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THE PHYSIOLOGY OF STEREOPSIS

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■ **Abstract** Binocular disparity provides the visual system with information concerning the three-dimensional layout of the environment. Recent physiological studies in the primary visual cortex provide a successful account of the mechanisms by which single neurons are able to signal disparity. This work also reveals that additional processing is required to make explicit the types of signal required for depth perception (such as the ability to match features correctly between the two monocular images). Some of these signals, such as those encoding relative disparity, are found in extrastriate cortex. Several other lines of evidence also suggest that the link between perception and neuronal activity is stronger in extrastriate cortex (especially MT) than in the primary visual cortex.

INTRODUCTION

A central problem faced by the visual system is providing information about a three-dimensional environment from two-dimensional retinal images. In many animals, one of the most precise sources of information arises from the fact that the two eyes have different vantage points. This means that the images on the two retinae are not identical (see Figure 1). The differences between the locations of matching features on the retinae are termed binocular disparities, and the ability to perceive depth from these disparities is stereopsis. This review focuses on the neuronal basis for such depth judgements and so does not discuss all published studies of disparity selectivity. A more encyclopedic review of much of this material has appeared recently (Gonzalez & Perez 1998b).

Before it is possible to determine the disparity of an image feature, it is essential to match features in the left eye with appropriate features in the right eye (see

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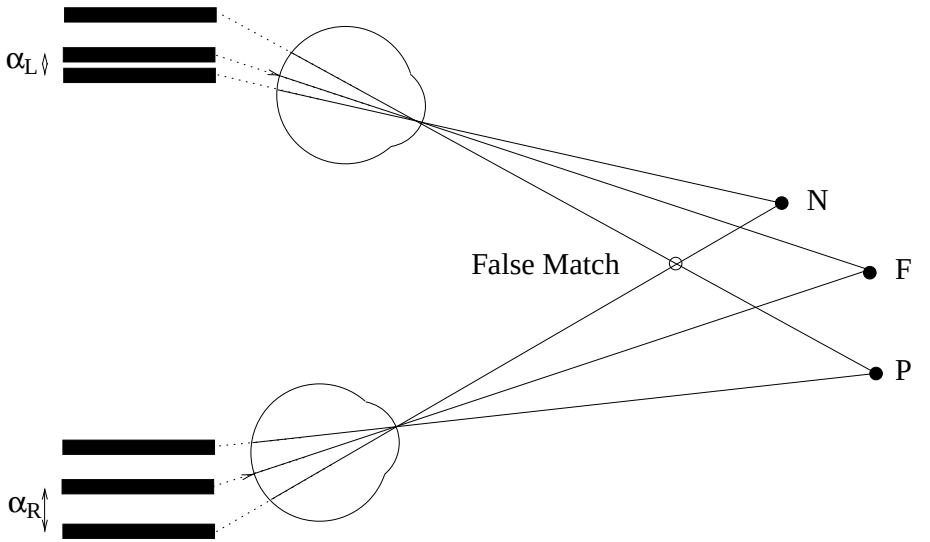

Figure 1 Geometry of binocular vision. Both eyes fixate bar F, so the image of F falls on the fovea in each eye. The images of a nearer bar, N, fall on noncorresponding retinal locations. The angular distances from the fovea (a convenient reference, defining corresponding locations) are marked by α_L and α_R, and the difference between these angles is the binocular disparity of N. This also illustrates the correspondence problem: The image of N in the right eye combined with the image of P in the left eye forms a binocular image with a disparity corresponding to the open circle labeled "false match." No object is perceived at this depth because the brain matches only correctly corresponding features on the two retinae.

Figure 1). This "stereo correspondence problem" was highlighted by the random dot stereogram (RDS) (Julesz 1971). Here a set of random dots is shown to each eye. The dots within a region of one eye's image are displaced a small distance horizontally, thus introducing a binocular disparity. When fused, this gives rise to a vivid depth sensation, even though the two monocular images look homogeneous, with no distinctive features. Although it was the work of Julesz that led to the modern use of the RDS for studying stereopsis, the phenomenon had been noticed 100 years earlier by Cajal (Bergua & Skrandies 2000).

In the primary visual cortex (V1), a good understanding of the mechanism of disparity selectivity has been achieved in recent years, so the first half of the review focuses on this. The second half describes those properties of extrastriate areas that suggest a greater involvement in depth perception.

