Ocular Dominance Peaks at Pinwheel Center Singularities of the Orientation Map in Cat Visual Cortex

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Crair, Michael C., Edward S. Ruthazer, Deda C. Gillespie, and Michael P. Stryker. Ocular dominance peaks at pinwheel center singularities of the orientation map in cat visual cortex. *J. Neurophysiol.* 77: 3381–3385, 1997. In the primary visual cortex of monkey and cat, ocular dominance and orientation are represented continuously and simultaneously, so that most neighboring neurons respond optimally to visual stimulation of the same eye and orientation. Maps of stimulus orientation are punctuated by singularities referred to as ''pinwheel centers,'' around which all orientations are represented. Given that the orientation map is mostly continuous, orientation singularities are a mathematical necessity unless the map consists of perfectly parallel rows, and there is no evidence that the singularities play a role in normal function or development. We report here that in cats there is a strong tendency for peaks of ocular dominance to lie on the pinwheel center singularities of the orientation map. This relationship predicts but is not predicted by the tendencies, previously reported, for pinwheels to lie near the center lines of ocular dominance bands and for iso-orientation bands to cross ocular dominance boundaries at right angles. The coincidence of ocular dominance peaks with orientation singularities is likely to reflect a strong underlying functional link between the two visual cortical maps.

INTRODUCTION

Hubel and Wiesel described maps for both orientation and eye preference in visual cortex and proposed a unified model in which the representation of ocular dominance ran orthogonal to bands of like orientation preference (Hubel and Wiesel 1974), assuring representation of all orientations through both eyes. While later imaging studies revised this model in detail (Blasdel and Salama 1986; Grinvald et al. 1986; Hubel et al. 1978), revealing singularities of unknown function in the orientation map around which all orientations were represented (Blasdel 1992; Bonhoeffer and Grinvald 1993; Rojer and Schwartz 1990), one of its features, the tendency for iso-orientation lines (along which orientation preference does not change) to cross the boundaries of ocular dominance domains at right angles, was confirmed in monkey (Bartfeld and Grinvald 1992; Obermayer and Blasdel 1993). The same imaging studies also revealed a tendency for pinwheel center singularities of the orientation map to lie along the center lines of ocular dominance bands. Similar results have been reported in cat (Hubener et al. 1995).

We sought to determine whether a closer relationship might exist between the representations of eye preference and stimulus orientation than those previously reported. We found such a relationship, which not only predicts the earlier findings but also yields some insight into development and possible function.

METHODS

Optical imaging

Optical intrinsic signal responses were measured using standard techniques (for review, see Bonhoeffer and Grinvald 1996). Briefly, reflectance of primary cat visual cortex (AP −2.0 to 2.0, close to the V1/V2 border, illuminated with 610-nm light) following monocular presentation of moving high-contrast square wave gratings (0.1–0.2 cycles/deg, 1 cycle/s, 8 orientations separated by 22.5 deg in pseudorandom order) was captured at 192 × 144 pixel resolution through a matching 610-nm filter by a cooled slow scan CCD Camera (Princeton Instruments, NJ). Images were high-pass filtered (1.2-mm kernel) and smoothed (50 μm kernel) when necessary. Cortical responses to the presentation of different stimulus orientations were combined and summarized using a single pseudocolor representation referred to as an angle map. Ocular dominance (OD) ratio maps were computed by adding up the responses to all stimuli presented to the left eye and dividing by the sum of the responses to stimuli presented to the right eye. Orientation images used in this paper were responses to a particular oriented stimulus divided by the average response to all orientations through either eye (sometimes referred to as a ''cocktail blank'' normalization).

Analysis

The center lines of ocular dominance bands were computed from OD ratio maps using the medial axis transform (IDL, Research Systems). To determine unambiguously the positions of the peaks of the functional ocular dominance domains, the centroids of regions within the full-width, half-maximum response contour of the band-pass filtered OD ratio maps were computed. The positions of pinwheel singularities were defined as the points where the integral of the orientation differences around a pixel was ±180°. Angle maps were smoothed when necessary using a 3-bin Lee filter (IDL) to prevent identification of spurious pinwheels.

