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Research Note

Correlations between directional and orientational tuning of cells in cat striate cortex

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Summary. Simple (N = 284) and complex cells (N = 125) in the central projection area (0–5° eccentricity) of the striate cortex of cats were stimulated with moving light bars and the responses to different directions of movement were recorded and plotted as polar-plots. Fourier analysis was applied to polar plots (SDO-analysis, Wörgötter and Eysel 1987; Wörgötter et al. 1990) to determine the general sensitivity (S) of the cells to visual stimulation, the directional (D) and orientational (O) tuning strength as well as preferred direction (PD) and preferred orientation (PO). Statistical distributions of the S, D and O parameters were determined for simple and complex cells of the cortical layers II–VI. Simple cells were more strongly tuned for direction and orientation than complex cells, whereas complex cells had a greater general sensitivity to visual stimulation. Directional tuning was significantly stronger in layer VI than in layer IV simple cells, otherwise no differences were detected between these two layers. We found that cells with large D and small O components are generally rare. The D and O components were plotted against each other to determine any possible correlation between the tuning strengths. The correlations were statistically significant for simple and complex cells but the correlation coefficients were very small ($r < 0.3$). It is suggested that only a very weak coupling between directional and orientational tuning exists, preferentially in the deeper layer simple cells.

Key words: SDO-analysis – Tuning curves – Preferred direction – Preferred orientation – Cat

Introduction

Directional and orientational tuning have been treated as independent features of visual cortical cells since they were first described by Hubel and Wiesel (1962). The question if both properties are based on different mechanisms has been investigated in the studies of Hammond and MacKay (Hammond 1978; Hammond and MacKay 1977). They demonstrated differences in the responses of visual cortical cells to a moving oriented bar or a moving noise field lacking all orientation information, and these results were interpreted as evidence that direction and orientation specificity are mediated by different mechanisms. Further evidence for this hypothesis was provided by Sillito (1977, 1979) who showed that directional and orientational tuning of cortical cells in many cases could be independently influenced by microiontophoretic blockage of GABAergic inhibition with the GABA antagonist bicuculline applied directly at the recorded cell. In addition, it has been demonstrated that the direction specificity of a cell can be removed by remote inactivation of a small volume of cortical tissue at a distance of approximately 1 mm lateral to the recorded cell without affecting the orientational tuning (Eysel et. al. 1988), the reverse effect – removing orientational tuning without affecting directionality – however, was never observed. This suggested that some degree of orientation specificity is required without which no directional tuning can be expressed.

An analysis of the correlation between tuning strengths could provide a relatively simple test of this hypothesis. Intuitively, a strong correlation between the strength of directional and orientational tuning would indicate a link between the underlying mechanisms, while a lack of correlation would suggest independence. However, correlation analysis can merely show statistical dependence which cannot directly be interpreted in terms of causality.

When correlating the commonly used direction index (DI) and half-width-at-half-height (HWHH) orientational tuning parameters (see Orban 1984), however, difficulties can arise due to the entirely different procedures used to compute the two parameters. When

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applying Fourier analysis of cortical tuning curves (Thibos and Levick 1985; Swindale et al. 1987, SDO-analysis; Wörgötter and Eysel 1987), which allows determination of the directional (D) and orientational (O) tuning strength, the resulting D and O parameters are revealed by a uniform computational process which validates a correlation analysis between both. This, finally, makes it possible to investigate interactions between directional and orientational tuning strength.

In this report we will demonstrate a negligible correlation between the strength of directional and orientational tuning in visual cortical cell responses. The only clear effect observed is that cells with strong directional but weak orientational tuning are rarely found in area 17.

Methods

The same methods were used as in a previous paper appearing in the same volume (Wörgötter and Eysel 1991) and only a brief outline will be given here.

The data for this study were obtained from extracellular microelectrode recordings in area 17 of the visual cortex from 34 adult cats stimulated with moving bars. The orientation of the moving bar was changed in 30° steps and tuning curves were measured and plotted as polar-plots.

The general sensitivity, directional and orientational components (S, D, O) of the responses were extracted by Fourier analysis of polar-plots (SDO-analysis) as described in the previous paper (Wörgötter and Eysel 1991). Briefly, the orientational tuning curve can be interpreted as a periodical function with 360° periodicity; the first harmonic (A_1 and B_1; Eq.1) is then regarded as the directional and the second harmonic (A_2 and B_2; Eq.1) as the orientational component (i.e. first and second moment of a circular distribution, Batschelet 1981). The gain (Gi; Eq.2) and phase (Pi; Eq.3) values define the directional (or orientational) tuning strength and the preferred direction (or preferred orientation).