Measuring Disparity Selectivity

Before discussing the possible roles of disparity-selective neurons in stereopsis, it is important to recognize some of the difficulties in establishing that individual neurons signal disparity. This is usually assessed by presenting some stimulus at a range of disparities, and neurons are classified as disparity-selective if they fire

more action potentials in response to some disparities than in response to others. There are two potential pitfalls in this approach. First, in the absence of any change in the visual scene, changes in the animals' fixation distance (convergence) alter the disparity of the retinal stimulus. Second, changes in the disparity of a stimulus are inevitably associated with changes to at least one of the monocular images presented, so it is vital to dissociate binocular and monocular effects of manipulating disparity.

Eye Movements In preparations that involve a paralyzed, anesthetized animal, the vergence state is probably stable over short periods of time (long enough to characterize disparity selectivity in one cell), but is likely to drift slowly over the course of a long experiment. This problem has been circumvented in some studies by use of a reference cell technique—a second neuron is recorded from a different electrode and held as long as possible. Repeatedly plotting the receptive field (RF) locations of the reference cell allows compensation for drifts in eye position (Hubel & Wiesel 1970, Ferster 1981). Although this technique compensates for changes in vergence, it still does not permit absolute calibration of vergence state. Thus, it is not possible to say with certainty that a neuron's preferred disparity is crossed (nearer than the fixation point), uncrossed (farther than the fixation point), or zero. In some studies, visual identification of retinal landmarks has been used to determine corresponding locations and hence to determine eye position. However, this is fairly imprecise compared with the precision of disparity tuning in many cells.

In an awake animal, the vergence state may change within the course of a single trial; thus, knowing the position of both eyes is essential for the interpretation of disparity tuning data. If the animal is converging correctly, then the absolute value of stimulus disparities is known. Early studies of awake monkeys that recorded the positions of both eyes clearly demonstrated the existence of neurons selective for nonzero disparities in primate V1 (Poggio & Talbot 1981). Other studies have recorded the position of only one eye (e.g. Poggio & Fisher 1977, Trotter et al 1996, Janssen et al 1999), under the assumption that if the animal is fixating with one eye, it is probably also converging correctly. This assumption is not always secure, since small changes in vergence (and therefore disparity) can have a significant effect on firing rate in sharply tuned cells.

Monocular and Binocular Effects of Disparity Changing the disparity of a stimulus inevitably changes at least one of the monocular half-images. Consider a bar stimulus flashed at different disparities. As the disparity is changed, the monocular position of the bar changes. With a sufficiently large disparity the bar may fall completely off the RF in one eye (or even both eyes). Obviously the failure to respond to such a stimulus need not indicate disparity selectivity. Careful use of a sweeping bar can avoid its falling off the RF altogether, but changes in the monocular stimuli alone may still elicit changes in firing rate.

Some studies have applied criteria to the neural responses to reduce the chance of obtaining a misleading appearance of disparity selectivity. Hubel & Wiesel (1970)

and Hubel & Livingstone (1987) required that the disparity tuning width be much narrower than the RF width. But this criterion might exclude cells that are genuinely disparity selective. It may be for this reason that Hubel & Wiesel (1970, p. 42) "studied hundreds of cells in area 17" and "found no convincing examples of binocular depth cells."

Two different solutions to the problem of monocular artifacts have been effective. The first is to present a dichoptic bar stimulus at all possible combinations of positions in the two eyes. In this way the effects of disparity can be separated from the effects of monocular position. This is the approach taken in the reverse-correlation methods (Ohzawa et al 1990). The second approach is to use RDS stimuli (Julesz 1971), first applied to physiological recording in the pioneering work of Poggio et al (1985, 1988). Here, changes in disparity are not associated with any discernible changes in the monocular images. Disparity selectivity in response to such stimuli identifies a specific response related to binocular correlation.

Fortunately, most of the disparity-selective phenomena reported in early studies have been replicated with stimuli that eliminate monocular artifacts. However, there are certain observations that have only been reported using simple bar stimuli that should therefore be treated with caution. These include observations on the properties of near/far cells (see section on Classes of Disparity Tuning) and the combination of vertical and horizontal disparities (section on Horizontal and Vertical Disparities).

