

Prenatal and postnatal development of laterally connected orientation maps

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Abstract

Both environmental and genetic factors interact to produce the orientation maps found in adult primary visual cortex of mammals. However, it is not clear how this interaction occurs during development, or whether both factors are crucial. Previous computational models have focused on either environmentally driven or genetically driven development alone. In contrast, we show that a two-stage model of development can account for a wider range of experimental data. The model explains how environmental and genetic information can be incorporated into the same neural hardware, using a common set of learning mechanisms. Our results suggest that while either environmental or genetically driven development is sufficient for maps and selectivity to form, prenatal activity speeds up early development and makes it more robust against environmental variation.

Key words: Orientation maps, Spontaneous activity, Cortical modeling, Nature-nurture

1 Introduction

Experiments in mammals such as cats, ferrets, and monkeys have shown that the orientation map patterns and receptive fields in primary visual cortex (V1) are produced by an interaction between environmental and genetic factors. Genetic influences are clear when measuring neural responses in newborns, before any visual experience. Even at or before natural eye opening, orientation-selective cells and orientation maps can be detected in newborn kittens and ferrets [5, 8, 9, 11, 12]. The overall shape of the orientation map changes very little during subsequent normal visual experience [9, 11]. Based on this evidence, one might conclude that orientation maps are largely genetically specified.

At the same time, it is clear that altering the visual environment can have dramatic effects on how orientation-selective neurons and maps develop. For instance, if kittens are raised in environments consisting of only one orientation of contour (e.g. vertical lines) during a critical period, an abnormally large number of their V1 neurons become responsive to vertical orientations [4]. Kittens raised in this way develop orientation maps that with larger area devoted to the overrepresented orientation [14]. Cats whose visual environment was even more abnormal, e.g. with eyelids sutured shut during development, have few orientation-selective neurons at all in V1 [5, 11]. Even in normal adult animals, the distribution of orientation preferences is slightly biased towards horizontal and vertical contours [7, 10], mirroring the distribution of orientations in normal visual environments [17]. Such a bias is consistent with neurons learning orientation selectivity from the environment. Orientation selectivity also improves greatly after

birth, and the maps become smoother and more well organized [9, 11]. Based only on the postnatal experiments, one might conclude that orientation maps develop primarily through visual experience.

Taken together, the evidence indicates that both genetic and environmental influences interact to produce the adult orientation map. However, important questions remain. How does this interaction actually occur? Could adult-like maps develop from environmental or genetic cues alone, or are both necessary? These questions are difficult to answer through biological experiments. Computational modeling, however, can lead to valuable insights, because it is easy to separate environmental and genetic influences in computational experiments. Existing models have been used to simulate how orientation maps can develop from visual input alone (e.g. natural images; [6]) or genetic factors alone, such as spontaneous neural activity (e.g. noise [13]; for review of existing models of each type, see [16].) However, models have not yet shown how V1 can have an initial map at birth that becomes smoother and more selective due to postnatal visual experience, while retaining the original map shape. The visually driven and internally driven models also differ in many ways besides the source of activity, and thus it has been difficult to determine whether the activity patterns alone account for any differences between the results.

In this paper we construct a single model to show how an initial map can develop from spontaneous neural activity, then be refined through visual experience to reflect the environment. The model develops orientation maps and selective neurons for a very wide range of training patterns. This result suggests that the processing implemented in orientation maps is very general, and does not need to be encoded specifically in the genome. The role of spontaneous activity may primarily be to speed up development so that even newborns have functional neural processing. This ability may make development more predictable in unusual environments, and allow higher levels to organize sooner.

2 HLISSOM model

The simulations are based on the HLISSOM model [1], a version of the LISSOM model [15] extended to support natural images by modeling the LGN. The architecture is shown in figure 1, and will be briefly reviewed below. (For more details, see [3].) The model consists of a hierarchy of two-dimensional sheets of neural units modeling different areas of the visual system: a sheet of retinal photoreceptors, a pair of sheets of LGN units (ON-center and OFF-center), and a sheet of cortical units (“neurons”) representing V1. Because the focus is on the two-dimensional organization of V1, each neuron corresponds to a vertical column of cells through the six anatomical layers of the cortex.

