



Binocular disparity can explain the orientation of ocular dominance stripes in primate primary visual area (V1)

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Abstract

In the primate primary visual area (V1), the ocular dominance pattern consists of alternating monocular stripes. Stripe orientation follows systematic trends preserved across several species. I propose that these trends result from minimizing the length of intra-cortical wiring needed to recombine information from the two eyes in order to achieve the perception of depth. I argue that the stripe orientation at any point of V1 should follow the direction of binocular disparity in the corresponding point of the visual field. The optimal pattern of stripes determined from this argument agrees with the ocular dominance pattern of macaque and *Cebus* monkeys. This theory predicts that for any point in the visual field the limits of depth perception are greatest in the direction along the ocular dominance stripes at that point. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The perception of depth in primates relies on recombining information coming from both eyes. This is accomplished by a retinotopic mapping (Daniel & Whitteridge, 1961; Tootell, Switkes, Silverman & Hamilton, 1988) of the two retinal images onto the primary visual area V1. In many primates, neurons dominated by each eye are segregated into the system of alternating stripes known as the ocular dominance pattern (Hubel & Wiesel, 1968; Wiesel, Hubel & Lam, 1974). A complete reconstruction of the pattern in a macaque V1 is shown in Fig. 1 (LeVay, Connolly, Houde & Van Essen, 1985).

This pattern is not random: the orientation of the ocular dominance stripes on the cortical surface follows systematic trends found in other macaques (Horton & Hocking, 1996) and in *Cebus* monkeys (Rosa, Gattass, Fiorani & Soares, 1992). These trends are easiest to see when the ocular dominance pattern is transformed back into visual field coordinates by dividing all cortical distances by the local magnification factor. [The mag-

nification factor (Daniel & Whitteridge, 1961) gives the distance in millimeters on the cortex which corresponds to a 1° separation on the retina.] The transformed pattern shown in Fig. 2 [as obtained by LeVay et al. (1985) following Hubel and Freeman (1977)] reveals two major trends: in the parafoveal region stripes tend to run horizontally, while farther from the fovea stripes follow roughly concentric circles. These trends in the orientation of the stripes call for explanation.

Many theorists have successfully modeled the development of ocular dominance columns (Erwin, Obermayer & Schulten, 1995; Swindale, 1996; Wiskott & Sejnowski, 1998), and some have addressed the trends in stripe orientation. It was suggested originally by LeVay et al. (1985) and later investigated by others (Jones, Van Sluyters & Murphy, 1991; Goodhill & Willshaw, 1994; Bauer, 1995) that the mapping from the two almost circular LGN layers to the more elongated representation in V1 requires least stretching (or anisotropy of the magnification factor within ocular dominance stripes) if the stripes run perpendicular to the long axis of V1. However, this theory does not explain the different orientation of ocular dominance stripes in the parafoveal region (Goodhill, Bates & Montague, 1997). Moreover, it is unlikely that the

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shape of V1 dictates its internal organization; more probably, its internal organization will dictate its shape. Goodhill et al. (1997) have instead proposed that the global pattern of ocular dominance stripes arises from anisotropic and spatially non-uniform correlations in the neural input from the retinae. This seems like a plausible developmental mechanism, although anisotropic correlations have yet to be demonstrated experimentally.

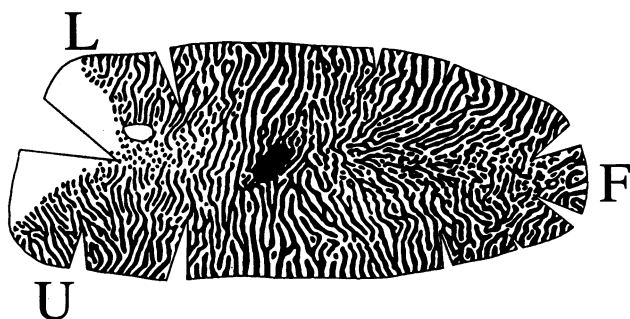


Fig. 1. The complete reconstruction of the ocular dominance pattern in macaque V1 by LeVay et al. Black/white stripes are composed of neurons dominated by the left/right eye. The retinotopic map is organized as follows. Most of the perimeter is the V1–V2 border which corresponds to the vertical meridian the upper end of which is marked by U and the lower by L. F designates the representation of the fovea. The horizontal meridian is represented along the long axis with the tilted black oval corresponding to the blind spot.

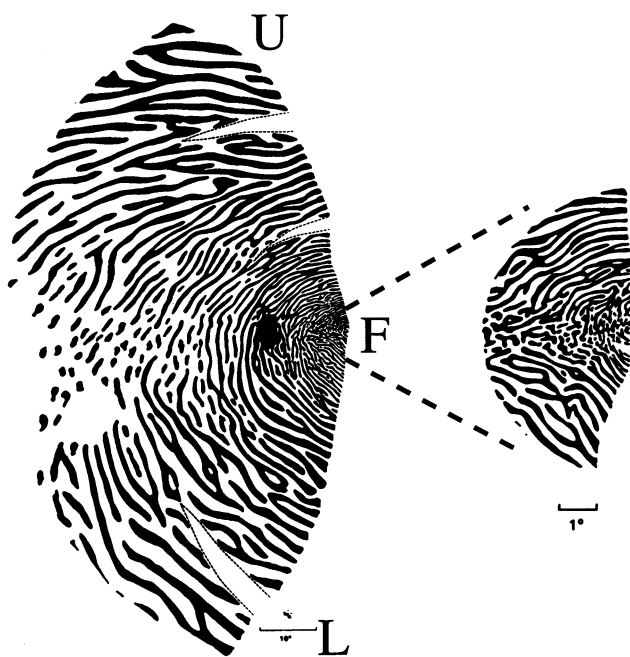


Fig. 2. The complete ocular dominance pattern from Fig. 1 transformed back into visual field coordinates by LeVay et al. The right boundary represents the vertical meridian with the fovea (F) in the middle. Notice two major trends in the orientation of the stripes. In the parafoveal region stripes tend to run horizontally. Farther from the fovea stripes follow concentric circles. The blow-up shows parafoveal region.