PRIMARY VISUAL CORTEX

Although the responses of many cells in the lateral geniculate nucleus can be modulated by stimuli in the nondominant eye (Suzuki & Kato 1966, Singer 1970, Marocco & McClurkin 1979, Rodieck & Dreher 1979), this does not produce disparity-selective responses (Xue et al 1987). V1 is the first site at which single neurons can be activated by stimuli in both eyes. The first studies to document disparity selectivity in V1 (Pettigrew et al 1968, Barlow et al 1967) used sweeping bar stimuli in anesthetized cats. These studies demonstrated that some V1 neurons encode information specifically about the relationship between the images in the two eyes. The data are compatible with a variety of different mechanisms. At one extreme is the possibility that the monocular processing is complicated: A distinctive "trigger feature" such as an oriented edge is identified (Barlow et al 1967), and the neuron responds maximally when this feature appears at the preferred disparity. At the other extreme is a trivial possibility that these neurons are activated whenever any excitatory stimulus is present in each monocular RF. Although such neurons could carry some information about disparity, it would be confounded by effects of monocular stimulus location.

Between these extremes is the possibility that each monocular RF performs a relatively simple operation on the image, and the cell fires maximally when this

calculation produces a large result in both eyes. In this scheme it does not matter whether the visual stimulus is the same in both eyes, only that the stimulus in each eye produces a strong output from the monocular filter. An important consequence of such a scheme is that the monocular RF shape largely determines the shape of the disparity response, whereas a scheme based on trigger features requires no special relationship between the structure of the monocular RF and the shape of the disparity tuning function. We now examine these relationships for the two main physiological cell types in V1: simple cells and complex cells.

Simple Cells

A defining characteristic of simple cells is that they show linear spatial summation (Hubel & Wiesel 1962, Movshon et al 1978b). Thus, their responses to monocular stimuli can be summarized by a RF map that describes the response to small bright and dark spots presented at different locations in space (Jones & Palmer 1987, DeAngelis et al 1993a). These RF maps are well described by Gabor functions (a sinewave multiplied by a Gaussian envelope), and the response of a simple cell can be reasonably well predicted by convolving a visual pattern with the RF map (Jones & Palmer 1987, Field & Tolhurst 1986, DeAngelis et al 1993b). (Convolving here means multiplying the image brightness at each point with the value of the RF at that point and summing all the products.) Disparity selectivity in simple cells might then be understood as follows. A convolution is performed in each eye, and the results are added (so a negative result in the left eye can cancel excitation from the right eye). After this binocular summation, the output is half-wave rectified (negative values are discarded). The cell will fire roughly in proportion to the result of this binocular summation. In such a scheme, the key to understanding disparity selectivity would be to understand the differences between the two monocular RFs.

Ohzawa & Freeman (1986b) performed the first quantitative comparison of monocular and binocular responses at different disparities in simple cells. They presented sinusoidal luminance gratings and used the monocular responses to drifting gratings to predict binocular responses to a range of interocular phase differences. The majority of responses were well described by this linear model, and nearly all could be explained by a linear interaction followed by a threshold. [An earlier study, using bars, suggested the same conclusion (Ferster 1981).]

Up until this time, it had generally been thought that neurons had closely matched RF profiles in the two eyes (e.g. Hubel & Wiesel 1973, Maske et al 1984). Disparity selectivity was thought to result from these RFs being placed in different positions on the two retinae. Ohzawa & Freeman (1986b) pointed out that similar disparity selectivity could be produced by cells that have RFs in corresponding retinal locations but that have different RF shapes in the two eyes (see Figure 2). Indeed Bishop et al (1971) had noted such differences in some cells in the cat. To investigate this possibility explicitly, Freeman and colleagues (DeAngelis et al 1991, Ohzawa et al 1996) fitted Gabor functions to RF profiles