RESULTS

Maps of orientation and ocular dominance from seven cats (P26-P55) with normal visual experience were obtained by imaging intrinsic optical signals (Bonhoeffer and Grinvald 1993, 1996). Figure 1 shows a typical activity pattern in a cat. Response to oriented stimuli is patchy and heterogeneous, with different areas of cortex responding to different stimulus orientations. In total, this response tiles the cortex into a single orientation map, which consists of regions of smooth change in orientation preference and singularities
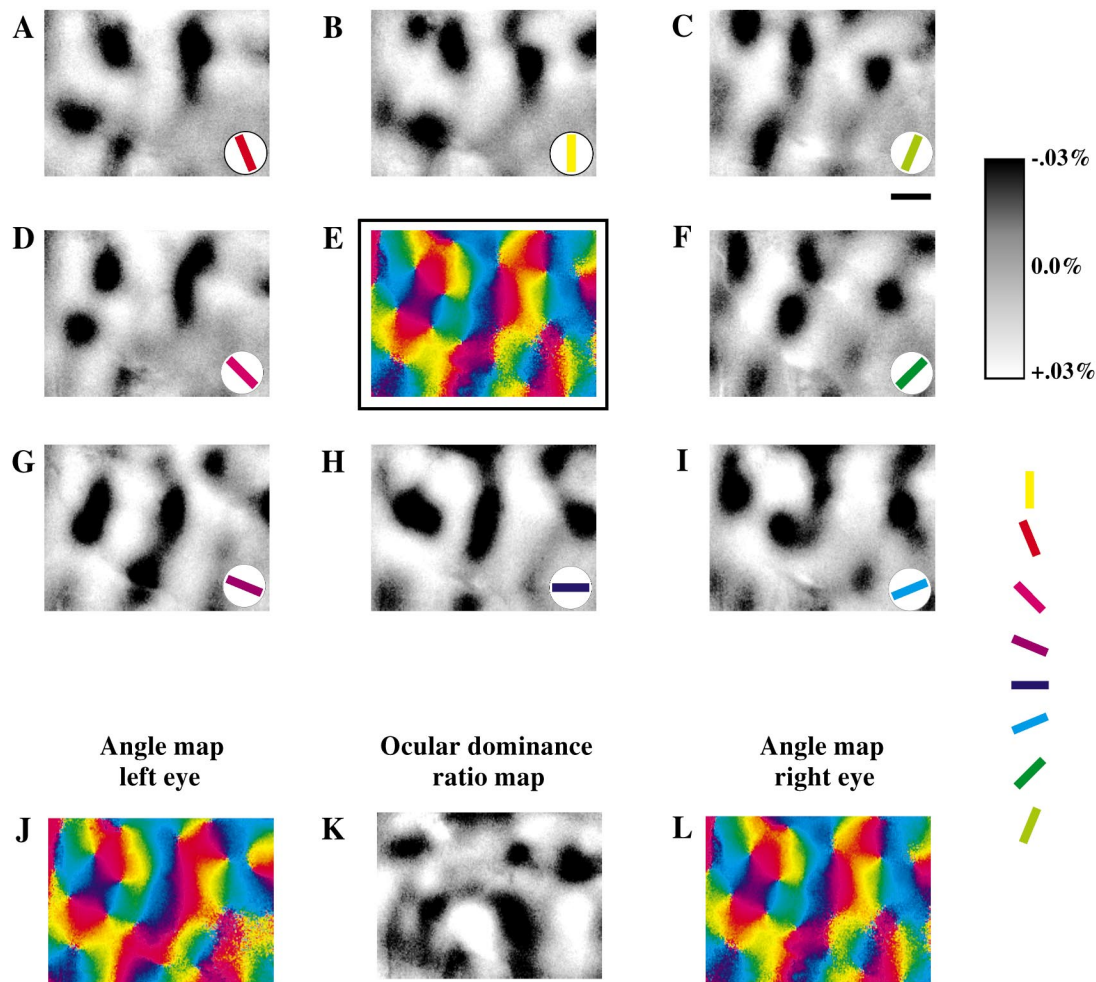
FIG. 1. Gray-scale images (*A–D, F–I*) show sum of 2 eyes' responses to stimulation at orientation indicated by colored bar insets. Dark regions are areas of strong neuronal response. Angle map (*E*) shows preferred stimulus orientation (scale at *right*). Angle maps for 2 eyes shown separately (*J* and *L*) are similar. In dark regions of ocular dominance (OD) ratio map (*K*), left eye responds better than right eye. Scale bar, 500 μm. Medial up, anterior to right.