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

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

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

The zero order component A_o reflects the average sensitivity (S) of the cell to visual stimulation. D and O components are normalized with respect to S (i.e. given in % of S).

Note: Fourier analysis requires two data points per full period to retrieve the corresponding frequency component (Sampling theorem). 30° orientation steps correspond to 12 data points in 360° or six data points in 180° which is the periodicity of the orientation domain. Such a threefold oversampling should be entirely sufficient to retrieve the correct orientational tuning even of narrowly tuned simple cells (cf. Wörgötter et al. 1990). This validates the use of the apparently coarse 30° sampling steps.

The commonly used direction index (DI) and half-width-at-half-height orientational tuning parameter (HWHH) can be obtained from the SDO-parameters with the following empirical equations:

$$DI = 60.9 \log_{10}(D) - 38.7 \quad (4)$$

$$HWHH = -63.1 \log_{10}(O) + 137.9 \quad (5)$$

The correlation r was found to be better than 0.85. The diagrams from which those empirical equations were derived and a detailed comparison of the parameters from SDO-analysis with the commonly used parameters is given elsewhere (Wörgötter et al. 1990).

Error probabilities were calculated applying the two-tailed Student-t-test. The strength of correlation between different parameters was determined by the Spearman rank correlation coefficient.

Results

Statistical distribution of tuning strengths

The distributions of the S, D and O components were determined for 284 simple and 125 complex cells. The histograms in Fig. 1 show distinct differences between both cell classes. Simple cells tend to have a low sensitivity to visual stimulation with many cells having an S component close to zero (Fig. 1A). The overall responsiveness of complex cells is higher (Fig. 1B), however, their directional (Fig. 1D) and orientational tuning (Fig. 1F) is on average lower than that of simple cells (Fig. 1 C, E). A similar number of cells were found in both cell classes that had no directional tuning (Fig. 1C, D); cells with no orientational selectivity, however, are in general relatively rare, particularly in the group of simple cells (Fig. 1E, F). All distributions are unimodal indicating that there is no subgrouping within the simple or complex cell classes. The mean values show a significant difference ($p < 0.0001$) between simple and complex cells. A comparison of simple cells of layer IV with those of layer VI (not shown) revealed no significant difference for the S and O components. There is, however, a significant tendency for layer VI simple cells to be more strongly tuned for direction than the simple cells in layer IV ($p < 0.05$).

Correlation analysis between directional and orientational tuning strengths

To test a possible correlation between the strength of directional and orientational tuning the D and O components for simple and complex cells were plotted against each other (Fig. 2A,B). The Spearman-rank-correlation coefficient was significantly different from zero for both graphs (simple cells: $N = 284$, $r = 0.27$, $p < 0.001$; complex cells: $N = 125$, $r = 0.21$, $p < 0.01$). The low values of the correlation coefficients indicate a low degree of statistical dependence of D and O in the two samples of cortical cells. Only a relatively small number of cells was found above the dashed lines in Fig. 2A,B. This region of the graph represents cells with a low O and a high D component. While only a few cells with this parameter combination could be detected more cells exhibited the reverse situation, i.e. low D and high O components. No significant difference was found for the subgroups of complex cells in layers IV and VI but the subgroup of simple cells in layer VI displayed a tendency towards a more pronounced correlation ($r = 0.4$).

In comparison to complex cells (Fig. 2B), the distribution for simple cells is shifted to higher O components (Fig. 2A) which was already evident from the histograms in Fig. 1. Typical examples of cortical response characteristics of simple (Fig. 2C) and complex cells (Fig. 2D)