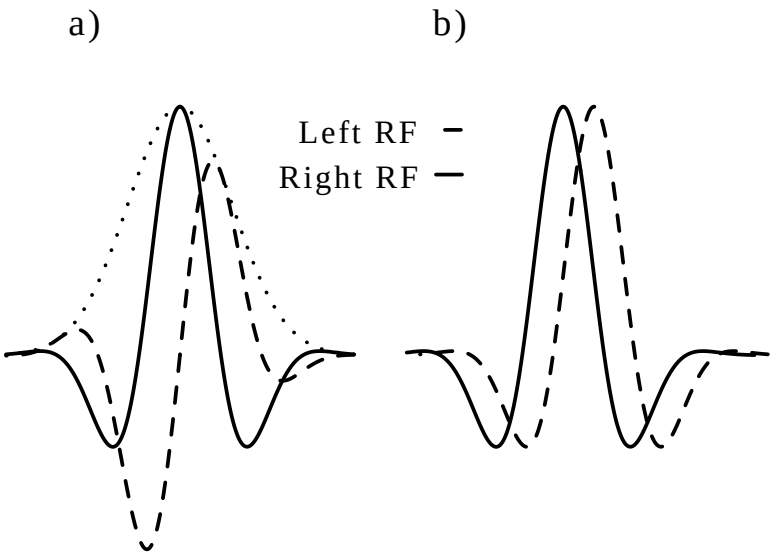

Figure 2 Phase and position disparity mechanisms. Receptive field (RF) profiles in the left eye (dashed lines) and right eye (solid lines) are shown for two possible binocular neurons. The profiles are Gabor functions, the product of a sinewave and a Gaussian envelope (dotted line). In (*a*), the location of this envelope is the same in both eyes, but the phase of the sinusoidal component is different (by $\pi/2$ here). In (*b*), the RF has the same shape (determined by the phase of the sinewave relative to the envelope) but different positions in the two eyes.

measured separately for each eye. Differences in the internal structure of the RF were quantified as a difference in the phase of the sinusoidal component relative to the center of the Gaussian envelope (see Figure 2). This revealed a wide range of interocular phase differences, called phase disparities, in binocular simple cells.

Anzai et al (1999b) went on to compare monocular and binocular responses of simple cells by showing uncorrelated one-dimensional noise patterns to the two eyes. Monocular RF profiles were constructed by computing the average effect of black or white lines at different locations in each eye separately. Binocular RF profiles were constructed independently from looking at the average effect of lines of the same contrast polarity in the two eyes (black-black or white-white pairs) compared with the effect of lines of opposite polarity in the two eyes. They found a good agreement between the monocular RF structure and the shape of the binocular disparity response. Taken together, these studies clearly showed that phase differences between monocular RFs do occur in simple cells, and that these differences account for the shape of the binocular interaction profile. However, this conclusion does not imply that position disparities are not also used, as discussed below.

Complex Cells

For complex cells, it is much less straightforward to understand disparity selectivity in terms of monocular RF structure because these neurons are spatially nonlinear. They respond to oriented contours over a range of positions, but are nonetheless quite selective for the luminance structure of the stimulus (Hubel & Wiesel 1962). With monocular sinusoidal gratings, complex cells are insensitive to the spatial phase of the grating yet remain selective for the spatial frequency. For disparity-selective complex cells, this gives rise to an interesting property: They are insensitive to the phase of the grating when tested in either eye alone, yet they are sensitive to the phase difference between the eyes (Ohzawa & Freeman 1986a).

An extension of the earliest model of complex cells (Movshon et al 1978a) to the binocular case provides a possible explanation of this phenomenon. This disparity "energy" model (Ohzawa et al 1990) simply proposes that a complex cell is constructed from a set of simple cells. As shown in Figure 3, all of the constituent simple cells have the same disparity tuning, but their monocular RFs are in quadrature (meaning that all spatial frequency components are shifted by $\pi/2$, so that the responses are orthogonal). If a stimulus is at the complex cell's preferred disparity, then at least one of the simple cells is activated, no matter where in the RF a stimulus falls. However, if a stimulus is at the null disparity, none of the simple cells is active, so the complex cell does not fire either. This model produces a complex cell that is sensitive to the correlation between images in the two eyes (Qian 1994, Fleet et al 1996).

This model explains many properties of disparity-selective neurons in V1. First, it explains the results obtained with sinusoidal gratings by Ohzawa & Freeman (1986a). Second, it explains the shape of disparity tuning functions measured with broadband stimuli: Because the RF profiles of the constituent simple cells are well described as Gabor functions, the shape of the disparity tuning curve is as well (Ohzawa et al 1990, 1997; SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication). In the energy model, the spatial period of the Gabor function describing the disparity response is closely related to the monocular spatial frequency tuning. In practice, however, only a weak correlation has been observed between these two measures (Ohzawa et al 1997; SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication).