known as ''pinwheels'' around which all orientations are represented locally. OD ratio maps in cat (Fig. 1*K*), like monkey (Bartfeld and Grinvald 1992; Obermayer and Blasdel 1993), show regions of cortex that respond more strongly to stimulation of one eye than the other and correspond closely to anatomic OD columns (Ts'o et al. 1990). OD maps in the cat are less regular than the parallel stripes found in much of monkey visual cortex.

Using automated techniques described in METHODS, we identified the locations of pinwheel center singularities in the orientation maps (open star in Fig. 2*A*), as well as the center lines of ocular dominance bands (thin white or black lines in Fig. 2*D*). We then measured the separations between pinwheel center singularities and the center lines of ocular dominance bands. Figure 3*A* summarizes these data in the form of a cumulative probability distribution. Visual inspection of the exemplary maps shown in Fig. 2 and the quantitative analysis in Fig. 3*A* reveals that there is a statistically significant tendency for pinwheels to lie near the center lines of the ocular dominance bands. Using the same pinwheel center positions and ocular dominance maps, but shuffling the positions of pinwheel centers with respect to the ocular

dominance maps by rotating them 180°, produced a greater average separation (*P* < 0.0025, Kolmogorov-Smirnov test), indicating that the pinwheels lie nearer the ocular dominance band centers than expected by chance. A Monte-Carlo analysis of the pinwheel to ocular dominance band separation in which pinwheels were placed at random positions on the ocular dominance map also resulted in a greater average distance than that actually observed (*P* < 0.005, Kolmogorov-Smirnov test). The actual mean distance from pinwheels to the nearest ocular dominance band center line was 99 μm. In the shuffled maps, it was 132 μm, and in the Monte-Carlo analysis, it was 117 μm. Thus there is a real tendency, which can be appreciated by visual inspection, for pinwheels to lie near the center lines of ocular dominance bands in cat, though the tendency is not large nor always obvious.