Rather than modeling development, I have taken a different approach to explain the orientation of ocular dominance stripes. I propose that the stripe orientations follow from V1's role in depth perception according to the principle of wiring economy. In other words, I focus on understanding why the stripes are arranged as they are, rather than *how* they become so arranged.

The wiring economy principle amounts to the following (Covey, 1979; Mitchison, 1991; Cherniak, 1992; Young, 1992; Cajal, 1995; Chklovskii & Stevens, 2000): because of limitations on head size, there is pressure to keep the volume of the cortex to a minimum. This implies that wiring, i.e. axons and dendrites, should be as short as possible, while maintaining function. In general, the function of a given cortical circuit specifies the connections between neurons. Therefore the problem presented by the wiring economy argument is to find, for a given set of connections, the spatial layout of the neurons that minimizes wiring length. This problem is extremely difficult, computationally, because the large number of neurons in a cortical region leads to an astronomically large number of possible combinatorial arrangements. However, the columnar organization of the cortex (Mountcastle, 1957) allows me to consider the layout of cortical columns (each consisting of a large number of neurons with similar properties) rather than individual neurons, reducing the problem to two dimensions and making it treatable.

The wiring economy principle has been used to explain the retinotopic map (Covey, 1979; Kaas, 1997) and ocular dominance stripes (Mitchison, 1991; Chklovskii & Koulakov, 1999) in V1. In the first case, the construction of receptive fields requires connections between neurons representing neighboring points in the visual field. Topographic mapping of the visual field minimizes the length of these connections. In the second case, each cortical neuron connects more often to cortical neurons dominated by the same eye than to neurons dominated by the opposing eye. Thus the segregation of neurons into alternating monocular stripes minimizes the total length of intra-cortical connections under certain conditions.

Here I use the principle of wiring economy to find the optimal orientation of the ocular dominance stripes (given they exist) from the function of V1 in processing binocular disparity. Disparity arises when an object closer or farther than the point of fixation forms images on the two retinae that are in different positions relative to the fovea. Because the cortex is retinotopically mapped, the left and the right eye representations of this object in the cortex will fall some distance away from each other, as determined by the magnitude and direction of the retinal separation. Recombining these representations requires extensive wiring between cortical columns.

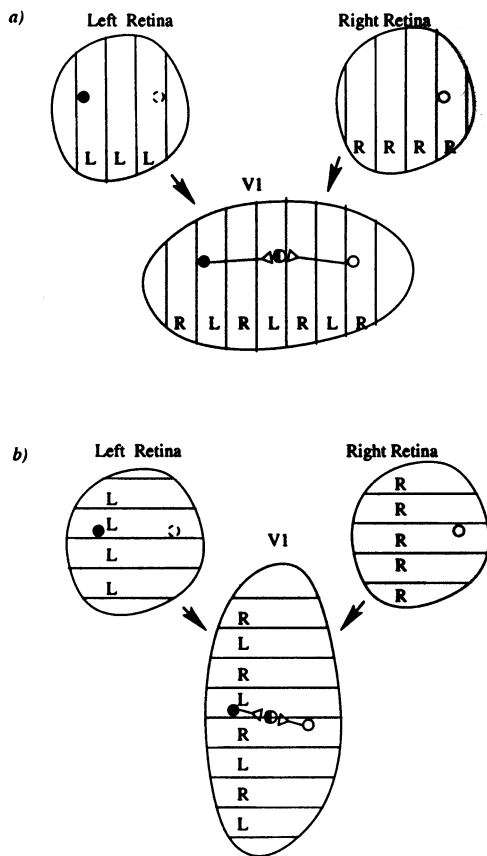


Fig. 3. Alignment of ocular dominance stripes with the disparity direction in the cortex minimizes wirelength. Filled and empty circles designate left and right retinal images of the same object. Dashed circle is the point of the left retina corresponding to the right-eye image. Separation between the filled and the dashed circle is the retinal disparity. Shown are the two limiting cases of the retino-cortical mapping with ocular dominance stripes perpendicular (a) or parallel (b) to the disparity direction. The two images are recombined in V1 (for example by projecting onto a binocular cell, half-filled circle). Because of the double-coverage perpendicular to the ocular dominance stripes, alignment of ocular dominance stripes with the disparity direction (b) places the right/left representations of the same object closer than (a).

In Section 2, I show that the left and right eye representations in V1 will be closer if the ocular dominance stripes run parallel, rather than perpendicular, to the direction of retinal separation. Therefore I argue that in order to minimize wirelength, the orientation of the stripes should correspond to the direction of binocular disparity. However, for any given point on the cortex the disparity in the corresponding point of the visual field depends on the viewing conditions, that is, direction of gaze and distance to the object. In Section 3, I calculate a distribution of disparities averaged over viewing conditions. I obtain a map of typical disparities in the visual field which then determines the optimal orientation of the ocular dominance stripes.

