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UNDERSTANDING OCULAR DOMINANCE DEVELOPMENT FROM BINOCULAR INPUT STATISTICS

Zhaoping Li

Hong Kong University of Science and Technology, Computer Science Dept.
Clear Water Bay, Kowloon, Hong Kong,
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ABSTRACT

It is hypothesized that the striate cortex is concerned with, among other things, removing binocular correlations in the inputs. This theory is applied to explain the different ocular dominance column (ODC) formations observed after visual developments under strabismus, excessive binocular correlations, normal environment, and monocular deprivation. These ODC formations are shown to be consequences of decorrelation coding strategies for different binocular input statistics. Experimental tests of the theory are suggested.

1 INTRODUCTION

Recoding sensory inputs to remove the input redundancy has been advocated as a sensory preprocessing goal and is argued to have cognitive advantages [1]. An overwhelming source of redundancy in visual inputs is the pair-wise image pixel correlation, and binocular correlation is one of them. We recently developed a theory proposing that the striate cortex is concerned with, among other things, decorrelating the binocular inputs [10]. It predicts a distribution of monocular/binocular and disparity selective cells and their relationship with the receptive field sizes and orientations. They agree well with experimental observations (e.g., [2, 5, 3, 8]), and are motivating experimental tests [12].

Visual developments under strabismus, excessive binocular correlation, normal environment, and monocular deprivation give very different ocular correlation structures. This paper applies the stereo coding theory to explain the consequent differences in the ODC formations and demonstrates that they are caused by the different coding strategies to remove their respective input ocular correlations. Decorrelation principle has also been applied successfully to explain the spatio-chromatic coding in the retina [9].

2 ODC FORMATIONS AFTER DIFFERENT DEVELOPMENTAL CONDITIONS

The binocular inputs are $S^L(\underline{x})$ and $S^R(\underline{x}')$, at locations $\underline{x}$ and $\underline{x}'$ in the left and right eyes respectively. A point in (or outside) the fixation plane induces $S^L(\underline{x}')$ and $S^R(\underline{x}')$ at $\underline{x} = \underline{x}'$ (or $\underline{x} \neq \underline{x}'$). Taking the Fourier amplitude $\tilde{S}^a(\underline{f})$ of the image $S^a(x)$ at spatial frequency $\underline{f}$, the ocular correlation is captured under translation invariance by $R_x^{ab}(\underline{x}, \underline{x}') \equiv < S^a(\underline{x}) S^b(\underline{x}') >$ where $a, b = L, R$, and brackets denote average over inputs[10]. For instance $R^{LR}(\underline{f} = 0)$ is the correlation between the mean light levels in the two eyes, and $R^{LL}(\underline{f})$ is the left eye signal power for frequency $\underline{f}$. Explicitly, $\begin{pmatrix} R^{LL}(\underline{f}) & R^{LR}(\underline{f}) \\ R^{RL}(\underline{f}) & R^{RR}(\underline{f}) \end{pmatrix} \equiv \begin{pmatrix} 1 & r \\ r & a \end{pmatrix} R(\underline{f}) \equiv \mathbf{R} \cdot R(\underline{f}),$, where $R(\underline{f}) = R^{LL}(\underline{f})$, $r \equiv R^{LR}/R^{LL}$, $a \equiv R^{RR}/R^{LL}$, and the boldfaced $\mathbf{R}$ denotes the 2×2 binocular correlation matrix.

We then have

$$\begin{array}{rcc} \text{Normal environment :} & a = 1 & r = r_{normal} \\ \text{Strabismus:} & a = 1 & r < r_{normal}, r \approx 0 \\ \text{Excessive ocular correlation :} & a = 1 & r > r_{normal}, r \approx 1 \\ \text{Monocular deprivation :} & a < 1 & r \approx \sqrt{a} r_{normal} < r_{normal} \end{array} \tag{1.1}$$

Right eye deprivation gives $R^{RR} < R^{LL}$ and $a < 1$; symmetry between the two eyes gives $R^{RR} = R^{LL}$ or $a = 1$. Ocular correlation is smaller under strabismus, $r_{strabismus} < r_{normal}$, or monocular deprivation, $r_{mono-deprivation} < r_{normal}$, and larger $r_{excessive} > r_{normal}$ when two ocular inputs are artificially correlated with synchronous stimulations of the optic nerves[6]. Our measurements [10] show that r is highest between mean light levels and decreases as spatial scales get smaller, and can be approximated by $r(\underline{f}) = r_o e^{-f/f_o}$. $1/f_o$ is roughly the object disparity range or average image alignment.

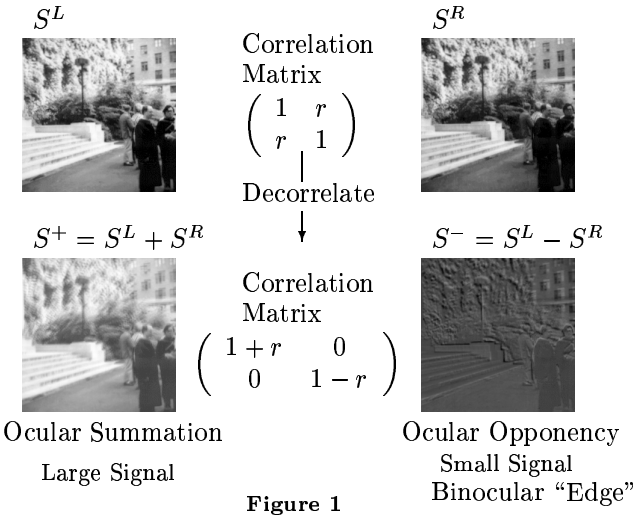

Figure 1

2.1 Strabismus

Under extreme strabismus, average image misalignment $\Delta X_{strabismus}$ is larger than most cell receptive field sizes. Consequently, $r(\underline{f}) \approx 0$ for $\underline{f} \geq 1/\Delta X_{strabismus}$, and there is practically little binocular correlation to be removed in the corresponding scales. Information from the two eyes should then be processed independently, giving monocular cells and, if we assume that cells segregate ocularly, stark ODCs. This is indeed observed in animals whose eyes are misaligned surgically or optically during development (e.g., [2]). In less severe cases, some cells can still be binocular when their receptive fields are large enough to cover the image misalignment, providing the subjects some residual stereopsis.