Ocular dominance bands are not uniform along their course. Periodic peaks in the density of innervation are evident in transneuronal labeling studies (Anderson et al. 1988; Murphy et al. 1995; Shatz and Stryker 1978). Similar peaks are also evident in the intensities of the optical signal evoked by monocular stimulation, as shown by the contours drawn in Fig. 2*C*. Automated identification of these peaks of ocular
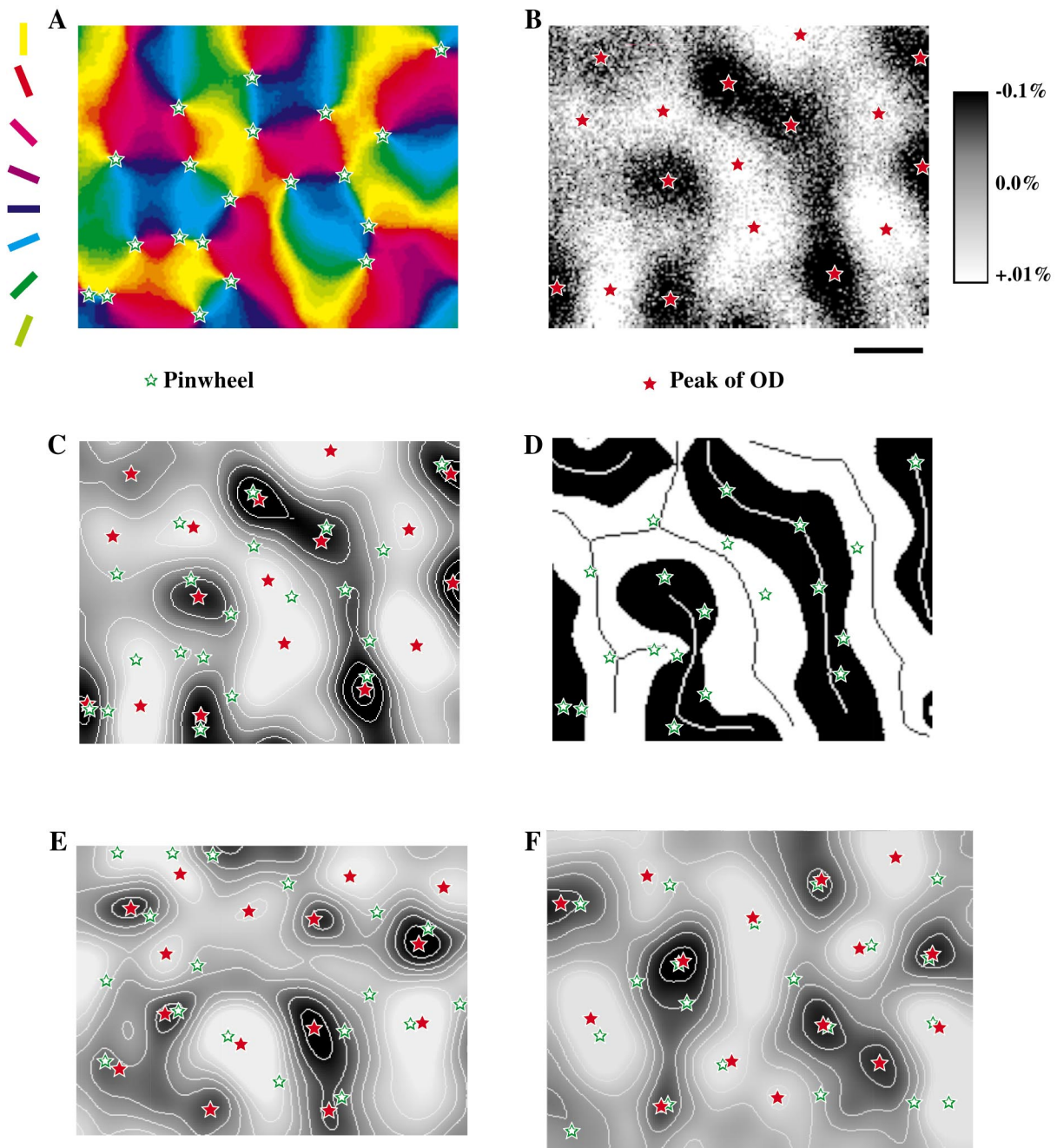
FIG. 2. Open star, positions of pinwheel centers identified automatically in angle map (*A*). Filled star, peaks of OD ratio maps (*B, C, E,* and *F*). OD center lines shown as thin black and white lines (*D*). Relationship between pinwheels (open star) and OD peaks (filled star) apparent in typical example (*C*), worst case (*E*), and best case (*F*). Scale bar, 500 μm. Medial up, anterior to right.