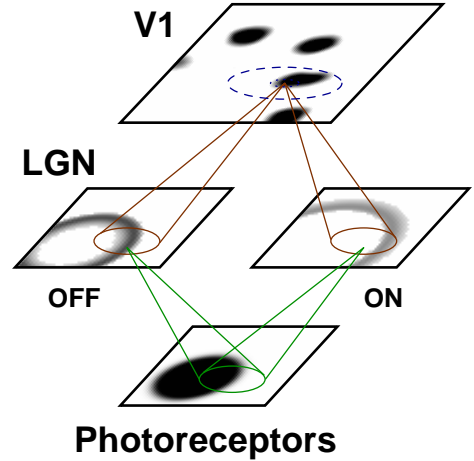
The input to the model consists of a series of activity patterns on the sheet of photoreceptors, such as grayscale photographic images. Each LGN unit (i, j) computes its response η_{ij} as a scalar product of a fixed weight vector and its receptive fields on the photoreceptor sheet:

$$\eta_{ij} = \sigma \left(\sum_{\rho ab} \gamma_{\rho} X_{\rho ab} w_{ij, \rho ab} \right), \quad (1)$$

where ρ specifies which input sheet to use (the photoreceptors, in this case), σ is a piecewise linear sigmoid activation function, γ_{ρ} is a constant scaling factor, $X_{\rho ab}$ is the activation of input unit (a, b) on sheet ρ at timestep t , and $w_{ij, \rho ab}$ is the corresponding weight value. Each V1 neuron computes its initial response like that of an LGN unit, except that ρ specifies one of the

Fig. 1. HLISSOM model of orientation map development.

The model is a hierarchy of sheets of neural units, modeling the early visual pathway. There are two sheets of LGN units. The LGN units receive input from their circular receptive fields (RFs) on the photoreceptors. Connections to a sample photoreceptor RF are plotted for two LGN units. Similarly, neurons in V1 have circular RFs on both LGN sheets; connections to two of the RFs are shown. V1 neurons also have lateral excitatory (small dotted circle) and lateral inhibitory (large dashed circle) connections to their neighbors. Input patterns are drawn in a grayscale bitmap on the photoreceptor sheet, and the ON and OFF LGN units compute their activity. Once all LGN units have been activated, initial V1 activity is computed from the LGN responses, and the activity then spreads laterally within V1. Both afferent and lateral V1 weights are adapted when the activity settles.



ON or OFF LGN sheets. After the initial response, the V1 activity settles through short-range excitatory and long-range inhibitory lateral interaction:

$$\eta_{ij}(s) = \sigma \left(\sum_{\rho ab} \gamma_{\rho} X_{\rho ab}(s-1) w_{ij, \rho ab} \right), \quad (2)$$

where ρ identifies either an LGN sheet or the lateral excitatory or inhibitory weights to V1, γ_{ρ} is a constant scaling factor for each ρ (negative for inhibitory lateral weights), and $X_{\rho ab}(s-1)$ is the activation of input unit (a, b) during the previous settling step. The V1 activity pattern starts out diffuse, but within a few iterations of equation 2, converges into a small number of stable focused patches of activity, or activity bubbles. After the activity has settled, the connection weights of each V1 neuron are modified. All V1 weights adapt according to the Hebb rule, normalized so that the sum of the weights from each sheet ρ is constant for each neuron (i, j) :

$$w_{ij, \rho ab}(f+1) = \frac{w_{ij, \rho ab}(f) + \alpha_{\rho} \eta_{ij} X_{\rho ab}}{\sum_{ab} [w_{ij, \rho ab}(f) + \alpha_{\rho} \eta_{ij} X_{\rho ab}]}, \quad (3)$$

where η_{ij} stands for the activity of neuron (i, j) in the final activity bubble, $w_{ij, \rho ab}(f)$ is the connection weight from the previous fixation, α is the learning rate for each type of connection, and $X_{\rho ab}$ is the presynaptic activity. The larger the product of the pre- and post-synaptic activity $\eta_{ij} X_{\rho ab}$, the larger the weight change. At long distances, few neurons have correlated activity and therefore most long-range connections eventually become weak. The weakest connections are eliminated periodically, resulting in patchy lateral connectivity similar to that observed in the visual cortex.