The orientation of stripes predicted by this theory agrees with actual patterns obtained from macaque and

Cebus monkeys, see Section 4. My results show that the two major trends of stripe orientation result from two main contributions to disparity. In the parafoveal region, binocular disparity is due mainly to the horizontal displacement of the eyes, consistent with the horizontal stripes in the (transformed) ocular dominance pattern. Farther from the fovea, the pattern consists of isoeccentric lines. These are explained by binocular disparity due to unequal rotation of the eyeballs around the gaze line (cyclotorsion).

2. Disparity direction determines orientation of ocular dominance stripes

Because the left and the right eye pathways do not converge before V1, the existence of binocular neurons in V1 (Hubel & Wiesel, 1970) suggests that the information from both eyes is recombined there. Moreover, many binocular neurons in V1 are disparity-tuned (Barlow, Blakemore & Pettigrew, 1967; Poggio & Fischer, 1977; Cumming & Parker, 1999). This requires intracortical wiring which connects cortical columns containing left/right eye representations of an object. To minimize the wirelength, the distance between these columns should be as small as possible.

For a given magnitude of binocular disparity, the distance between the columns containing left/right representations of an object depends on the orientation of ocular dominance stripes relative to the separation of the columns. To see this consider two alternative arrangements: ocular dominance stripes oriented perpendicular (Fig. 3a), or parallel (Fig. 3b) to the separation of the columns. One can think of V1 as being composed of interleaved stripes cut from the two topographic maps belonging to the two eyes (Blasdel & Fitzpatrick, 1984). If one were to move across the stripes the representation of every point in the visual field is encountered twice: once in a right-eye column, once in a left-eye column. Therefore the separation between the two columns containing left/right eye representations of the object is twice as big if the stripes are perpendicular compared to parallel to the separation between the columns. Thus for a given magnitude of disparity in the visual field the length of inter-eye connections is minimized if the ocular dominance stripes run in the direction corresponding to the disparity direction.

Several assumptions were made in this argument. First, I assumed the absence of stretching within the stripes which could change the distances across versus along the stripes. To see whether this is a valid assumption I restate the argument in terms of the cortical magnification factor which has been measured experimentally. The separation between the two columns in V1 is given by the retinal disparity times the magnification factor. If the magnification factor across the stripes

is greater than that along the stripes, the separation between the columns and hence the length of inter-eye connections is minimized by aligning the stripes with the disparity direction.

Several experiments have studied the anisotropy of the cortical magnification factor. Although, Daniel and Whitteridge (1961) reported initially that the magnification factor is isotropic, most subsequent investigations came to a different conclusion. Van Essen, Newsome and Maunsell (1984) found, electrophysiologically, that the magnification factor was anisotropic (approximately, by a factor of two) along the vertical meridian. Although they did not image the ocular dominance pattern, we know that ocular dominance stripes run perpendicular to the vertical meridian. Thus their observation shows that the magnification factor across the stripes is about twice as big as that along the stripes. Their observation about the isotropic magnification factor along the horizontal meridian is difficult to interpret because the direction of ocular dominance stripes is variable. Tootell et al. (1988) used radioactive deoxyglucose infusion and ruled out the possibility of an isotropic magnification factor. Their results are compatible with the doubling of the magnification factor across the stripes within the accuracy of the measurements. Recently, Blasdel and Campbell (1998) have shown with optical imaging that the magnification factor across the stripes is 1.5 times greater than along. Therefore, even though some stretching seems to be present, there is enough anisotropy for my argument to remain valid.

Second, I did not include wirelength of intra-eye connections in the cortex. These connections are responsible for monocular functions of V1 such as processing of contour orientation and color. The reason for neglecting these connections is their isotropy, that is they do not depend on the direction in the visual field. Therefore, orientation of the ocular dominance stripes should not affect the length of intra-eye connection.

Third, I neglected a possible specificity of inter-eye connections in respect to monocular functions of V1 such as orientational selectivity. Binocular neurons are likely to receive information from neurons with the same preferred orientation. Moreover this preferred orientation should correlate with the disparity direction. However, this effect should not affect my argument because it averages out. Once all the possible orientations are included, the combined connections should be non-specific because different orientations are approximately equally represented.

Fourth, I assumed retinotopic mapping in V1. Although there is scatter in the receptive field location in a given cortical column, the magnitude of the scatter does not exceed the period of the ocular dominance pattern (Hubel & Wiesel, 1974). Because I rely on retinotopy on the scales of several stripe widths (Fig. 3) the argument remains valid.

Thus, I showed that the orientation of ocular dominance stripes should follow the direction of disparity for the corresponding point of the visual field. To determine the optimal pattern of ocular dominance stripes I need to find disparity for all points in the visual field. This leads me to the calculation of a binocular disparity map.

3. Calculation of the typical disparity map

In Section 2, I argued that the ocular dominance pattern should follow the map of binocular disparity in order to minimize the length of intra-cortical wiring. However the direction and magnitude of the disparity for a given point in the visual field depends on the viewing conditions such as the distance to the object and the direction of gaze. Therefore, I need to average disparity over these variables. The typical direction of disparity should determine the optimal orientation of ocular dominance stripes.

In order to find the disparity map, I consider the origins of disparity in some detail. This is done in several steps by first considering a primate with the gaze direction fixed at straight ahead and then gradually adding degrees of freedom available to the eyeballs.

