

Dimensional selectivity of neurons in the dorsolateral visual area of the owl monkey

STEVEN E. PETERSEN, JAMES F. BAKER and JOHN M. ALLMAN

Division of Biology 216-76, California Institute of Technology, Pasadena, Calif. 91125 (U.S.A.)

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The discovery of a large number of extrastriate cortical visual areas has led to the hypothesis that each area performs its own set of functions in visual perception or visuomotor coordination^{1-3,10,13,16}. Owl monkey visual cortex contains at least 9 topographic representations of the visual field^{1,3}. We have found in one of these areas, the dorsolateral crescent (DL), that more than two-thirds of the neurons are selective for the spatial dimensions of visual stimuli within excitatory receptive fields much larger than the preferred stimulus dimensions. In preliminary results from other extrastriate areas, such neurons are much less common.

Single neurons were recorded from 4 extrastriate areas of two chronically-prepared owl monkeys. One-hundred-and-nine neurons were studied quantitatively (52 from DL; 30 from the middle temporal area (MT); 13 from the dorsomedial area (DM); 14 from the medial area (M)). Recording techniques were similar to those described in Allman et al.² with the exception that both eyes were fixed and brought into binocular alignment, and the visual stimuli were presented on a tangent screen 28.5 cm from the animal. Also, the animal's sedation was maintained with small doses of ketamine-HCl (3 mg/kg/h i.m.).

A receptive field map of the exposed cortex was constructed and electrode penetrations were placed in a particular area by comparison to the published maps of Allman¹ and Allman and Kaas³. Electrolytic lesions were placed in selected penetrations. Electrode placements and the borders of areas were later verified by histological reconstruction of Nissl-stained and myelin-stained sections. Responses of units in identified areas were first studied qualitatively by hand-controlled stimuli, then quantitatively using computer-controlled stimuli. The computer presented stimuli in pseudorandomly-ordered sequences of bars of various lengths (the dimension orthogonal to the direction of movement), widths (the dimension parallel to the direction of movement), and spots of various diameters. All spike information was computer-collected and stored on magnetic disk for later analysis. Response magnitude was calculated as the difference between the mean impulse rate during the stimulus presentation and the mean spontaneous rate. Nearly all extrastriate neurons exhibited

