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## **Relation Between Retinotopical and Orientation Maps in Visual Cortex**

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**A recent study of cat visual cortex reported abrupt changes in the positions of the receptive fields of adjacent neurons whose preferred orientations strongly differed (Das & Gilbert, 1997). Using a simple cortical model, we show that this covariation of discontinuities in maps of orientation preference and local distortions in maps of visual space reflects collective effects of the lateral cortical feedback.**

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Theoretical analysis of the role of lateral interactions in the cooperative behavior of neuron ensembles resulted in two main conclusions:

1. Lateral interactions may create a continuum of localized stable states (Ben-Yishai, Bar-Or, & Sompolinsky, 1995).
2. Inhomogeneities in lateral connections break the continuity of these states, leading to clustering at particular locations in the neural net (Tsodyks & Sejnowski, 1995).

The visual cortex clustering would imply that receptive fields of nearby neurons exhibit discontinuities in their features.

We tested this hypothesis by simulating a network of interacting neocortical neurons with the architecture of primary visual cortex. In such a network, the receptive field properties of a neuron result from both the pattern of external inputs from lateral geniculate nucleus (LGN) and the pattern of lateral connections (Ernst, Pawelzik, Wolf, & Geisel, 1997).

The network is formed by  $n_x \times n_y$  columns consisting of excitatory (index e) and inhibitory (index i) neuronal populations, each receiving afferent input  $I^{aff}$  from the LGN, lateral excitatory input  $I_e^{lat}$ , and lateral inhibitory input  $I_i^{lat}$ . The population dynamics for column  $j$  reads,

$$\tau_e \cdot \frac{dA_e(j, t)}{dt} = -A_e(j, t) + g_e(I_{ee}^{lat}(j, t) + I_{ie}^{lat}(j, t) + I_e^{aff}(j, t)), \quad (1)$$

$$\tau_i \cdot \frac{dA_i(j, t)}{dt} = -A_i(j, t) + g_i(I_{ei}^{lat}(j, t) + I_{ii}^{lat}(j, t) + I_i^{aff}(j, t)). \quad (2)$$

$g_e$  and  $g_i$  are piecewise linear gain functions (threshold linear neurons) with firing thresholds  $t_e, t_i$  and slopes  $s_e, s_i$ , and  $\tau_i, \tau_e$  are time constants. We assume that the connections  $W$  from one subpopulation to excitatory and inhibitory subpopulations do not differ significantly except for the total interaction strengths  $w$ , and therefore define the synaptic input as:

$$I_{ee}^{lat}(j, t) = w_{ee} \cdot \sum_{k=0}^N W_e(j, k) A_e(k, t) \quad (3)$$

$$I_{ei}^{lat}(j, t) = w_{ei} \cdot \sum_{k=0}^N W_e(j, k) A_e(k, t) \quad (4)$$

$$I_{ie}^{lat}(j, t) = w_{ie} \cdot \sum_{k=0}^N W_i(j, k) A_i(k, t) \quad (5)$$

$$I_{ii}^{lat}(j, t) = w_{ii} \cdot \sum_{k=0}^N W_i(j, k) A_i(k, t). \quad (6)$$

We assume that the strength of lateral connections depends on the proximity of the columns and relative angle between their preferred orientations:

$$W_e(j, k) = W_e^0 \cdot \exp\left(\frac{-|\vec{r}(j) - \vec{r}(k)|^2}{2 \cdot \sigma_e^2}\right) \exp\left(\frac{-|\Phi(j) - \Phi(k)|^2}{2 \cdot \sigma_e^{\Phi^2}}\right) \quad (7)$$

$$W_i(j, k) = W_i^0 \cdot \exp\left(\frac{-|\vec{r}(j) - \vec{r}(k)|^2}{2 \cdot \sigma_i^2}\right) \exp\left(\frac{-|\Phi(j) - \Phi(k)|^2}{2 \cdot \sigma_i^{\Phi^2}}\right). \quad (8)$$

The constants  $W^0$  normalize the coupling matrices  $W$  such that the average coupling strength to other neurons is one. The LGN inputs  $I^{aff}$  were assumed to originate from retinotopic locations uniformly distributed over

the visual field and to include an orientation bias given by a map of preferred orientations obtained by optical imaging (Bonhoeffer & Grinvald, 1991). The visual field has the same dimensions  $n_x, n_y$  such that one unit square corresponds to one column in the cortex.

$$I^{aff}(j, t) = \sum_{k=1}^N M(k) \cdot \left[ (1 - \epsilon) + \epsilon \cdot \exp \left( -\frac{|\Phi_{stim}(k) - \Phi(j)|^2}{2 \cdot \sigma_{rf}^2} \right) \right] \quad (9)$$

$$\cdot \exp \left( -\frac{|\vec{r}(k) - \vec{r}(j)|^2}{2 \cdot \sigma_{rf}^2} \right) \quad (10)$$

$$I_e^{aff}(j, t) = w_e^{aff} \cdot I^{aff}(j, t) \quad (11)$$

$$I_i^{aff}(j, t) = w_i^{aff} \cdot I^{aff}(j, t). \quad (12)$$

$M(k)$  denotes a stimulus mask that is 0 if there is no stimulus at position  $\vec{r}(k)$  in the visual field and 1 otherwise. The model cortex has been stimulated with gratings of radius  $\rho = 2$  in eight different orientations at each position of the visual field. While presenting these localized oriented stimuli, the network was allowed to converge to a solution. Receptive fields were obtained as the set of locations where presentation of stimuli lead to activation of a neuron (see Figure 1).