Consider two eyes fixating at optical infinity. Then, by definition, the images of the fixation point fall on the foveae of the two eyes. Moreover, all objects at infinity are imaged on the retinal locations which are the same distance and direction from the fovea in both eyes. Such locations send afferents to adjacent cortical columns and are called corresponding. [In reality, images of infinite objects may not fall on exactly corresponding points. For example, there is a 2° tilt of the vertical meridians (Volkman, 1859; Helmholtz, 1962). In this paper I neglect these deviations because they do not alter the results qualitatively.] Physiologically, stimulation of corresponding points results in a single perception of the object. Objects at a finite distance away, however, are imaged at different retinal locations relative to the fovea, called non-corresponding. Binocular disparity is defined as a displacement of the left-eye image from the location on the left retina corresponding to the right-eye image of the same point object. Physiologically, finite-distance objects may still appear single due to sensory fusion if the disparity falls within a range called Panum's fusional area. Otherwise the doubling of the perception or diplopia is experienced.

When the eyes fixate at optical infinity all the infinitely removed objects appear with zero disparity. To find the disparity of other objects, I use a geometrical construction illustrated in Fig. 4. I fix the direction of gaze at straight ahead. The image of point *O* in the right eye falls on the retinal point *R* which belongs to the line passing through *O* and the nodal point of the

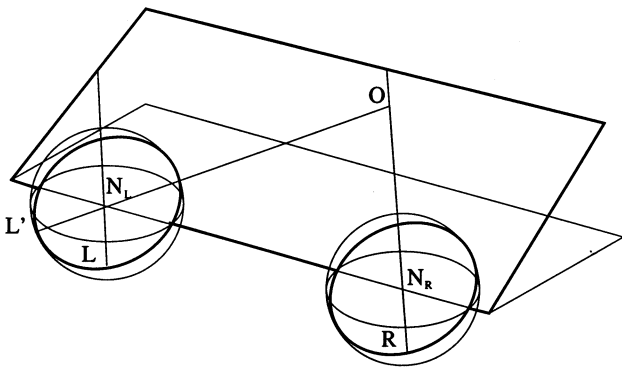


Fig. 4. Epipolar lines (thick circles) determine the direction of disparity for fixation at optical infinity. They are formed by the intersection of the retinae and an epipolar (visual) plane (thick rectangle), which passes through fixation point and the centers of the two eyeballs.

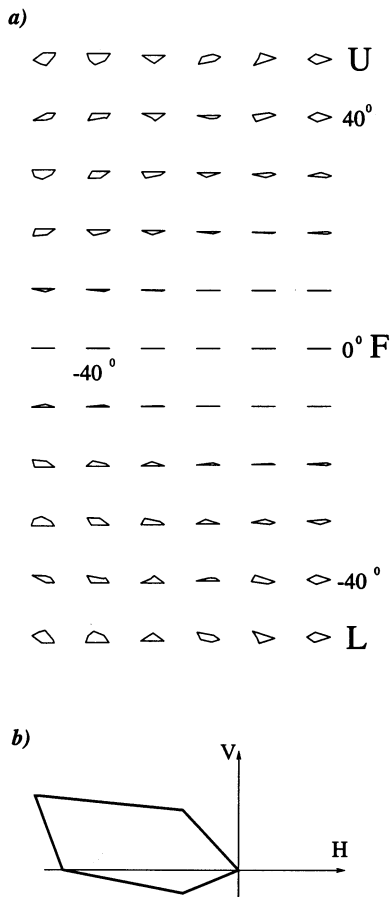


Fig. 5. Weighted disparity direction map for the left visual hemifield. The calculation is based on Listing's law. I assume a uniform distribution of gaze directions within 30° azimuth from the primary position. (a) The grid of polar plots is arranged in the azimuth-elevation plane of the retina. (b) A blow-up of a typical polar plot. The distance from the origin represents the number of gaze directions with disparity direction falling into the corresponding sector. Horizontal axis corresponds to purely horizontal disparity, while the vertical axis corresponds to purely vertical disparity.

right eye N_R . The image of point O in the left eye falls on the retinal point L' . A line passing through the left-eye nodal point N_L and parallel to OR intersects the retina at the point L , a point corresponding to R . The arc LL' is the binocular disparity of point O . This arc belongs both to the retina and to a plane that passes through point O and the nodal points of the two eyes, known as an epipolar plane. The common of the epipolar plane and the retina is called an epipolar line. Therefore the direction of disparity LL' is along the epipolar line while its magnitude depends on the distance to point O . If point O had a different elevation its disparity direction will be aligned with another epipolar line formed by the intersection of another epipolar plane and the retina. Therefore possible directions of disparity in the visual field are along epipolar lines formed by great circles passing through the interocular line. I call this disparity translational because it results from the horizontal displacement of the eyes.

Now I allow eyes to change the direction of gaze in the horizontal plane, while assuming that the center of rotation of an eyeball coincides with its nodal point. Then point O is projected onto the same locations L' and R in head-centered coordinates. Point L remains corresponding to R . However the eyes, and hence the retinae rotate under those points. Therefore, the direction of disparity in the retinal coordinates changes depending on the gaze direction. I calculate the frequency distribution of disparity directions by averaging over a uniform distribution of gaze directions within $\pm 30^\circ$ of straight ahead.