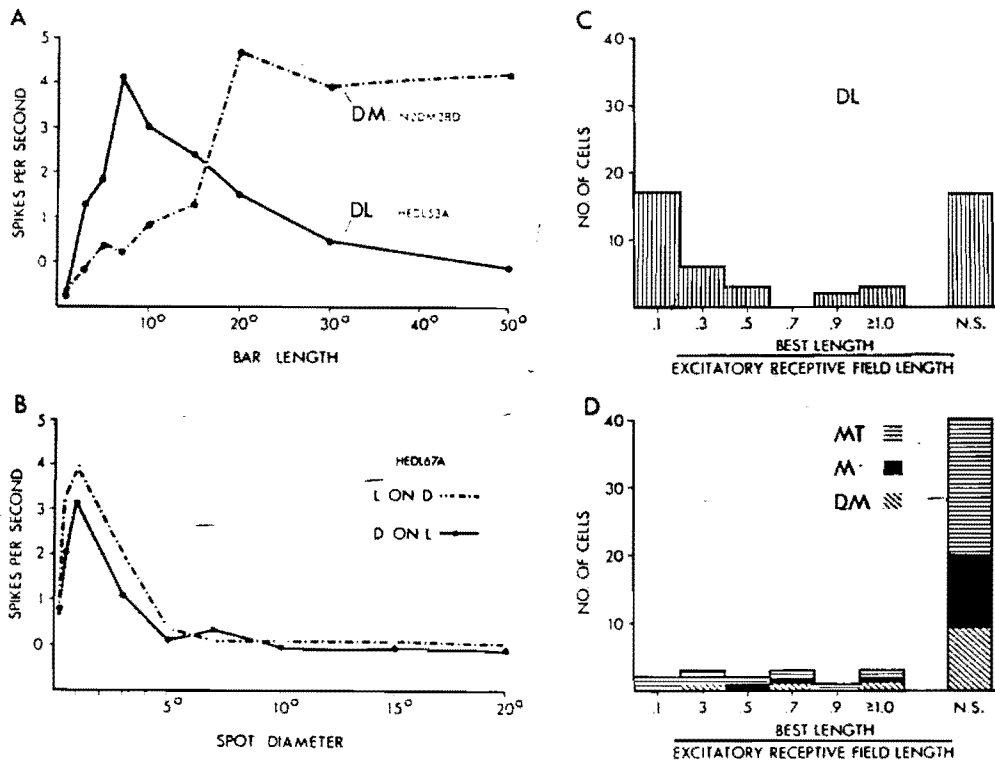


Fig. 1. A: responses of two units to different bar lengths. Each data point is the average of 5 stimuli presented in pseudorandom order. HEDL53A (solid line) was recorded from DL and shows marked selectivity. N2DM28D (dashed line) illustrates the typical response profile for cells outside of DL, in which the cell summates up to a certain value, whereupon the response levels off. The length of the excitatory receptive field for both cells was 20°. B: responses of a DL neuron to light (open circles) and dark (closed circles) spots of different diameters. Responses to stimuli of the same size were virtually the same regardless of contrast. C and D: optimal bar length is expressed as a percentage of the comparable dimension of the excitatory receptive fields. Cells with a length selectivity index of less than 0.5 were considered to be non-selective and are represented by the bins at the right. The average length of the excitatory receptive fields in DL was 20.3° with a S.D. of 9.5°, while the combined average for the other areas was 15° with a S.D. of 7.4°.

some direction, orientation, and velocity sensitivity⁵, and the dimension series were run at the optimal velocity in the preferred direction of each neuron studied.

Most DL neurons were sharply dimensionally-selective: they responded well only to stimuli which had near optimal dimensions (see Fig. 1a (DL cell) and Fig. 1b). Most cells outside of DL showed response summation up to a certain stimulus value, but were unaffected by further increases (Fig. 1a, DM cell). An index of stimulus dimension selectivity was calculated using the formula:

$$I = \frac{\text{response to the largest stimulus dimension tested}}{\text{response to the optimal stimulus dimension tested}}$$

For length and spot diameter, DL cells were significantly more selective than cells in DM, M, and MT, and were significantly more selective for width than MT neurons. The statistical test used was a one-way analysis of variance with comparisons being

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Fig. 1
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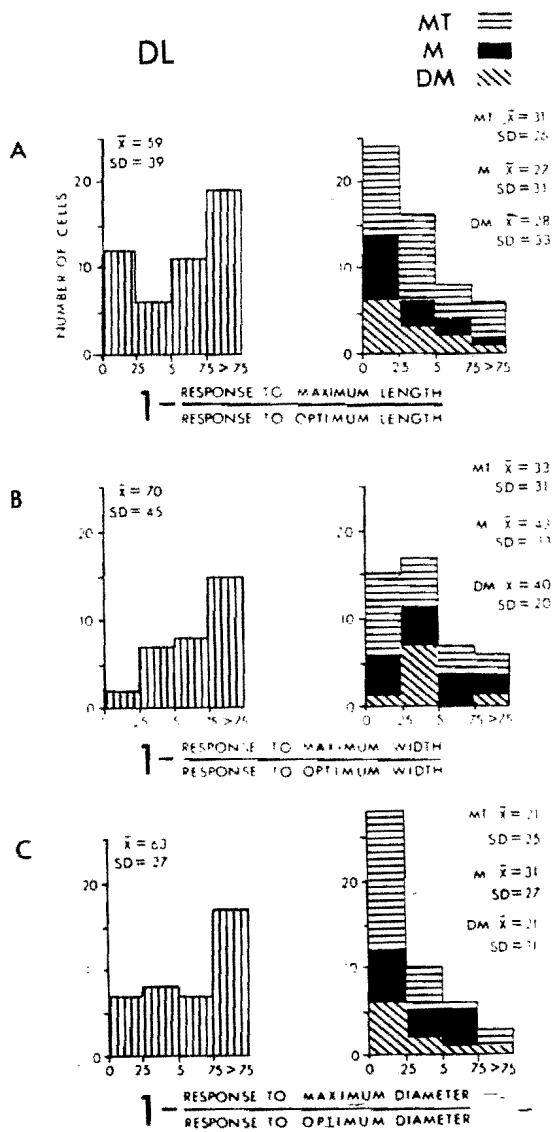