2.2 Excessive ocular correlation

The other extreme is given by binocularly synchronized optic nerve stimulations [6], causing very large binocular correlation $r \approx 1$. As can be easily checked, the correlation in $\mathbf{R} = \begin{pmatrix} 1 & r \\ r & 1 \end{pmatrix}$ can be removed by the new variables (see Fig. 1) $S^{\pm} = (S^L \pm S^R)/\sqrt{2}$. The ocular *summation* signal S^+ is analogous to the "mean-light-level" in space, and has a larger signal power than the ocular

opponent signal S^- — the binocular "edge". A strong ocular correlation $r \approx 1$ gives a negligible signal power to S^-. Accordingly, S^- should be ignored, and processing the S^+ channel alone gives ocular smoothing, analogous to the spatial image smoothing when noise is significant. Since S^+ receives equally weighted inputs from the two eyes, most cortical cells are binocular, making it difficult to form ODCs as observed physiologically [6].

2.3 Normal visual developmental condition

The amount of ocular correlation in normal conditions is in between those in the two extreme cases above, predicting cells with a whole spectrum of ocular dominance indices (ODI) as observed physiologically [2, 5]. The essential coding steps are

$$S^{L,R} \xrightarrow{\text{decorrelate}} S^{\pm} \xrightarrow{\text{gain control}} g^{\pm}S^{\pm} \xrightarrow{\text{multiplex}} g^+S^+ \pm g^-S^- = (g^+ \pm g^-)S^R + (g^+ \mp g^-)S^L$$

The gain control gives binocular edge enhancement $g^- > g^+$, when S^- is significantly larger than noise, and binocular smoothing $g^+ > g^-$ otherwise. The multiplexing achieves "locality" in coding (see details in [10]), and the ODI can be derived from the cell input gains $g^+ \pm g^-$ from the two eyes. $S^{\pm}$ have signal powers $(1 \pm r(\underline{f}))R(\underline{f})$, where both ocular correlation $r(f)$ and $R(f) \sim 1/f^2$, the monocular power spectrum [7], decay with $\underline{f}$. Consequently, as receptive field sizes of the cortical cells decrease or their optimal frequencies $\underline{f}$ increase, binocular edge enhancement $g^- > g^+$ and ocular umbalance are replaced by binocular smoothing $g^+ > g^-$ and ocular balance [10].

2.4 Monocular deprivation

A deprived right eye gives a correlation structure $\mathbf{R} = \begin{pmatrix} 1 & r \\ r & a \end{pmatrix}$ with $a < 1$. The decorrelated signals become $S^+ = S^L + \beta S^R$ and $S^- = -\beta S^L + S^R$, where $\beta < 1$. The binocular symmetry is broken: S^+ is strong-eye-dominant, and S^-, the binocular edge, is weak-eye-dominant and easily overcome by noise. In fact, S^- has a negligible signal power for most scales under severe monocular deprivation when $a \ll 1$. This gives a majority of the strong-eye-dominant cells and a thicker corresponding ODC, as observed in physiology (e.g., [4]).

3 DISCUSSION AND SUGGESTED EXPERIMENTAL TESTS

Deccorelation of binocular inputs is shown here to cause different ODC formations in the primary visual cortex in different input environments. It predicts stark ODCs, a failure of ODC formation, a whole spectrum of ODIs, and unequal sizes of ODCs, respectively, for visual developments under strabismus, excessive ocular correlation, normal environment, and monocular deprivation. These predictions agree well with experimental observations [2, 4, 6, 5], and demonstrate that many neural coding properties can be understood from visual input statistics [10].

In addition, the theory is predicting neural properties not yet explored systematically in experiments, and motivating experimental tests. First, a transition from monocularity to binocularity is predicted as the cortical receptive field sizes decrease (see section 2 and [10]). There are some experimental evidences supporting the prediction [5, 11] and more systematic tests are desired. Second, we predict that cortical cells preferring horizontal orientation are more likely binocular [10]. This is because these cells access input variations in the vertical direction, and these variations are more correlated ocularly (or less strabismus-like) compared to those in the horizontal direction since our eyes are aligned vertically. This prediction has motivated a recent physiological investigation, which is producing an encouraging support to the theory [12]. Third, we predict that the cortical cells adapt under low light levels to become more binocular or ocularly cooperative. In particular if the non-dominant eye inputs to a monocular cell normally inhibit inputs from the dominant eye, the inhibition should be reduced or even switched to facilitation as the cell adapts to low light levels. This is understood by noting that a small signal-to-noise under low light adaptation discourages binocular edge enhancement or neurons detecting ocular input differences (i.e., g^- should be small), and encourages ocular summation to integrate the signal. An experimental test of this prediction will be crucial to the theory.

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