The result is shown in Fig. 5 as a grid of polar plots each of which corresponds to a particular point in the retinal coordinates. Each polar plot shows the frequency of different directions of disparity for a given point on the retina. The distribution of disparity exhibits strong anisotropy and the dominant disparity direction can be easily determined for all the retinal locations. If the only movements allowed to the eye were rotations around the vertical axis then this would be a complete disparity map. The optimal ocular dominance pattern would be determined by transforming this map into cortical coordinates by using the magnification factor.

A comparison with Fig. 2 shows that this map only partially agrees with the macaque data. It reproduces correctly the horizontal stripe orientation in the parafoveal region. However, the map fails to capture the isoecentric trend in stripe orientation at higher eccentricity.

Inclusion of different gaze elevations eliminates this disagreement. Naively, one may expect that the disparity map remains intact because the interocular line is the axis of rotational symmetry. However, vertical eye movements are accompanied by cyclotorsion (Enright, 1980; Nakayama, 1983), or rotation of the eyeballs around the direction of gaze. The amplitude of cyclo-

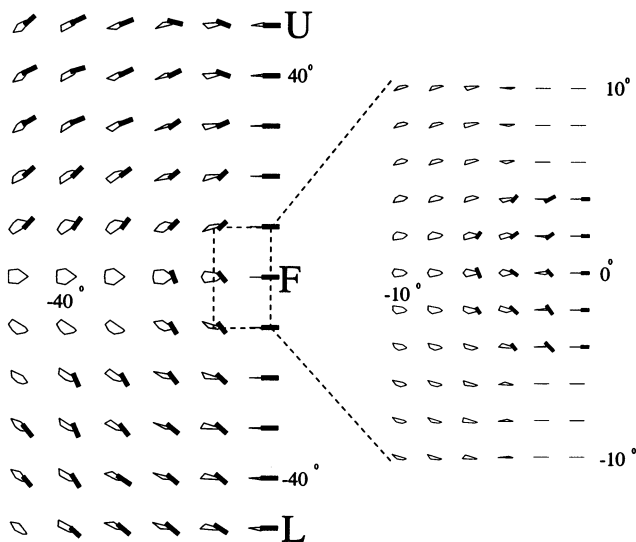


Fig. 6. Weighted disparity map for fixation at infinity and including cyclotorsion occurring for different gaze elevations. The grid of polar plots showing the distribution of disparity directions is in azimuth-elevation visual field coordinates. Both cyclotorsional and translational components of disparity are included in the calculation. Notice that the dominant disparity directions are similar to the pattern of ocular dominance represented by black bars. The blow-up shows the parafoveal region. The direction of ocular dominance stripes near the vertical meridian was fixed to be horizontal in accordance with anatomical data.

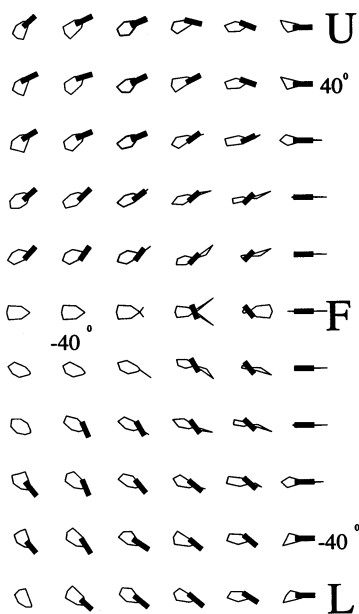


Fig. 7. Weighted disparity map for fixation at arm's length from the eyes including cyclotorsion. Notice that the dominant disparity directions are similar to the pattern of ocular dominance represented by black bars.

torsion depends on the direction of gaze as specified by Listing's law. [Listing's law states that to determine the amplitude of cyclotorsion for an arbitrary direction of gaze one has to rotate the eye into that direction from

the primary position around an axis which lies in a (Listing) plane.] According to the recent measurements (Bruno & van den Berg, 1997) the amplitude of cyclotorsion is often unequal in the two eyes. Thus, although points L' and R remain fixed in the head-centered coordinates, point L corresponding to R rotates around the gaze direction. This causes a cyclotorsional contribution to disparity which is oriented along concentric circles around the fovea.

The full binocular disparity includes cyclotorsional and translational contributions. Because the magnitude of the translational contribution depends on the distance to an object while the cyclotorsional contribution does not, the direction of disparity depends on the distance to an object. Therefore, finding the typical disparity direction requires specifying a plausible range of distances to relevant objects.

This range of distances can be found from the following argument. First, images of objects with cortical disparities much greater than the width of ocular dominance stripes cannot be recombined in V1: these objects should be excluded from the disparity calculation. Second, images of objects with cortical disparities much smaller than the width of ocular dominance stripes can be recombined independent of the stripe orientation. These objects should be excluded as well. Only objects with cortical disparities in the intermediate range of cortical disparities [a ; b] are affected by the stripe orientation.

To determine the values of a and b which define the relevant object location I use the data on the size of Panum's fusional area. It has been found that Panum's fusional area multiplied by the cortical magnification factor is independent of eccentricity (Rovamo & Virsu, 1979; Hampton & Kertesz, 1983), thus supporting the hypothesis that the recombining of images from the two eyes takes place in V1.

In calculating the disparity map I use the measurements of Panum's fusional area as a function of eccentricity by Hampton and Kertesz (1983). The typical disparity map for fixation at infinity is shown in Fig. 6. Although results of the calculation depend on the choice of parameters, they do not change qualitatively (see Section 4).