Fig. 2. Distributions of stimulus dimension selectivity indices for length (A), width (B), and spot diameter (C). The distributions for DL cells are on the left, and the distributions for MT, M and DM cells are on the right. Statistics comparing these distributions; *df* for length = 3,94; width = 3,66; spot diameter = 3,81. *S*-values for length, width and spot diameter selectivity, respectively: DL vs MT = 3.42*, 3.91*, 8.66*; DL vs M = 3.14*, 1.53, 3.44*; DL vs DM = 2.76*, 1.55, 4.94*; MT vs M = 0.05, 0.21, 0.29; MT vs DM = 0.03, 0.07, 0.01; M vs DM = 0.01, 0.02, 0.21. *, *P* < 0.05.

made between areas using Scheffe's multiple comparisons (see Fig. 2 for *S*-values)¹⁴. We assumed that recordings made in the same area of different animals were from the same population. Fig. 2a, b and c shows the distribution of selectivity indices for the 4 areas.

The dimensional selectivity of DL cells was independent of the amount or sign of contrast in the receptive field. Eight cells which responded well to either contrast were tested using both light-on-dark and dark-on-light stimuli and the results were

invariably similar (Fig. 1b). Varying stimulus contrast over a 1.5 log unit range likewise had little effect on a unit's responsiveness. The optimal length and width were typically considerably smaller than the mapped excitatory receptive field. This is illustrated in Fig. 1c and d which shows distributions of optimal lengths as a proportion of receptive field length. Cells which had a selectivity index of 0.5 or less were considered as non-selective and are represented in the columns at the right. The dimensional selectivity of DL cells was also independent of stimulus position in the receptive field.

DL neurons had a wide range of preferred sizes. The optimal length varied from 1° to 30° , and the optimal width from 0.25° to 7° . The length and width preferences appeared independent of each other for 21 cells in which both dimensions were tested. Of the 17 cells in DL from which complete data for all 3 spatial tests were available, 14 responded better to the best rectangular stimulus than to the best spot.

Many examples of cells sensitive to the spatial dimensions of visual stimuli have been reported. In most cases, the cells reported exhibit major differences from the cells found in DL. The cells in the rabbit temporal lobe⁷, and the convex edge detectors in the frog optic nerve and tectum¹², are not independent of contrast, in that they fire only to dark-on-light stimuli. The local edge detectors in the cat and rabbit retinae^{8,11}, the spot cells in V-II of the macaque⁴, and the lower-order hypercomplex cells of the visual cortex of the cat¹⁰ are strongly dependent on the position of the stimulus in the receptive field. Most of the cells, including the neurons in the superficial layers of the superior colliculus of the macaque¹⁵, lack the orientation specificity, and the independent specification of length and width preferences of DL neurons. One type of higher-order hypercomplex cell (see Figs. 23-25 in Ref. 10) found by Hubel and Wiesel in V-III of the cat closely corresponds to the neurons found in DL. However, we have found no evidence, other than the DL cells' preference for rectangular stimuli, that DL cells show the characteristic higher-order hypercomplex pattern of selectivity to orientations 90° apart. The strongest similarities exist between DL neurons and the neurons of the medial bank of the lateral suprasylvian sulcus in the cat studied by Camarda and Rizzolatti⁶, and there is a striking similarity in the percentage of dimensionally-selective cells in the two regions (about 70%).

The dimensional selectivity of DL neurons suggests that DL contributes to form or shape perception. This hypothesis is consistent with the observation that DL has the most expanded central visual field representation of all of the owl monkey's cortical visual areas¹.

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