The energy model also explains the responses of complex cells to stimuli of opposite polarity in the two eyes. Most complex cells can be activated monocularly both by dark bars (against a grey background) and by bright bars. But when a dark bar is shown to one eye, while a bright bar is shown to the other eye at the preferred disparity, disparity-selective cells are generally suppressed. Similarly, they show activation for those disparities where same-polarity bars produce inhibition (Ohzawa et al 1990). This occurs because in each simple cell subunit, the maximum binocular response occurs when the bar in both eyes causes maximum excitation. If the polarity of a bar in only one eye is reversed, then that bar

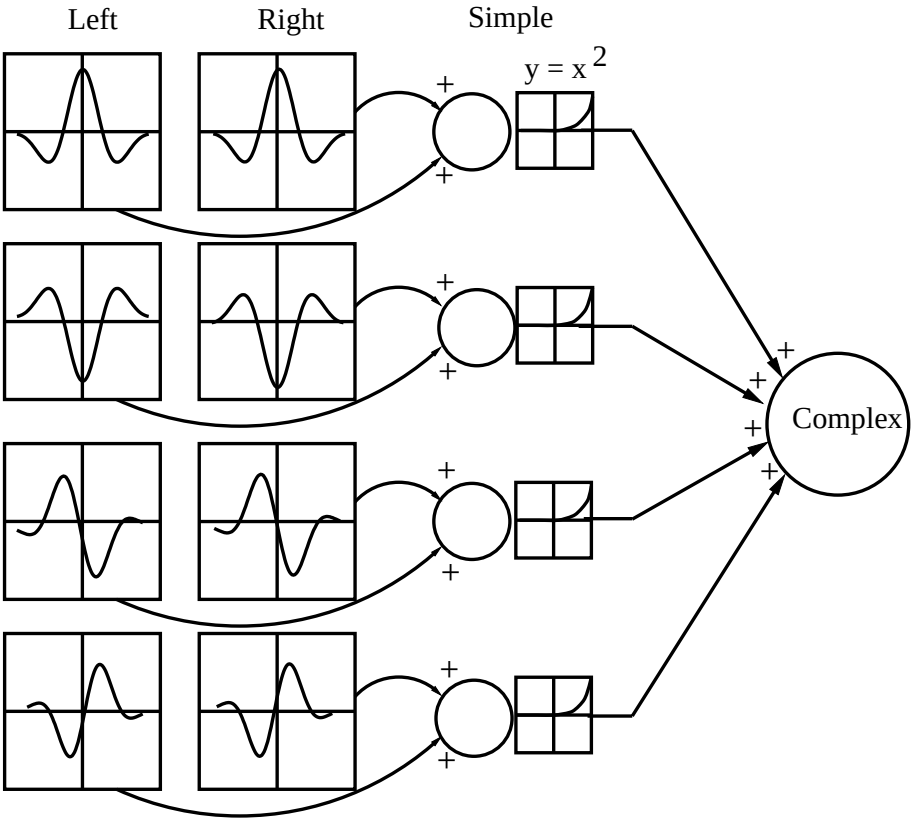

Figure 3 A model for disparity selectivity in complex cells. Each complex cell receives inputs from a minimum of four simple cells. These consist of two pairs that are in quadrature, so that the sum of outputs is invariant to monocular spatial phase. At least one simple cell is activated by a stimulus in any phase. Those simple cells that are inhibited contribute nothing to the response (because the output of each simple cell is rectified). Thus all stimulus phases are excitatory. In this example, the receptive field (RF) profiles are identical in both eyes, so the complex cell is maximally activated by stimuli at zero disparity. If a stimulus is presented with a disparity equal to one half cycle of the RF, then the monocular responses cancel one another in each simple cell. Because responses from the two eyes are added before rectification, there is no response to this disparity. Hence this model explains the preservation of sensitivity to interocular phase differences, despite an insensitivity to spatial phase in each eye. If the same interocular phase shift or position shift is added to each of the simple cells, then the complex cell is maximally activated by nonzero disparities. If vairables L and R are the results of convolving the stimulus in each eye with the corresponding RF profile, then the output of each simple cell is $(L + R)^2 = L^2 + R^2 + 2LR$. Thus, by virtue of the last term in this expression, the half-squaring nonlinearity makes the cell sensitive to binocular correlation. Adapted from Ohzawa et al (1990).

becomes a suppressive stimulus. The position of this monocular stimulus must then be altered to produce excitation. Since this position change is required for only one eye, it results in a change in disparity.

