

## Reorganization of neural circuitry during growth of cat visual cortex

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The contribution of plasticity to normal development remains unsolved. Cortical growth may involve substantial modifications of neural circuitry, thus enabling to study cortical plasticity under natural rearing conditions. Here, we present experimental evidence for reorganization of ocular dominance (OD) column layouts during postnatal cortical growth. Furthermore, we show that the observed mode of reorganization is predicted by a large class of models for activity dependent development of neural circuitry. We conclude that cortical plasticity remodels columnar organization in normal development.

We test three conceivable scenarios of how the layout of OD columns might change during cortical growth: i) Balloon like isotropic expansion of cortex and OD domains, ii) anisotropic expansion of cortex by which OD domains would elongate in the direction of stretching, and iii) isotropic or anisotropic expansion accompanied by bending of OD domains resulting in a more isotropic layout of OD domains. Notice that, in contrast to i and ii, scenario iii requires remodeling of OD in parts of the neuronal population.

In experiment, we observed a considerable reorganization of OD columns during the late phase of postnatal cortical growth consistent with scenario iii, but inconsistent with either scenario i or ii. We used an image analysis method based on wavelets to analyze the two-dimensional spatial organization of OD columns in flat mount sections of 2-DG labeled OD columns in cat visual cortex. We found that the size of area 17 increased by 50% between postnatal week 4 and 10. However, during this period the mean spacing between adjacent OD columns showed only a weak and transient increase of about 10%. Consequently, the total number of OD domains in area 17 increased by more than ~30%. Moreover, the bandedness, a parameter quantifying the degree of anisotropy of layouts, decreased considerably over this time course. The absence of a persistent increase of column spacing excludes the balloon hypothesis (scenario i) while the decrease of the bandedness excludes anisotropic stretching as a possibility (scenario ii). However, isotropic expansion following reorganization (scenario iii) appears consistent with these data. To obtain a better understanding of scenario iii, we analyzed it in a model study.

Scenario iii is indeed predicted by most models for OD column development that have been proposed so far. It represents the generic behavior upon isotropic expansion under the presence of intracortical Mexican-hat like linear interactions of constant range. The basic mechanism is that the system tries to maintain its intrinsic spatial scale and the simplest way to achieve this is by bending its domains. This behavior is known under the name zigzag instability. For the sake of specificity, we analyzed the effect of cortical expansion on columnar layouts in the elastic net model and compared it to the degree of reorganization observed experimentally. Under various expansion conditions, the elastic net model indeed showed stereotypical behavior of a zigzag instability with bending and reorganization of OD domains. Consistent with experiment, the spacing of OD columns increased only transiently and the bandedness measure decreased over the same period. The degree and duration of reorganization strongly depended on the amount of expansion. For a realistic expansion scenario the predicted period of reorganization fairly matched that period in the visual cortex.

In conclusion, we observed a specific mode of columnar reorganization in cat visual cortex that appears to be induced by cortical expansion during growth. This mode of reorganization is predicted by most models for the activity dependent development of OD columns suggesting that cortical plasticity remodels columnar organization in normal development.