

Meridional differences in orientation sensitivity in monkey striate cortex

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Recent physiological investigations^{1-3,5} have suggested that in humans there is greater sensitivity and discrimination for horizontally and vertically oriented edges and gratings than for diagonal ones. Several investigations have looked for a neurophysiological counterpart of this effect in striate cortex of the cat and monkey. Two hypotheses have been proposed:

(1) Neurons with horizontal and vertical orientation selectivity are more common in visual cortex than are neurons selective for obliques.

(2) All orientations are equally represented but cells responding to horizontal and vertical orientations are more selective for orientation.

Recent work on the cat by Rose and Blakemore⁷ suggests that simple cells with vertical and horizontal axes of orientation are more tightly tuned than those with diagonal axes. A more provocative finding reported recently by Mansfield⁶ suggests that in monkey foveal striate cortex, cells sensitive to horizontally and vertically oriented edges are more numerous than cells for other orientations. This finding implies a columnar organization somewhat different from that proposed by Hubel and Wiesel⁴ in that it would necessitate more space or columns allocated to meridional and fewer columns to diagonal orientation specificity.

In view of these findings, as part of a more general effort⁸, we investigated a sample of 673 neurons in 226 penetrations perpendicular to the cortical surface and 11 penetrations at 10° or 20° to the cortical surface from the parafoveal striate cortex in 45 monkeys which were flaxedilized and artificially respired with 30% O₂-70% N₂O. To determine if any meridional variations in cell number or orientation specificity existed, we assessed (1) cell number according to optimal orientation and (2) orientation tuning specificity for different axes. The orientation tuning function was derived from a smoothed curve of average response to presentation of a bar or edge stimulus swept across the receptive field at various orientations in a randomized sequence. The width of tuning in degrees at 71% of maximum response was the measure employed.

Fig. 1A shows a plot of the number of cells having optimal responses at various orientations. Only cells between 2° and 5° from the fovea, primarily representing the lower visual field, are included in this sample. In Fig. 1B the data were pooled adding

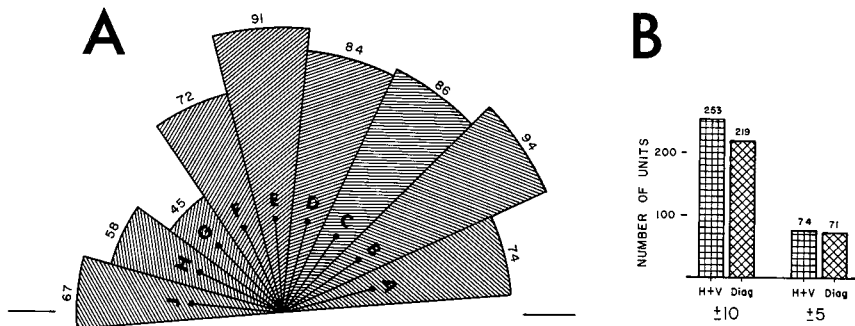


Fig. 1. A: proportions of cells having optimal response at various orientations. Each category represents a 20° orientation range. The orientation of a bar was defined as 0° (H) if it was tangent to the outer edge of wedge A; those oriented at 90° (V) were tangent to wedge E. B: relative numbers of cells having horizontal or vertical preferred orientations to obliques. The first bar graph represents numbers of cells with a broad definition of horizontal and vertical *versus* diagonal preferred orientation ($\pm 10^\circ$). The second graph uses a more stringent criterion ($\pm 5^\circ$).

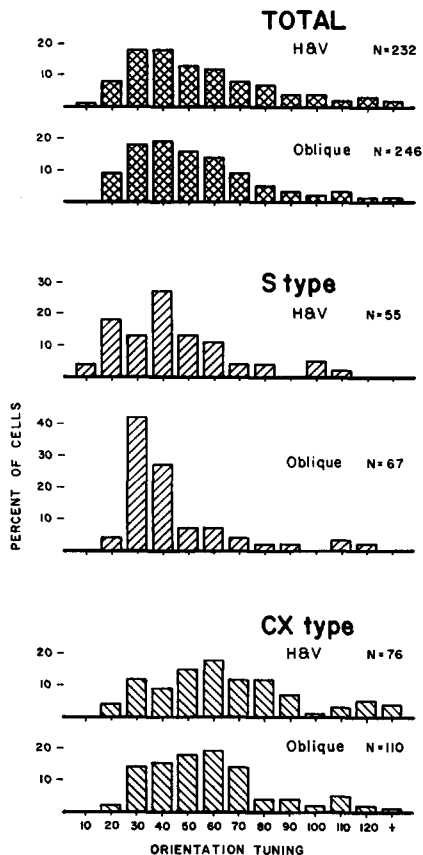


Fig. 2. The orientation tuning ranges of horizontals and verticals *versus* obliques for all cells, S-type cells, and CX-type cells. The orientation tuning score of each cell was derived from the responses obtained to moving bars of different orientations, and represents the width, in degrees, of a smoothed tuning curve at the 71% level of the maximum response rate. All cells having their maximum response rate within 20° of horizontal or vertical form the H and V group; all others form the oblique group. Neither the total nor S-type nor CX-type cell groups show significant differences in tuning for horizontal-vertical *versus* oblique.

all orientations between 0 ± 10 and 90 ± 10 for verticals and horizontals, and between 40 ± 10 and 130 ± 10 for diagonals. These data show that in our sample there are not significantly more cells with optimal orientations near vertical or horizontal at 2–5° retinal eccentricity than there are those preferring diagonal orientations. There are significantly more cells with preferred orientations of 40 ± 10 than 130 ± 10 ; the reason for this asymmetry is unclear.

Tuning specificity for different visual axes was assessed by pooling all cells having their optimal orientation within 20° of either the horizontal or vertical axes and comparing them to the rest of the cells. The orientation tuning specificity obtained in this fashion for horizontally and diagonally oriented units is shown in Fig. 2. Simple (S-type) and complex (CX-type) cells were also analyzed separately. In our sample neither S-type nor CX-type cells show significant differences in tuning specificity for the horizontal–vertical orientations *versus* the oblique orientations. We also recorded from 24 foveal cells in two tangential penetrations. Of these 10 were selective for horizontal and vertical (H, ± 20 ; V, ± 10) and 12 for diagonal (± 15). Specificity for sharpness of tuning did not differ significantly among these cells (median = 18 for horizontals and verticals; median = 22 for diagonals).

We conclude that if meridional differences in orientation sensitivity do indeed exist in the monkey, they are not reflected in the properties of striate cortex neurons representing the visual field from 2° to 5° from the fovea. The small sample of cells collected from foveal striate are not encouraging in revealing such specialization. We did not, however, explore this central region as systematically as Mansfield⁶ has done.

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