dominance (filled star in Fig. 2, *B, C, E,* and *f*) shows clearly that they tend to fall on or near pinwheels. The tendency for the peaks of ocular dominance columns to fall on or near pinwheel center singularities was striking (Fig. 3*B*) and much stronger than the tendency for pinwheels to lie near the center lines of ocular dominance bands ($P < 0.0001$ for OD peak-pinwheel vs. $P < 0.0025$ for pinwheel-OD center line, Kolmogorov-Smirnov test between experimental and shuffled data). Measurements of the distance between the peaks of ocular dominance and the nearest pinwheel center singularities clearly reflect this strong relationship, with a

mean peak to pinwheel separation of 202 μm as compared with 295 μm in shuffled maps ($P < 0.0001$) and 293 μm in Monte-Carlo maps in which pinwheels were placed at random positions on the center lines of ocular dominance bands ($P < 0.00001$). The median separation between OD peaks and pinwheels was 138 μm, only 47% of the median distance in the shuffled maps.

DISCUSSION

We describe here a striking and highly significant tendency for the peaks of monocular responsiveness along the
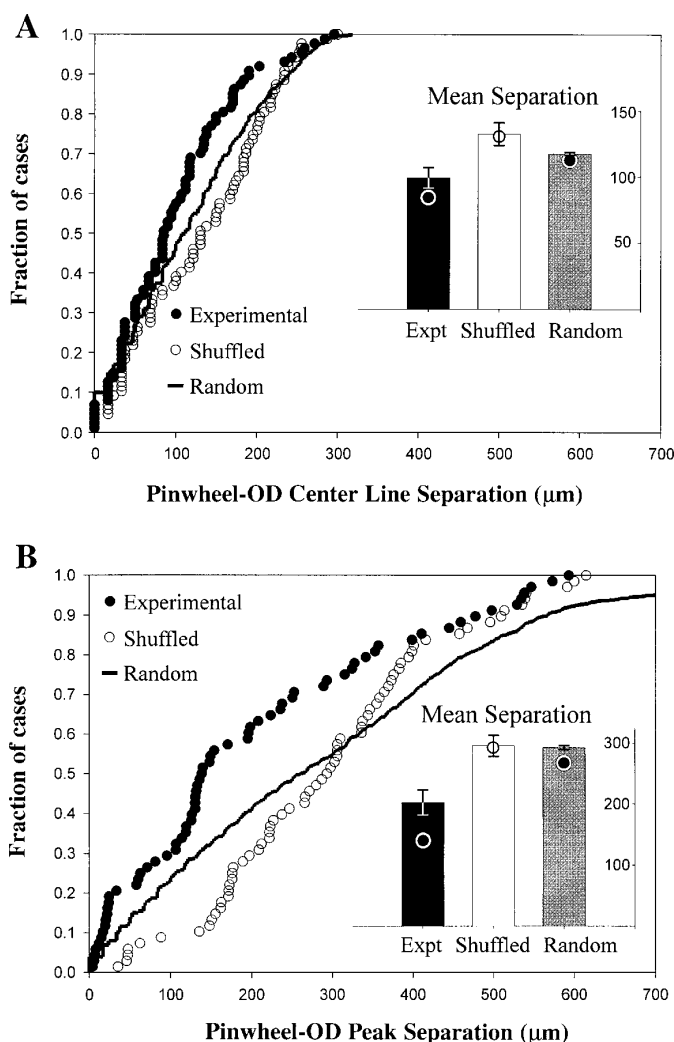
A

B

FIG. 3. Distributions of distances between experimental (●), shuffled (○), and randomly placed pinwheels (−) and nearest OD center line (A). Distributions shown of distances between automatically identified OD peaks and experimental (●) and shuffled (○) pinwheels and pinwheels randomly placed on OD center lines (−; B). *Insets*: error bars show standard error of mean; dots show median.

course of ocular dominance columns to lie close to singularities in the orientation map in cat visual cortex. Because OD peaks naturally lie near OD center lines, the close relationship between peaks and pinwheels accounts for the tendency of pinwheels to lie near OD center lines. The Monte-Carlo analysis reveals that the converse is not true: random placement of pinwheels on OD center lines (Fig. 3B ''random'') does not account for the experimentally observed proximity of OD peaks to pinwheels, because it fails to place the pinwheels on the peaks of ocular dominance and allows them instead to lie anywhere along their length.