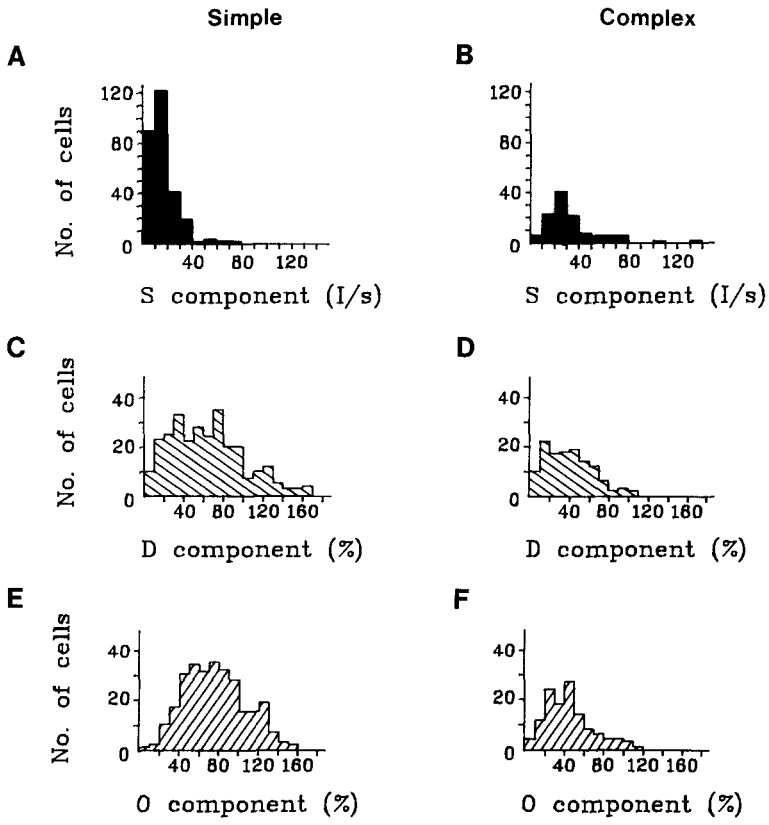

Fig. 1A–F. Distributions of tuning strengths for simple (**A, C, E**) and complex cells (**B, D, F**). Distribution of the S components (**A, B**), the D components (**C, D**), and of the O components (**E, F**) are shown. Simple cells on average displayed a lower S but higher D and O components than complex cells. Mean values: (**A**) $\bar{S}_{simple} = 16.1 \pm 11.4$ I/s; (**B**) $\bar{S}_{complex} = 33.7 \pm 23.4$ I/s; (**C**) $\bar{D}_{simple} = 63.7 \pm 37.0\%$; (**D**) $\bar{D}_{complex} = 39.9 \pm 24.2\%$; (**E**) $\bar{O}_{simple} = 76.8 \pm 30.4\%$; (**F**) $\bar{O}_{complex} = 44.7 \pm 24.1\%$