For the experiments reported in this paper, the 36×36 ON-center and the 36×36 OFF-center LGN sheets received input from a 54×54 photoreceptor array. Each ON/OFF unit had a fixed Difference of Gaussians receptive field (RF) within the photoreceptor array. Initially, the afferent weights of the 96×96 V1 neurons were random, and the lateral weights had a smooth circular Gaussian profile. The learning parameters were the same as in our earlier V1 orientation model [2], generated for this cortex size and input patterns using a systematic scaling methodology [1].

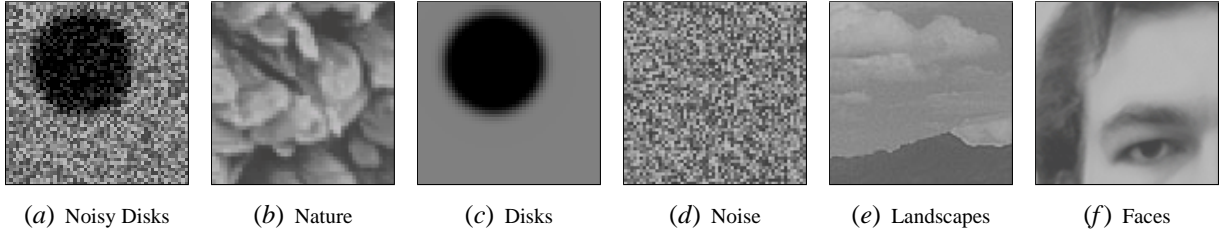


Fig. 2. **Training patterns.** The network was trained prenatally on 1000 noisy, disklike activity patterns, as in (a), followed by 9000 images of natural objects and natural scenes, as in (b). The prenatal training is intended to model retinal waves, which have spatially coherent patches. We also tested a series of control patterns, including the disks alone (c), random noise alone (d), horizontally biased images (e), and vertically biased images (f). Results with these other patterns show what features of the prenatal and postnatal activity are most important.

3 Experiments

To study how prenatal and postnatal learning together produce the adult organization, we simulated a two-stage process of development. In the prenatal phase of 1000 input presentations, input patterns consisted of noisy patterns of neural activity (figure 2a). These patterns were chosen to match retinal waves, which are the best-characterized source of spontaneous activity in early development. However, they can also represent any other spontaneous activity that includes large patches that are spatially coherent. The patterns consisted of uniform random noise combined with a large “disk” of activity representing a local patch of highly responding neurons (a retinal wave). Figure 2a shows an example. For the 9000 iterations in the postnatal phase, we used images of natural objects and scenes, modeling eventual visual experience (see example image in figure 2b).

Figure 3 shows that this network first develops an orientation map through spontaneous activity, then gradually refines it based on experience with natural images, without changing the overall shape of the map. The orientation preference distribution is also biased towards horizontal and vertical, as seen in ferret visual cortex [10]. These results are the main novel component of this work. To our knowledge, only one other computational model has been tested in this way; the postnatal training was found to entirely rearrange the map in that model [6], unlike in animals.

In further experiments, we explored how different pattern types can change the map organization. These three experiments act as controls for the main results, helping to determine what features of the model are crucial. Details are presented in [1], but the results are summarized here. First, we tested different postnatal training conditions, to see how different environments can change the outcome. Skewed data sets were indeed reflected in the maps, as found for ferrets [14]. For instance, for the Landscapes dataset (figure 2e), containing many horizontal contours, the orientation histogram became biased towards horizontal. For the Faces dataset (figure 2f), more neurons became tuned to vertical orientation. These findings replicate the experimental results from animals raised in biased environments, and suggest that the postnatal component of training is important because it allows the map to adapt to the actual environment of the animal.

Second, we tested different patterns of prenatal training activity, to determine what features of the noisy disks were crucial. Both the disks alone (figure 2c) and random noise alone (2d) resulted in orientation maps with locally coherent patches of orientation-selective neurons. How-