In summary, the responses of disparity tuned cells can be explained with the energy model or some similar model in which there is no substantial nonlinearity in monocular processing prior to binocular combination. There is no need to postulate any complex feature detection prior to the representation of disparity in V1.

Horizontal and Vertical Disparities

Although we have discussed disparity encoding as if it were one-dimensional, RFs are two-dimensional. Thus, responses of the energy model depend on both horizontal and vertical disparities. A plot of responses to all combinations of vertical and horizontal disparities will reflect the structure and orientation of the monocular RFs (see Figure 4). A binocular neuron with perfectly matched RFs in the two eyes will be maximally activated by an RDS stimulus at zero disparity, and applying either a horizontal or a vertical disparity will reduce the response. The response should change more rapidly when disparities are applied orthogonal to the RF orientation because the structure of the monocular RFs changes most rapidly in that direction. However, if the visual stimulus is one-dimensional, such as a bar or a grating, then disparities applied parallel to the stimulus orientation have no effect (Figure 4*f*). Therefore, when evaluating responses to vertical and horizontal disparities, it is important to use stimuli that are orientation broadband, like RDS. With such stimuli, the energy model predicts that disparity tuning depends on RF orientation, phase disparity, and position disparity (both horizontal and vertical components).

This prediction of the energy model remains largely untested: The only study using combinations of vertical and horizontal disparities used bar stimuli (Maske et al 1986). It is an important prediction to test because stereopsis does not require equally precise information about all types of disparity. In most viewing situations, disparities in the central part of the retina will be larger horizontally than vertically. If the primary function of such cells is stereopsis, this should be reflected in the direction of neuronal disparity preferences. Alternatively, V1 neurons may measure binocular correlation for disparities in all directions. Such measurements would be useful for many binocular functions, including stereopsis and the control of vergence eye movements (which maintain vertical and horizontal alignment of the eyes). In this view, one would expect V1 neurons to represent horizontal and vertical disparities equally (isotropic).

Although data in the format of Figure 4 have not been obtained with RDS, two other experimental approaches have been used to determine whether disparity encoding is isotropic. The first has been to examine whether there is a relationship between orientation preference and the strength of disparity tuning. All the studies that have examined this quantitatively have found no correlation (Ohzawa &