Results of a similar calculation performed for fixation at arm's length are shown in Fig. 7. Details of the calculation are given in Appendix A.

4. Discussion

Orienting ocular dominance stripes in the direction locally corresponding to the typical disparity optimizes the length of intra-cortical wiring needed for the perception of depth. Therefore, the wiring economy principle predicts that the ocular dominance pattern follows

the map of typical disparities. This prediction agrees with the data as can be seen by comparing the map of typical disparities for fixation at infinity to the orientation of ocular dominance stripes in Fig. 6. This is also true for the disparity map calculated for fixation at arm's length, Fig. 7. The map of typical disparities reproduces correctly the two major trends in the data: in the parafoveal region stripes tend to run horizontally, farther from the fovea, the pattern consists of isoeccentric stripes.

These trends result from the two major components of disparity: translational, due to the horizontal displacement of the eyes, and cyclotorsional, due to unequal rotation of the eyeballs around the gaze line (cyclotorsion). The relative magnitude of the two components depends on the distance to the fovea, Fig. 8. In the parafoveal region, cyclotorsional disparity goes to zero linearly with eccentricity because rotational displacement is proportional to the radial distance from the axis of rotation passing through the fovea. At the same time, translational disparity remains finite for objects closer or farther than the point of fixation.

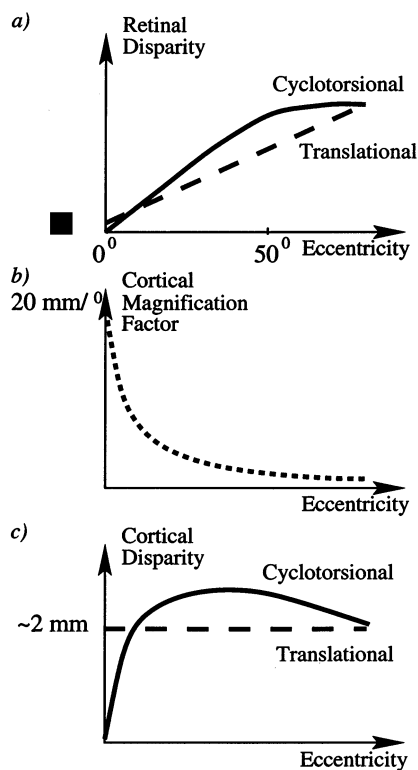


Fig. 8. Relative importance of the two contributions to disparity depend on the eccentricity. (a) Magnitude of translational and cyclotorsional disparity components in retinal coordinates as a function of eccentricity along the horizontal meridian. Notice that the cyclotorsional disparity goes to zero linearly with eccentricity while the translational disparity remains finite in the parafovea. (b) Cortical magnification factor as a function of eccentricity. (c) Translational and cyclotorsional disparity components in cortical coordinates as a function of eccentricity along the horizontal meridian.

Therefore, translational disparity dominates in the parafoveal region. Since the translational disparity is mostly horizontal, this explains the horizontal trend in the stripe orientation in parafoveal region. Farther from the fovea, the cyclotorsional component of disparity may (or may not) become dominant depending on several parameters: the amplitude of cyclotorsion, the frequency of different viewing conditions, and the typical limit of depth perception. Along the horizontal meridian, cyclotorsional disparity is vertical, while translational is horizontal. Hence, the direction of the ocular dominance stripes must switch at the point where the cyclotorsional component of disparity takes over the translational. This switch is evident in the macaque data, Fig. 2 at about 8° eccentricity.

These trends in the orientation of ocular dominance stripes are not qualitatively affected by assumptions made in the calculation. For example, I assumed a uniform distribution of the gaze directions. Any reasonable bell-shaped distribution should lead to the same two trends in the ocular dominance pattern. Also Fig. 7 shows that the same trends are present for fixation at arm's length from the eyes.

The functional significance of these trends in the stripe orientation is supported by their generality. Ocular dominance patterns imaged in several macaques (Horton & Hocking, 1996) show the two trends in the stripe orientation. Rosa et al. (1992) transformed into visual field coordinates a complete ocular dominance pattern of *Cebus* monkeys. They found that the pattern was qualitatively similar to macaque with the stripe orientation switching at $\approx 6^\circ$ and the first trend sometimes lacking. Preliminary data (Horton & Hocking, 1998) on the ocular dominance pattern in humans is hard to analyze because precise topography in V1 is not known. Although the two trends are present, there is a significant interpersonal variability, possibly indicating varying significance of the two contributions to disparity from person to person.

Although this theory reproduces the two major trends in the data, there is an unexplained trend in the macaque (LeVay et al., 1985; Horton & Hocking, 1996) and *Cebus* monkey (Rosa et al., 1992) data. In the foveal region, less than 1° eccentricity, the orientation of stripes differs from the typically horizontal disparity there. In the context of the current theory, I see a couple of possible explanations for this disagreement. First, the assumption that the fovea is represented on the V1–V2 border may be incorrect. This would happen if there is a duplication in coverage of the visual field by the left and the right hemispheres. Because the size of such overlap cannot be big ($< 1^\circ$) this has to be verified by a precise mapping of V1 topography together with the ocular dominance mapping. Second, the fusional area may not be symmetric around the fixation point. For example, the convexity of most natural

objects may favor a displacement of the fusional area towards greater distances.