Similar reasoning also reveals that the relationship between OD peaks and pinwheels is not predicted by the previously described tendency for iso-orientation lines to cross ocular dominance column boundaries at right angles (Bartfeld and Grinvald 1992; Hubener et al. 1995; Obermayer and Blasdel 1993). In fact, the relationship described here predicts the earlier finding, given weak constraints on smoothness in the orientation maps.

Because of the general continuity of the mapping of preferred orientation, knowledge of the position of pinwheel singularities is effectively equivalent to a specification of the entire orientation map (Wolf et al. 1993). Therefore, the present description of a simple relationship between the map of ocular dominance and pinwheel center singularities amounts to a comprehensive description of the entire relationship between the two maps.

We see three possible explanations for the present finding. One hypothesis is that there is some special structural or neurochemical feature responsible for both the peaks of monocular responsiveness and the orientation singularities. A natural candidate is the koniocellular geniculocortical projection to the cytochrome oxidase-rich blobs (Boyd and Matsubara 1996; Hendry and Yoshioka 1994; Murphy et al. 1995), which may act independently to create both orientation singularities and peaks of monocular responsiveness. It will be important to search for anatomic or neurochemical features that distinguish the pinwheel centers from other regions of cortex, particularly at the relevant times during early development.

A second hypothesis is that mechanisms that are responsible for the development of orientation and ocular dominance columns also cause them to be coupled. For example, if these mechanisms act to maximize locally correlated neuronal activity (Miller et al. 1989), then regions around orientation singularities would be at a disadvantage because not all cells at pinwheels are driven well by the same oriented contours (if oriented stimuli excited cells at one edge of the singularity, they would inhibit the cells on the other side). Monocular inputs to the pinwheel singularities, which may come for instance from spontaneous retinal activity, thus would be their greatest possible source of local correlated input. Models of the conjoint development of orientation and ocular dominance columns have explored these issues (Obermayer et al. 1995; E. Erwin and K. Miller, unpublished data).

Alternatively, the mechanisms of development may act to keep as nearly constant as possible the total variability among all stimulus dimensions represented (Durbin and Mitchison 1990; Kohonen 1989). The present finding is a partial confirmation of this hypothesis in that the regions in which ocular dominance is most nearly constant (OD peaks) tend to lie on the regions of the most rapid change in orientation (pinwheels). Evidence has been presented, however, that this tradeoff in variance among the modalities represented does not extend to topography (Das et al. 1995), and it is not yet clear how the optimality criteria that led to these models would operate in terms of the cellular mechanisms, architecture, and activity patterns that are actually responsible for the development of cortical maps.

Does a similar relationship between the orientation and ocular dominance maps exist in monkey? In the visual cortical representation of the periphery (LeVay et al. 1985), or much more widely after monocular deprivation (Horton and Hocking 1997), OD columns in the monkey wax and wane or break up into patches that are always centered on cytochrome oxidase (CO) blobs and that resemble OD columns in cats. This suggests that OD peaks in monkeys would lie under the CO blobs. If OD peaks are colocalized with pinwheels in the monkey, as we have found in the cat, then

the observation that CO blobs do not colocalize with pinwheels (Bartfeld and Grinvald 1992) is surprising.

The relationship described here between OD peaks and pinwheels powerfully constrains the relative arrangement of the orientation and ocular dominance maps. It will be interesting to determine whether similar relationships characterize other stimulus features that may be mapped onto the visual cortex, such as direction preference, spatial frequency preference, and preference for ON or OFF stimuli.

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