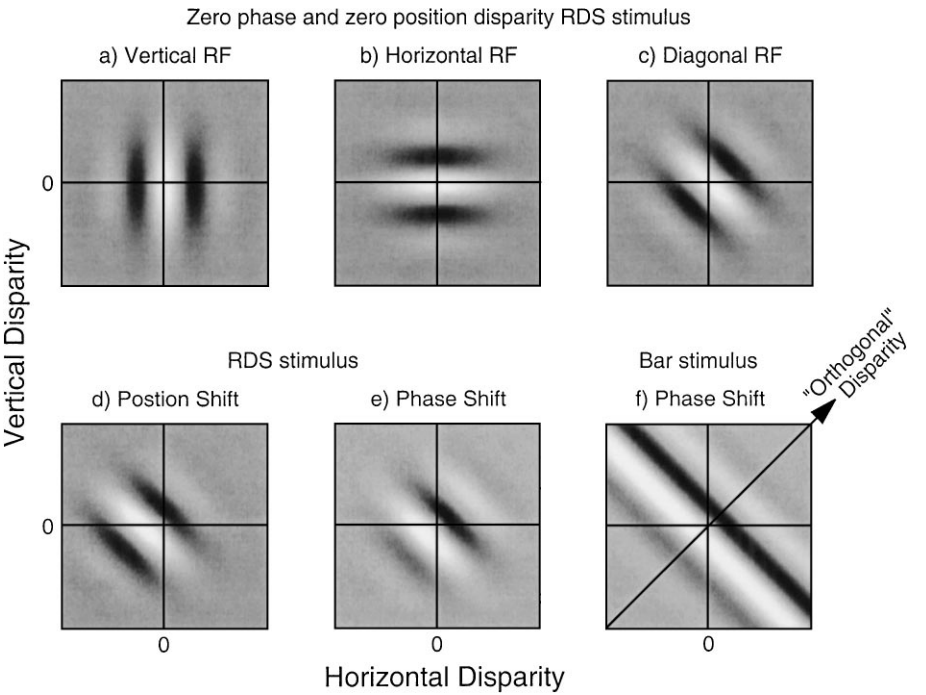

Figure 4 Responses of the energy model to vertical and horizontal disparities. The brightness of each point represents the response to a combination of horizontal and vertical disparity. Bright areas are strong responses; dark areas are weak responses. (*a–e*) Responses to orientation broadband stimuli [like random dot stereogram (RDS)]; (*f*) Responses to a one-dimensional (e.g. oriented bar) stimulus. (*a*) Responses of a neuron with identical RFs in the two eyes and a vertical preferred orientation are shown. Such a neuron is most sensitive to small changes in horizontal disparity. (*b*) Responses of a cell with matched RFs and a horizontal orientation. Because of its Gaussian envelope, this cell can also signal horizontal disparity for broadband stimuli. Note, however, that the most rapid changes in response result from vertical disparities (orthogonal to the RF orientation). (*c*) Responses of a cell with matched RFs and a diagonal RF orientation. (*d*) The effect of adding a horizontal position disparity to the neuron in (*c*). Note that the response profile has a diagonal axis of mirror symmetry because there is no phase disparity. The disparity that produces the greatest response is a horizontal disparity because the position shift is horizontal, but disparities orthogonal to the RF orientation produce the steepest change in response. (*e*) The effect of adding a phase disparity to the neuron in (*c*). Now, there is no axis of mirror symmetry parallell to the RF, and the neuron's largest response is produced by a combination of horizontal and vertical disparities along the direction orthogonal to the RF orientation. (*f*) When a long bar stimulus is used, only disparity changes orthogonal to the stimulus orientation elicit changes in response. Displacements parallel to the bar produce no change in the stimulus within the RFs. For this reason, many studies using oriented bars or gratings have only applied disparities orthogonal to the stimulus orientation.

Freeman 1986a,b; Smith et al 1997; SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication).

The second approach has been to look for a relationship between orientation preference and the range of disparities encoded. This approach is hazardous in anesthetized animals because the measured range can be influenced by drifts in eye position. Perhaps this explains why several studies of anesthetized cats have obtained conflicting results (e.g. Barlow et al 1967, Nikara et al 1968, von der Heydt et al 1978, Maske et al 1986). The only quantitative study of awake animals found no relationship between orientation preference and the range of disparities encoded (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication). One measurement that is not influenced by slow drifts in eye position is the interocular phase difference between the two monocular RFs. In simple cells from cat V1, DeAngelis et al (1991) found that neurons preferring near-vertical orientations exhibited a larger range of phase differences than those preferring horizontal orientations. A similar, but less clear, correlation was observed by Anzai et al (1999b). However, in complex cells Anzai et al (1999c) found a correlation in the opposite direction (vertically oriented cells showed smaller phase differences). In awake monkeys, Prince et al (SJD Prince, BG Cumming, AJ Parker, submitted for publication) found no correlation between orientation preference and either phase shift or horizontal position shift.

Overall, then, there is limited evidence to support the view that V1 preferentially represents the directions of disparity that are most useful for stereopsis. However, no single study has gathered all the data needed to test this hypothesis conclusively.

Phase and Position Mechanisms

Many complex cells have disparity tuning curves the shape of which indicates an interocular phase difference (Ohzawa et al 1990, 1997; Anzai et al 1999c; SJD Prince, BG Cumming, AJ Parker, submitted for publication). A tuning curve that is even-symmetric (like that labeled T0 in Figure 5) suggests that the cell has similar RF structures in the two eyes. A curve that has odd-symmetry (like those labeled FA and NE in Figure 5) indicates a 90° phase shift between the subunits in the two eyes. Another way to distinguish phase and position mechanisms is to measure disparity selectivity with sinewave gratings at different spatial frequencies. If only a position shift is present, then the peaks of the disparity tuning curves should coincide at a value equal to that shift. If only a phase shift is present, then the modulation in the disparity tuning should show a consistent phase of modulation (for discussion see Fleet et al 1996, Zhu & Qian 1996). Wagner & Frost (1993, 1994) reported that in the Wulst of the barn owl, multi-unit activity showed consistent peak positions, whereas using this method with single-cell recording in awake monkeys indicates both position and phase shifts (SJD Prince, BG Cumming, AJ Parker, submitted for publication). Furthermore, Prince et al found that the phase shift estimated by this method agreed with the estimate derived from analysis of tuning curve shape. Nieder & Wagner (2000) recently analyzed the shape of