This theory relates the ocular dominance pattern to the function of V1 allowing me to make several predictions. The location of the switch in the orientation of the ocular dominance stripes along the horizontal meridian should depend on the following parameters. Greater amplitude of cyclotorsion (or a greater frequency of gaze directions requiring cyclotorsion) increases cyclotorsional disparity and pushes the location of the switch in the stripe orientation towards the fovea. A greater extent of Panum's fusional area, b , achieves fusion for more objects with largely translational disparity. This should increase the eccentricity of the switch. Schwartz (1980) suggested that the size of Panum's fusional area and the width of the ocular dominance stripes are correlated between different species. If this is correct my theory implies that the species with greater width of ocular dominance stripes in the visual field should have the switch at higher eccentricity.

According to the theory, the functional significance of the orientation of ocular dominance stripes is in accommodating the typical disparity direction. Then processing of binocular disparity for any point of the visual field should be more efficient in the direction corresponding to the stripe orientation at that point. This predicts a greater number of disparity selective neurons for the direction of disparity corresponding to the stripe orientation as can be verified electrophysiologically. Also the limits of depth perception (for example, Panum's fusional area) should be greater in the direction along the stripes than across as can be tested psychophysically.

In conclusion, I argued that the orientation of the ocular dominance stripes optimizes the length of intracortical wiring needed to process binocular disparity for depth perception. This argument supports the utility of the wiring economy principle as a powerful tool in relating organization of the cortex to its function.

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Appendix A

Theoretical disparity maps were obtained numerically by using the following algorithm. A uniform grid of points was specified in the azimuth-elevation plane of the right retina. Real world points projecting onto each

retinal location sit on a line passing through that retinal location and the nodal point. I calculated the coordinates of a series of uniformly spaced reference points on this line. By drawing another line through the nodal point of the left eye and a reference point I found images of these points on the left retina.

The next step differs for the maps in Fig. 5a and in Figs. 6 and 7. For the map in Fig. 5a cyclotorsional disparity is neglected. The difference between the coordinates of the left and right retinal images gives binocular disparity. For fixation at infinity the disparity direction does not depend on the distance from the eyes to the object but only on the direction of gaze. To obtain the distribution of disparity directions I sum over a uniform distribution of gaze directions. Results are presented on the grid of polar plots in which the distance from the origin represents the number of gaze directions with disparity direction within the corresponding sector, Fig. 5b.

For the maps in Figs. 6 and 7 the cyclotorsional component of disparity is included. This is done by rotating the image of the reference point on the left retina by an amount proportional to the elevation angle. Because the magnitude of the translational component depends on the distance to the object while the cyclotorsional component does not, the direction of disparity is distance dependent in this case. Only reference points whose cortical disparity magnitude falls in the interval $[a; b]$ were included. To find the magnitude of cortical disparity I multiplied the retinal disparity by the local cortical magnification factor. I calculated the numbers of different disparity directions for each direction of gaze. Finally, I averaged over a uniform distribution of gaze directions. In the polar plots in Figs. 6 and 7 distance from the origin represents the number of reference points with disparity magnitude in the defined range and disparity direction falling into the corresponding sector averaged over different gaze directions.

I implemented the algorithm in MATLAB using the following parameters. The azimuth of the gaze directions as well as the elevation were uniformly distributed within 30° of straight ahead. The cyclotorsional misalignment was taken to be 10% of the elevation angle (Bruno & van den Berg, 1997). The point of fixation was at finite but large (2000 times interocular) distance for Fig. 6 25 times interocular distance for Fig. 7. The expression for the cortical magnification factor was chosen to be proportional to $1/(e + e_2)$ (Schwartz, 1980) where e is eccentricity and $e_2 = 2^\circ$ (Tootell et al., 1988). For the map shown in Fig. 6, I chose $a = 0.5b$ reflecting the relative anisotropy of the cortical magnification factor and $b = 0.13(e + e_2)$ corresponding to the diameter of Panum's fusional area (Hampton & Kertesz, 1983).

The experimental data of LeVay et al. (1985) were processed to obtain a map of ocular dominance stripe orientation using the following algorithm. The image in

Fig. 2 was locally Fourier transformed in a set of windows which were 10° wide and arranged on a grid used for the disparity map. By averaging over the absolute values of the Fourier coefficients I found the dominant wavevector magnitude. For the subset of Fourier coefficients for the wavevectors in the range from half to twice the dominant wavevector I found principal axes of the distribution. The direction of the minor axis gave the dominant local orientation of ocular dominance stripes. This algorithm was implemented in MATLAB. The results of the calculation in combination with the observation that the stripes are perpendicular to the vertical meridian gave a map shown by the black bars in Figs. 6 and 7.