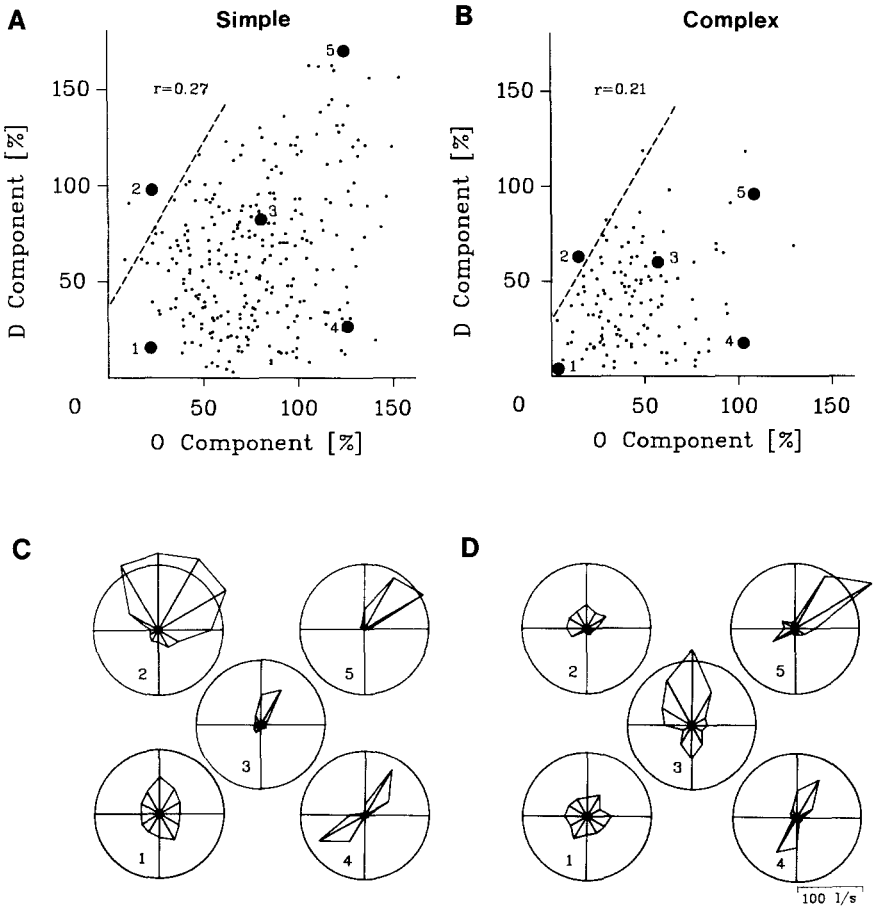

Fig. 2A–D. Correlation analysis between D and O components for simple (**A**) and complex cells (**B**) and examples of single cell tuning curves (**C, D**) which are shown in relation to their D and O components represented by the larger dots in the corresponding graphs. **A, B** The coupling between D and O is extremely weak with a Spearman-rank-correlation coefficient of: simple cells, $r = 0.27$, $p < 0.001$; complex cells, $r = 0.21$, $p < 0.01$. Only a few cells with high D and low O component are found (cells above the dashed lines). **C, D** The polar plots clearly demonstrate that the tuning strengths estimated by visual inspection are in a good correspondence with the results from SDO-analysis and that nearly every combination of D and O can occur in cells of cat's striate cortex

are shown as polar plots arranged according to the D and O components (indicated by the larger dots in the graphs above). Visual inspection of the polar plots reveals that the cells shown in the lower left corners (No. 1) display no directional and orientational tuning. The cells above (No. 2) belong to the rare examples which have a strong D but a weak O component. The majority of cells, however, is represented by the remaining three polar plots (No. 3–5) which exemplify the range from intermediate to strong directional and orientational tuning.

Discussion

The statistical treatment of the properties of visual cortical cells has been the aim of many studies in the field of visual neurophysiology (Heggelund and Albus 1978; Orban 1984; Orban et al. 1981; Rose and Blakemore 1974). The comparison of different features was commonly based on heuristic measures such as the direction index or the half-width-at-half-height orientational tuning parameter (see Orban 1984). The analysis of direction and orientation, however, can be based on a more solid theoretical background in realizing that direction has a periodicity of 360° and orientation of 180° in the visual field, in correspondence with the first and second harmonic in the Fourier analysis (SDO-analysis) of cortical tuning curves (Wörgötter and Eysel 1987). The present study is the first to apply SDO-analysis for a statistical determination of the properties within different cell classes in the visual cortex.

Our results showed that simple cells on average displayed a lower sensitivity to visual stimulation; their responses, however, are more strongly tuned for direction and orientation than the average responses of complex cells (Fig. 1). These results are entirely in agreement with previous findings showing that simple cells on average have a smaller half-width-at-half-height (Leventhal and Hirsch 1978) and a larger direction index (Bishop et al. 1971; Goodwin and Henry 1975) than complex cells while their mean peak response rate is lower (Leventhal and Hirsch 1978). The comparison of simple cells within layer IV and VI on the one hand revealed no difference concerning the S and O components, a result also observed by Leventhal and Hirsch (1978). Directional sensitivity, on the other hand, seems to increase slightly in layer VI as compared to layer IV, a property which is much more weakly expressed in cat than in monkey (Hawken et al. 1988). The effect, however, is significant and could be due to the generally observed preference of greater velocities in layer VI simple cells (Leventhal and Hirsch 1978) which is often coupled with a stronger directional tuning (Orban et al. 1981).

In reports applying the method of remote inactivation of cortical tissue (Eysel et al. 1990; Wörgötter and Eysel 1991, submitted), it has been demonstrated that orientational tuning cannot be influenced separately from the directional tuning. Contrary to previous findings (Hammond 1978; Sillito 1979), this result indicates that the mechanisms underlying directional and orientational tuning are not completely separated and that a certain functional and/or topographical overlap might exist. At least it could be possible that the mechanisms producing directional specificity are superimposed on (or "added to") those involved in the generation of orientational tuning. In the present paper we have tried to gain additional insight with a statistical approach and have determined the correlation between strength of directional and orientational tuning in large samples of cortical cells. Correlation analysis revealed low correlation coefficients which were, however, significantly different from zero. While this result does not support the hypothesis of a complete independence of D and O, it cannot be interpreted in terms of a strong coupling of the parameters either. Anyhow, high degrees of directional tuning are not associated with low or absent orientation specificity. Thus, unlike cells in area MT of the monkey (Albright 1984), cells in the striate cortex of the cat seem to require a certain amount of orientational tuning without which they cannot express any direction specificity. This is in particular valid for layer VI simple cells. This finding is in parallel with the observations that direction specificity does not persist after complete removal of the orientational tuning (Eysel et al. 1990; Wörgötter and Eysel 1991, submitted). In contrast, directional tuning can be experimentally abolished without any loss in orientational tuning (Eysel et al. 1988) which is reflected in the present statistical analysis by the existence of cells with strong orientational but no directional tuning.

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