Cortical Columns: A Multi-parameter Examination

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Columnar structure in the cerebral cortex has been demonstrated in numerous studies. However, in the visual system, it is not clear from imaging, basic physiological and anatomical approaches how multiple stimulus parameters are related within columns. We have analyzed recordings from pairs of neurons in the striate cortex of the cat using various spatial and temporal parameters. We find that most parameters are clustered within inferred columns with the exception of spatial phase. Diversity of phase could be useful for serial processing in central visual pathways.

Introduction

One of the basic organizing principles of the cerebral cortex is columnar structure (Mountcastle, 1997). This means that cells in a given sensory modality are organized in clusters perpendicular to the surface of the cortex. These slabs of cells share common response characteristics and neighboring columns are similar in specificity. In a lateral progression, the columns change in a regular, incremental fashion. In the visual cortex, a complete set of changes for all orientations and ocular dominance values for a given region of visual space constitutes a hypercolumn (Hubel et al., 1977).

Columnar structure has been identified for several visual parameters, including orientation and ocular dominance (Hubel et al., 1977) and direction selectivity (Payne et al., 1980); but see (Bonhoeffer et al., 1995; Shmuel and Grinvald, 1996). The standard methods that have been used to study columnar organization include single-cell recording, metabolic labeling and optical imaging. These approaches generally allow for a mapping of one or two response variables across visual cortex, with relatively poor resolution. A recent study has included orientation, ocular dominance and spatial frequency, but resolution is still low (Hubener et al., 1997). In addition to the problems with resolution, not all important visual variables have been studied by the standard imaging techniques. For example, receptive field shape (phase), response latency and temporal frequency selectivity are not amenable to analysis by imaging.

A different approach enables analysis of a variety of parameters with high resolution. The method involves recording simultaneously from pairs of adjacent neurons in the visual cortex and using a powerful visual stimulation and analysis technique that allows a number of parameters to be analyzed together. Comparisons can then be made between the two cells to find which parameters are similar and which are different. The assumption here is that both cells reside within a cortical column. Since columns are not being measured, per se, the inferences that are made are assumed to be applicable to columnar organization. The results of this approach, which have been published previously (DeAngelis et al., 1999) are reviewed here.

Methods

Pairs of neurons are isolated in the cat’s visual cortex, and spike discharge is amplified and processed for each cell using quantitative neurophysiological techniques. For this study all cell pairs are recorded from a single electrode. A reverse-correlation sparse-noise stimulation technique enables a full set of spatiotemporal receptive field parameters to be determined.

Two main types of analysis are used. In the first, a model-free process is used by which the degree of similarity between the receptive fields of a pair of neurons is assessed. This analysis provides a useful index of the degree of similarity between two receptive fields. However, it does not permit an analysis of how receptive fields of pairs of cells are different. To determine this, a second technique is used. This parametric model-based analysis provides data on specific relevant response parameters including spatial and temporal factors. A model is required for the second type of analysis. In this case, the model consists of two space-time separable receptive fields. Each is modeled as the product of a spatial and a temporal waveform. These two subunits are identical except for a 90º difference in spatial and temporal phases. The two receptive fields are combined to form a space-time inseparable unit. A weighting factor, applied in the combination, determines the degree of inseparability of the combined unit. Degree of inseparability is also an index of directional selectivity (DeAngelis et al., 1995, 1999). With this second method of analysis, it is possible to derive a series of spatial and temporal comparisons between every cell pair.

Results

Using the procedures described above, we may examine which response parameters are clustered in striate cortex. The most direct way to do this is to collect data in the form of a scatterplot in which the parameter for a given response characteristic of one neuron is compared to that for the second cell of the pair. This is done for several spatial and temporal parameters in Figure 1. The first parameter, shown in Figure 1A, is for orientation. A number of previous studies have identified orientation as one of the main columnar components (Hubel and Wiesel, 1974; Blasdel, 1992a,b). As the data in Figure 1A show, orientation is strongly correlated with a very high correlation between values for the two cells of each pair.