References

- Barlow, H. B., Blakemore, C., & Pettigrew, J. D. (1967). The neural mechanism of binocular depth discrimination. *Journal of Physiology (London)*, *193*, 327–342.
- Bauer, H. U. (1995). Development of oriented ocular dominance bands as a consequence of a real geometry. *Neural Computation*, *7*, 36–50.
- Bruno, P., & van den Berg, A. V. (1997). Relative orientation of primary positions of the two eyes. *Vision Research*, *37*, 935–947.
- Blasdel, G., & Campbell, D. (1998). *Symmetry of cortical magnification in Old and New World primates*. Preprint.
- Blasdel, G. G., & Fitzpatrick, D. (1984). Physiological organization of layer 4 in macaque striate cortex. *Journal of Neuroscience*, *4*, 880–895.
- Cajal, S.R.Y. (1995). *Histology of the nervous system* (pp. 116–124). New York: Oxford University Press.
- Cherniak, C. (1992). Local optimization of neuron arbors. *Biological Cybernetics*, *66*, 503–510.
- Chklovskii, D. B., & Koulakov, A. A. (1999). *Ocular dominance patterns in mammalian visual cortex: A wavelength optimization approach*. Preprint.
- Chklovskii, D. B., & Stevens, C. F. (2000). Wiring optimization in the brain. In S.A. Solla, T.K. Leen, K.R. Müller, Advances in Neural Information Processing Systems.
- Cowey, A. (1979). Cortical maps and visual perception: the Grindley Memorial Lecture. *Quarterly Journal of Experimental Psychology*, *31*, 1–17.
- Cumming, B. G., & Parker, A. J. (1999). Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity. *Journal of Neuroscience*, *19*, 5602–5618.
- Daniel, P. M., & Whitteridge, D. (1961). *Journal of Physiology (London)*, *159*, 203–221.
- Enright, J. T. (1980). Ocular translation and cyclotorsion due to changes in fixation distance. *Vision Research*, *20*, 595–601.
- Erwin, E., Obermayer, K., & Schulten, K. (1995). Models of orientation and ocular dominance columns in the visual cortex: a critical comparison. *Neural Computation*, *7*, 425–468.
- Goodhill, G. J., Bates, K. R., & Montague, P. R. (1997). Influences on the global structure of cortical maps. *Proceedings of the Royal Society of London B Biological Science*, *264*, 649–655.
- Goodhill, G. J., & Willshaw, D. J. (1994). *Neural Computation*, *6*, 615–621.
- Hampton, D. R., & Kertesz, A. E. (1983). The extent of Panum's area and the human cortical magnification factor. *Perception*, *12*, 161–165.
- Helmholtz, H.L.V. (1962). *Helmholtz's treatise on physiological optics*. (Translated from the 3rd German ed., J.P.C. Southall) New York: Dover.
- Horton, J. C., & Hocking, D. R. (1996). Intrinsic variability of ocular dominance column periodicity in normal macaque monkeys. *Journal of Neuroscience*, *16*, 7228–7239.
- Horton, J. C., & Hocking, D. R. (1998). Private communication.
- Hubel, D. H., & Freeman, D. C. (1977). Projection into the visual field of ocular dominance columns in macaque monkey. *Brain Research*, *122*, 336–343.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology (London)*, *195*, 215–243.
- Hubel, D. H., & Wiesel, T. N. (1970). Stereoscopic vision in macaque monkey. Cells sensitive to binocular depth in area 18 of the macaque monkey cortex. *Nature*, *225*, 41–42.
- Hubel, D. H., & Wiesel, T. N. (1974). Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor. *Journal of Comparative Neurology*, *158*, 295–305.
- Jones, D. G., Van Sluyters, R. C., & Murphy, K. M. (1991). A computational model for the overall pattern of ocular dominance. *Journal of Neuroscience*, *11*, 3794–3808.
- Kaas, J. H. (1997). Topographic maps are fundamental to sensory processing. *Brain Research Bulletin*, *44*, 107–112.
- LeVay, S., Connolly, M., Houde, J., & Van Essen, D. C. (1985). The complete pattern of ocular dominance stripes in the striate cortex and visual field of the macaque monkey. *Journal of Neuroscience*, *5*, 486–501.
- Mitchison, G. (1991). Neuronal branching patterns and the economy of cortical wiring. *Proceedings of the Royal Society of London B Biological Science*, *245*, 151–158.
- Mountcastle, V. B. (1957). *Journal of Neurophysiology*, *20*, 408–434.
- Nakayama, K. (1983). In: C. Schor, K. J. Ciuffreda, *Vergence eye movements: basic and clinical aspects* (pp. 543–566). London: Butterworths.
- Poggio, G. F., & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *Journal of Neurophysiology*, *40*, 1392–1405.
- Rosa, M. G., Gattass, R., Fiorani Jr, M., & Soares, J. G. (1992). Laminar, columnar and topographic aspects of ocular dominance in the primary visual cortex of Cebus monkeys. *Experimental Brain Research*, *88*, 249–264.
- Rovamo, J., & Virsu, V. (1979). An estimation and application of the human magnification factor. *Experimental Brain Research*, *37*, 495–510.
- Schwartz, E. L. (1980). Computational anatomy and functional architecture of striate cortex: a spatial mapping approach to perceptual coding. *Vision Research*, *20*, 645–669.
- Swindale, N. V. (1996). The development of topography in the visual cortex: a review of models. *Network: Computation in Neural Systems*, *7*, 161–247.
- Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *Journal of Neuroscience*, *8*, 1531–1568.
- Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. R. (1984). *Vision Research*, *24*, 429–448.
- Volkman, A. W. (1859). Die Stereoskopischen Erscheinungen. *Journal of Graefes Archives in Ophthalmology*, *2*, 1–100.
- Wiesel, T. N., Hubel, D. H., & Lam, D. M. (1974). Autoradiographic demonstration of ocular-dominance columns in the monkey striate cortex by means of transneuronal transport. *Brain Research*, *79*, 273–279.
- Wiskott, L., & Sejnowski, T. (1998). Constrained optimization for neural map formation: a unifying framework for weight growth and normalization. *Neural Computation*, *10*, 671–716.
- Young, M. P. (1992). Objective analysis of the topological organization of the primate cortical visual system. *Nature*, *358*, 152–155.