Orientation maps consist of regions where preferred orientation smoothly changes with the cortical location of neurons, separated by a set of discontinuities of preferred orientation called pinwheels and fractures. We assumed (see equation 8) that in accordance with anatomical evidence, lateral connections between a pair of neurons depend on their proximity in the cortex and the relative angle between their preferred orientations (Gilbert & Wiesel, 1985; Malach, Amir, Harel, & Grinvald, 1993). This implies that a pair of neurons located on opposite sides of a discontinuity have a weaker connection than the equally separated pair in the smooth region. Correspondingly, the localized stable states of the network will tend to cluster in the smooth regions, where interactions are stronger. Therefore, a stimulus moving across the visual field will cause a jump of activity across the fracture, leading to a corresponding jump in the locations of the receptive field centers (see Figure 1).

Our results demonstrate that lateral connections could play a crucial role in determining the retinotopic map in the visual cortex by causing a mismatch between the pattern of LGN inputs and the resulting receptive field properties. Subsequent development of connections between LGN and cortex could eliminate this mismatch (e.g., using Hebbian plasticity mechanisms).

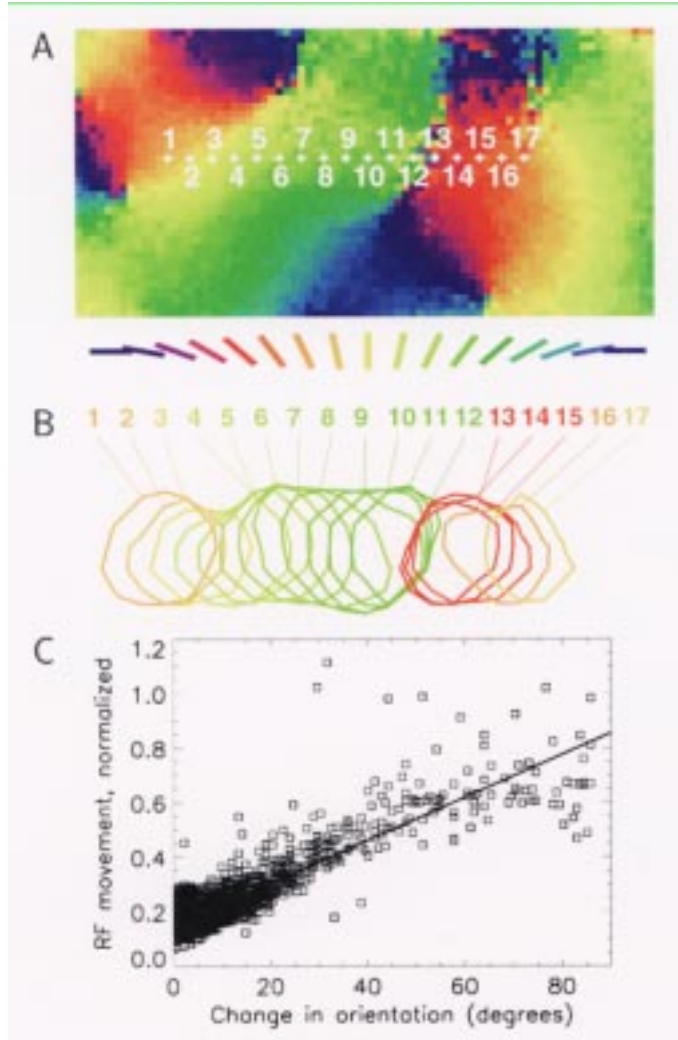


Figure 1: (A) Optical map of orientation preference with recording sites arranged on a line that crosses a fracture. A fragment of a map obtained in Bonhoeffer and Grinvald (1991) was used. Orientations are color coded according to the color bars below. (B) Receptive fields of neurons at the recording sites in A, shown with the color corresponding to their optimal orientations. (C) Shifts in the receptive fields positions, normalized by the size of the receptive fields, for nearby neurons versus change in their preferred orientations. The parameters for this simulation were  $n_x = 45$ ,  $n_y = 15$ ,  $\tau_e = \tau_i = 1.0$ ,  $s_e = 1.5$ ,  $s_i = 3.0$ ,  $t_e = 0.3$ ,  $t_i = 0.6$ ,  $w_{ee} = 1.3$ ,  $w_{ei} = 1.0$ ,  $w_{ij} = 0.2$ ,  $w_{ie} = 1.5$ ,  $\sigma_e^r = 1.5$ ,  $\sigma_e^\phi = 30^\circ$ ,  $\sigma_i^r = 3.5$ ,  $\sigma_i^\phi = 700^\circ$ ,  $\epsilon = 0.75$ ,  $\sigma_{rf}^r = 0.5$ , and  $\sigma_{rf}^\phi = 30^\circ$ .

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Received February 23, 1998; accepted June 17, 1998.