The influence of restricted orientation rearing on map structure in primary visual cortex

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ABSTRACT

Visual experience is critical to the development of the structure of the primary visual cortex and, in turn, normal functional vision. The primary visual cortex contains maps of multiple features of the visual input, and these maps are characterised by specific types of geometric relationships. Manipulations of the visual environment during development in animals such as ferrets, cats and monkeys provide an opportunity to probe the rules governing map formation via their effect on these relationships. Here we use a computational model of map formation based on dimension-reduction principles to predict the effect on map relationships of presenting only a single orientation to one eye and the orthogonal orientation to the other eye. Since orientation preference and ocular dominance are now tightly coupled one might expect orientation and ocular dominance contours to lose their normally orthogonal relationship and instead run parallel to each other. However, surprisingly, the model predicts that orthogonal intersection can sometimes be preserved in this case. The model also predicts that orientation pinwheels can migrate from the centre to the borders of ocular dominance columns, and that the wavelengths of the ocular dominance and orientation maps can become coupled. These predictions provide a way to further test the adequacy of dimension reduction principles for explaining map structure under perturbed as well as normal rearing conditions, and thus allow us to deepen our understanding of the effect of the visual environment on visual cortical development.

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Introduction

Visual experience is crucial to the development of the primary visual cortex (V1), and abnormal development can profoundly affect functional vision. For example, amblyopia is a common condition in humans that is characterised by a loss of visual acuity in one eye that is not caused by physical defects in the eye or any disease. The visual defects of human amblyopes have been reproduced in animal models through various manipulations of visual input such as monocular deprivation (Mitchell and Sengpiel, 2009). Electrophysiological and imaging studies of animals have also revealed the structural changes resulting from monocular deprivation that cause loss of acuity. More generally, manipulations of the visual environment of animals during their development have been used extensively to probe how environment and experience influence the structure and function of the visual system.

Neurons in V1 respond preferentially to stimuli with particular combinations of features. Amongst other features, neurons tend to prefer stimuli of a particular orientation (orientation preference, OP)

presented in one eye (ocular dominance, OD). In many mammals including cats (Crair et al., 1997a; Müller et al., 2000), monkeys (Blasdel, 1992a,b; Bartfeld and Grinvald, 1992; Obermayer and Blasdel, 1993) and ferrets (Müller et al., 2000), feature preferences co-exist in such a way that each combination of features is represented in the cortex (good coverage), while adjacent neurons across the surface of the cortex have similar response properties (good continuity) (Swindale, 1991). This results in feature maps, complex but stereotypical spatial patterns of response properties. Moving perpendicular to the cortical surface, cells tend to form columns with similar response properties (Hubel and Wiesel, 1977), and it is therefore often a good approximation to treat feature maps as two-dimensional.

These feature maps often have characteristic geometric relationships to each other. For instance, OP contours tend to intersect OD column borders perpendicularly in normal animals (Bartfeld and Grinvald, 1992; Blasdel, 1992b; Obermayer and Blasdel, 1993; Hübener et al., 1997; Kim et al., 1999; Müller et al., 2000). In addition, orientation pinwheels tend to be located at the centre of OD columns (Bartfeld and Grinvald, 1992; Obermayer and Blasdel, 1993; Hübener et al., 1997). However, manipulating the statistics of visual inputs in different rearing regimes challenges map formation and the relationships between maps. Such experiments probe the degree to which the

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structure of visual maps is intrinsic or influenced by sensory experience. While there is evidence that some aspects of map structure have an inherited component (Kaschube et al., 2002, 2003), other work has also demonstrated that visual inputs affect the structure of the relevant cortical map. For example, single orientation rearing causes the OP columns of the over-represented orientation to expand (Sengpiel et al., 1999; Tanaka et al., 2006).

"Dimension reduction" models have been successful at predicting and reproducing the structure of feature maps in V1 and the relationships between maps (Durbin and Mitchison, 1990; Goodhill and Willshaw, 1990; Obermayer et al., 1992; Erwin et al., 1995; Swindale, 1996; Goodhill et al., 1997; Swindale and Bauer, 1998; Goodhill and Cimponeriu, 2000; Carreira-Perpiñán et al., 2005; Yu et al., 2005; Farley et al., 2007). These algorithms map a high-dimensional feature space based on visual inputs onto a two-dimensional surface representing V1 under the competing constraints of good continuity and coverage. The models also reproduce the consequences of several experimental manipulations, including monocular deprivation and single orientation rearing (Goodhill and Willshaw, 1994; Carreira-Perpiñán et al., 2005).

An experimental manipulation that has not yet been explored by modelling is when individuals experience only horizontal lines in one eye and only vertical lines in the other eye. Several older experimental studies examined the effect on cat V1 of this rearing regime, but only with single-unit recordings (Hirsch and Spinelli, 1970, 1971; Stryker et al., 1978). These recordings revealed that neurons that responded to one eye were selective for vertical orientation while neurons that responded to the other eye were selective for horizontal orientations. However, whether the OP map altered to match the OD map or vice versa was not determined. Investigations of the consequences of this rearing paradigm using more modern optical imaging techniques are so far preliminary, and have only been presented in abstract form (Tani and Tanaka, 2008). In particular, the geometric relationships between the OD and OP maps arising from this rearing regime have not been fully explored, nor have the effects of the strength and duration of the orientation-restricted rearing on the resulting maps been investigated.