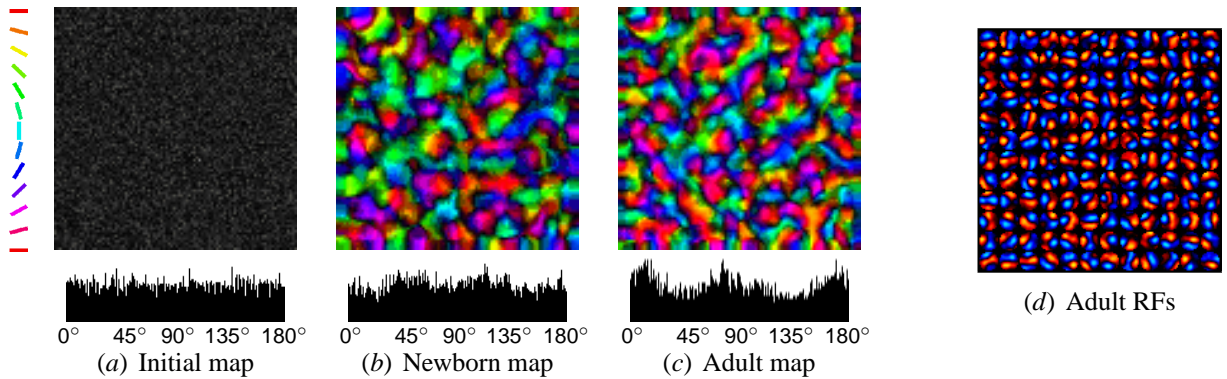


Fig. 3. **Two-stage development of the orientation map (color figure).** These plots show orientation maps for V1 at different stages of development in the model. Plots (a-c, top) show each V1 neuron colored with the orientation it prefers, according to the key at left. The brightness of the colors indicates how selective the neurons are — dark pixels represent unselective neurons, while bright pixels represent neurons highly selective for that orientation. At first, neurons are only weakly selective for orientation, because they have random receptive fields (a). After prenatal training, an orientation map has emerged, consisting of patches of neurons that prefer each orientation (b). Subsequent training with natural images increases the number of selective neurons, while keeping the same basic map shape (c). Receptive fields for every eighth neuron in the final map are shown in (d); areas where light excites the neuron are shown in red, while those where light reduces the response are shown in blue. Most neurons developed two or three-lobed receptive fields, as found in animals. The orientation histograms below each plot show that the initial and newborn maps have approximately flat distributions, but that the adult map has significantly more units that prefer horizontal (0° and 180°) and vertical (90°), as in animals and in the visual environment. These results show how genetic and environmental factors could interact to produce adult orientation maps and orientation-selective neurons.

ever, the receptive fields in the Disks case were much more selective than in typical newborn neurons. Thus including noise was crucial for obtaining realistic receptive fields. Yet for uniform random noise alone, the receptive fields were poorly selective, and primarily included receptive field types rarely reported in experimental studies of V1 (e.g. crosses). The orientation map was also less well organized than typical newborn maps. These results suggest that both spatially uncorrelated noise and spatially correlated activity determine how the prenatal map develops.

Third, we tested whether the prenatal training was crucial for developing orientation maps and selectivity, by training an initially random map only on natural images. Although the details of the final map organization differed from the normal case, the overall properties were very similar. Thus prenatal training is not required for a functional map to develop from natural image input.

4 Discussion and future work

The results presented in this paper show how environmental and genetic factors can interact to produce adult-like orientation maps. Both factors are crucial for explaining the experimental data, but the development of orientation maps and selectivity is very robust, i.e. maps can develop from a wide range of possible input patterns. The specific distribution of orientation preferences in the map reflects the distribution of orientations in the activity patterns, allowing the map to adapt to the environment.

Interestingly, prenatal training does not appear to be crucial for obtaining a well-organized final map, at least in normal environments. Thus it is not yet clear what roles the spontaneous activity and the maps found in newborns perform. They may help ensure, however, that maps develop normally in a wider range of possible environments. Prenatal training may also allow V1 to mature more quickly, which could be important for organizing higher levels of the visual system. Future studies will focus on how to distinguish between different types of internally generated activity from the resulting maps, in hopes of narrowing down the specific patterns responsible for the initial orientation maps in newborns.

5 Conclusion

The HLISSOM model shows how environmental and genetic factors can interact to produce adult orientation maps. Either factor alone is sufficient for developing the maps, but both are necessary to explain how newborns can have maps initially yet adapt to the environment. Orientation maps and selectivity appear to be very robust outcomes of developmental processes, and prenatal development may be important primarily as an optimization mechanism.

Acknowledgements

Supported in part by the National Institutes of Mental Health under Human Brain Project grant 1R01-MH66991, and by the National Science Foundation under grant IIS-9811478.

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