The other spatial parameters shown in Figure 1 are width, spatial frequency and spatial phase. In Figure 1B, receptive field width is also clearly clustered but not as strongly as orientation. Data for spatial frequency, in Figure 1C, are similarly clustered. The final spatial parameter, receptive field shape or phase, is clearly not clustered. Data for this variable, shown in Figure 1D, are completely scattered within the dashed line boundaries of the graph. This variable is circular and therefore the largest possible phase difference is 180º between a pair of receptive fields. It is for that reason that dashed line boundaries are included in Figure 1D.

Temporal data also exhibit clustering although the degree is relatively modest. For peak response latency (Fig. 1E), response duration (Fig. 1F) and temporal frequency (Fig. 1G), all three variables are significantly clustered. The final graph, for direction selectivity, indicates a lack of clustering for the index α. However, neighboring cells tend to prefer the same direction of
Figure 1. Correlations are shown for simultaneously recorded cell pairs in the striate cortex. Various spatial and temporal stimulus parameters are assessed. Open and closed symbols represent data from adult cats and from kittens at 4 weeks postnatal, respectively. (A) The strongest clustering is shown for orientation. Weaker but significant clustering is shown for receptive field (RF) width (B) and spatial frequency (C). Spatial phase values (D) are not clustered. The temporal values of latency (E), response duration (F) and temporal frequency (G) are clustered but not strongly. Direction index (H) is not clustered but adjacent cells tend to prefer the same direction of movement.
motion. This association in direction preference of neighboring neurons has been noted in single-cell studies (Tolhurst et al., 1981).

It is possible to quantify the degree of clustering for each parameter by using a statistical permutation test. To do this, a distribution of absolute pairwise differences is derived for each receptive field parameter studied. The median value of the distribution is then used to obtain a statistical value that may be called a grand random median. A clustering index may then be obtained; this is defined as the ratio of the grand random median to the paired median. If this ratio is large, then the clustering is strong. Details of this derivation are given elsewhere (DeAngelis et al., 1999).

Results of this quantitative analysis show that orientation is clustered to a far greater extent than any other parameter. Highly significant clustering is also exhibited for receptive field width and preferred spatial frequency. Weaker, but still significant, clustering is found for the temporal response measurements. This includes latency, duration and preferred temporal frequency. Clustering is not significant for the direction selectivity index, but, as noted above, paired cells tend to prefer the same direction of movement. The factor that stands out as not exhibiting significant clustering is receptive field shape, i.e. spatial phase. This may provide a significant coding and processing advantage, as noted below.

Discussion

In this study, an attempt has been made to determine which visual response parameters are clustered in the visual cortex. By inference, it is assumed that this information provides details of columnar organization in the visual cortex. Two types of analysis have been used. The first is a non-parametric type assessment of similarity between different receptive field parameters. The second is a model-based system by which a parametric analysis may be made that allows specific variables to be identified as the bases of receptive field differences.

The results of these analyses provide several interesting conclusions. The most basic question concerns the overall similarity of the spatiotemporal receptive fields of adjacent neurons. Analysis shows that adjacent simple cells are generally quite dissimilar if comparisons are made in the entire space-time domain. This does not fit the common notion of similarity between neighboring cells. Instead, it suggests that there is considerably less redundancy than what one would expect in the case of homogeneous columns.

Another interesting conclusion concerns the degree of clustering for different response parameters. Clustering is strong for orientation and spatial frequency and weaker for the temporal parameters of frequency, response latency and duration. The most important variable that accounts for differences between adjacent neurons is spatial phase or receptive field shape. Little variability between neighboring cells is accounted for by other receptive field parameters.

Finally, it is of interest to consider possible functional implications of the variability in spatial phase. The diversity in this parameter could be beneficial in the processing of information in central visual pathways. Specifically, the diversity of phase could be used in the hierarchical processing of information from simple to complex cells in the visual cortex.

Notes

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References