Here, we use an established model to explore this rearing regime and make novel predictions about joint OP and OD map development. Our results not only agree with the data from single-electrode recordings, but also extend previous work by visualising in full the effect on cortical maps as well as analysing the geometric relationships between maps. We predict that map development under restricted orientation rearing in the model proceeds in two stages. In the first stage, OP columns for the over-represented orientations form and precipitate the formation of OD columns perfectly aligned with the OP columns. In the second stage, other OP columns form at the OD column boundaries. This change in the OP map causes a concomitant rearrangement of the OD map and a change in the geometric relationships between the two maps. These results present a further opportunity to test the predictions of models based on trading off coverage and continuity constraints for explaining activity-dependent visual map development.

Methods

The elastic net algorithm

Many different computational models for visual map development have been proposed (Erwin et al., 1995; Swindale, 1996, 2003; Goodhill, 2007; Simpson et al., 2009). In most of these, including the elastic net used here, a set of visual inputs is mapped onto a two-dimensional array of cells representing V1. Many of these models have been shown to produce maps which closely match much of the experimental data regarding the structure of cortical maps and the relationships between maps. The elastic net in particular has

reproduced the experimentally observed effects on map structure of single orientation rearing (Carreira-Perpiñán et al., 2005), monocular deprivation (Goodhill and Willshaw, 1994; Carreira-Perpiñán et al., 2005) and angioscotoma representation (Giacomantonio and Goodhill, 2007).

Here we use the low-dimensional version of the elastic net model which treats each combination of input features, such as an oriented edge at a particular position in space, as a point in a 'feature' space. A net of points representing cortical cells occupies this feature space and the position of each cortical cell in this high-dimensional space $\mathbf{w}_j$ represents its full receptive field, e.g. (x-position, y-position, ocularity, orientation preference, orientation selectivity). This abstraction speeds up computation while still producing results in good agreement with the biological data (Erwin et al., 1995; Swindale, 1996).

At each iteration, feature points which uniformly sample the feature space are presented to the elastic net. The same set of feature points are presented simultaneously at each iteration (batch mode). This method speeds up the computation and generates smooth maps from only a relatively small number of feature points. It has previously been shown to generate maps which closely resemble those seen biologically (Goodhill and Willshaw, 1990, 1994; Goodhill and Cimponeriu, 2000; Carreira-Perpiñán et al., 2005; Giacomantonio and Goodhill, 2007). The 'activity', Φ, of each cortical cell $\mathbf{w}_j$ in response to the input feature $\mathbf{v}_i$ is related to the distance in feature space between the cortical point and the feature point, scaled by the parameter K:

$$\Phi\left(\|\mathbf{v}_i - \mathbf{w}_j\|, K\right) = \exp\left(-\frac{\|\mathbf{v}_i - \mathbf{w}_j\|^2}{2K^2}\right). \tag{1}$$

These activities are normalised so that each input feature elicits the same amount of activity in the cortex:

$$n_{ij} = \frac{\Phi\left(\|\mathbf{v}_i - \mathbf{w}_j\|, K\right)}{\sum_p \Phi\left(\|\mathbf{v}_i - \mathbf{w}_p\|, K\right)}. \tag{2}$$

The receptive field of each cortical cell $\mathbf{w}_j$ is then adapted towards each input feature by an amount proportional to the degree n_{ij} to which it responded to that feature:

$$\Delta\mathbf{w}_j = \alpha \sum_i n_{ij}\left(\mathbf{v}_i - \mathbf{w}_j\right) + \beta K \sum_{j' \in N(j)} \left(\mathbf{w}_{j'} - \mathbf{w}_j\right). \tag{3}$$

Here, $N(j)$ refers to the set of points in the cortical sheet that are neighbouring cortical point j. The first term is a summation of the influence of all input features on cortical cell j so that cell j adapts a little to each input feature simultaneously. The second term in Eq. (3) models the effect of lateral interactions which move neighbouring cortical points towards each other in feature space to keep the receptive fields of neighbouring cortical cells similar to each other (Dayan, 1993; Yuille et al., 1996; Carreira-Perpiñán and Goodhill, 2004).

The mapping procedure attempts to improve a trade-off between good coverage and good continuity, two properties of real cortical maps (Swindale, 1996). The cortical points must adequately sample the feature space in order to avoid perceptual blind spots (good coverage) and neighbouring cortical points must be close together in feature space to produce the smooth maps observed in V1 (good continuity). The relative strengths of the coverage and continuity terms are controlled by the ratio α/β.

K is reduced over the course of a simulation. As a result, the effect of each feature point on cortical points is increasingly local (Eq. (3), first term). At each iteration, every feature point pulls on every cortical point, contributing a component to the net displacement