple and 66% of the complex cells (Table 1). These results disagree with the findings of Henry et al. (1974a, b). The effect reported in our study, however, critically depended on the spot size and sometimes required spots as small as 0.1°, which were just covering the central receptive field zone, whereas the smallest spot size used in the studies of Henry et al. (1974a, b) was 0.43°. Additionally, accurate placement of the stimulus, so that it's trajectory follows the elongated receptive field center, was found to be critical and Fig. 4 demonstrates that a common 'axis specificity' and the widening of the orientational tuning reported by Henry et al. can be induced merely by stimulus displacement. Both requirements – small spots and accurate placement – could explain the difference between our findings and those of Henry et al. Hence, responses to a moving spot or bar normally do not show a common "axis specificity", therefore, the nomenclature of Henry et al. (1974a) cannot be used consistently. Instead, we propose that the term *axis specificity or axial selectivity be used to describe any response that can be elicited along the long-axis of the receptive field.* This terminology should allow the distinction between responses that are elicited along the receptive field axis (axial responses), and those evoked by an oriented flashing or moving stimulus (orientational responses).

In our findings such an axial selectivity, associated with the spot-response-axis in our report, was even more pronounced in simple than in complex cells and we propose that this may be due to the separate excitatory and inhibitory receptive field regions of simple cells. With separate receptive field regions, however, one might expect all simple cells to exhibit axial selectivity. The lack of a spot response component in the remaining 16% can be explained either by very low responsiveness of the cell to a light spot or by the fact that the movement of the light spot has to be aligned exactly with the excitatory receptive field center. Thus, for simple cells with very narrow receptive fields, particularly in layer IV, the stimulus in some cases may have partially missed the central zone. This explanation may also hold for the observation that mainly simple cells with large receptive fields showed strong spot responses because for cells with narrow fields even the smallest spots might have extended into inhibitory flanks of the receptive field while moving along the orientational axis. For complex cells axial selectivity is much weaker and particular cells with very large receptive fields and extremly pronounced complex cell characteristic did not express axial tuning. However, many complex cells show at least some separation between ON and OFF zones (Dean and Tolhurst 1983), so that in these cases an axial selectivity can be expected. Thus, separated receptive field regions may be a major requirement for the expression of axial selectivity.

The preferred orientation of cortical cells has been reported to be independent of bar length (Henry et al. 1973; Henry et al. 1974a, b), while orientational tuning strength increased when stimulating with longers bars (Henry et al. 1974a, b; Orban et al. 1979; Rose 1977). This can be interpreted differently on the basis of our present observations. For cells with a pronounced axial selectivity there was a strong tendency for intermediate bar lengths to elicit responses which contain both – axial and orientational – response components. Decreasing the bar length often resulted in a gradual rotation of the preferred direction of bar movement towards the spot-response-axis (Fig. 2). This suggests that cells with a strong spot response component average between axially and orientationally elicited responses, weighting both components according to the bar length. In some extreme cases the response to a moving spot contained both components as if added linearly (Fig. 3). The receptive fields of most cortical cells are relatively small and often have adjacent inhibitory zones, so that such an averaging effect in many cases should remain restricted to a small range of different bar lengths. Nevertheless, a gradual transition could be detected, although sometimes only weakly expressed, in a large number of cells. The decreasing orientational tuning in response to decreasing bar length reported by Henry et al. (1974a, b) can be explained by the above mentioned superposition of orientational and axial responses. The associated regular change of the preferred direction, however, indicates that the altered response characteristic for short bars is not merely a quantitative loss in tuning strength but a qualitative change in the response properties. This might be due to the involvement of a mechanism different from that responsible for the orientation dependent response. For most cells the directional tuning for a bar and a spot were clearly different (Fig. 2). This further supports the view that two distinguishable mechanisms are involved in the generation of both response components. In particular, directionality elicited by the long bar seems to be generated at least partly by influences lateral to the receptive field region (Eysel et al. 1987, 1988) which cannot account for any direction sensitive responses evoked by a moving spot.

The strong interactions between axial and orientational responses at intermediate bar lengths suggest that axial selectivity must be included in the description of the complete response characteristic of a visual cortical cell, because stimulation with bars that are too short will result in incorrectly estimating the orientational axis (Fig. 2A, 2.8° bar). In particular, for the determination of end-stopping the axial and orientational response components must not be confused, because end-stopping is only defined for orientationally dependent responses. However, a valid determination of the orientational axis is unequivocal only when performed by a stationary flashing stimulus, because any moving stimulus, in principle, can evoke spot response components and for cells with large receptive fields this may even occur for fairly long bars. An incorrect estimation of the orientational axis, however, would also lead to incorrectly estimating the end-stopping, especially for those cells (Fig. 3C) that show a response to a moving spot which is stronger than that seen to any of the bars (Rose 1977).

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