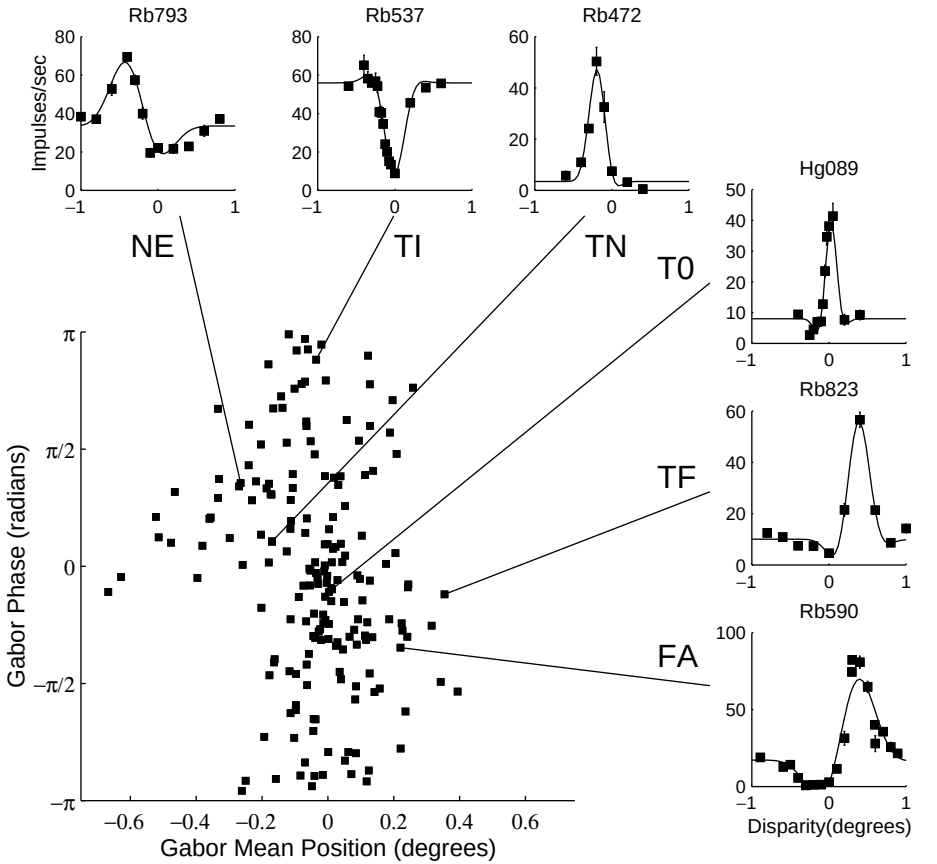

Figure 5 Distribution of phase and position disparities in a population of disparity-selective neurons (SJD Prince, BG Cumming, AJ Parker, submitted for publication). Tuning curves for horizontal disparity in random dot stereograms were fitted with Gabor functions. (Such curves are equivalent to horizontal cross sections through the surfaces shown in Figure 4.) For each neuron, the fitted phase is plotted against the fitted position of the Gaussian envelope. Examples of each of the classes identified by Poggio and collaborators are shown: NE, near; TI, tuned inhibitory, TN, tuned near; TO, tuned zero; TF, tuned far; FA, far. However, there is no tendency for a grouping around any of these shapes. Rather, the shapes of disparity tuning curves for V1 seem to form a continuum.

tuning curves recorded from the Wulst of the barn owl, and reported a range of phase shifts similar to that found in the cat and monkey. Taken together, these observations suggest that the study by Wagner and Frost probably underestimated that contribution of phase shifts.

Two studies have compared the relative contributions of phase and position mechanisms. Anzai et al (1997) used a reference cell method, recording from simple cells in anesthetized cats. In awake monkeys, Prince et al (SJD Prince,

BG Cumming, AJ Parker, submitted for publication) looked at responses of simple and complex cells to horizontal disparities in RDS. The phase and position of fitted Gabor functions were used to estimate underlying phase and position disparities. The data from both studies is shown in Figure 6: When converted into equivalent position shifts, phase shifts encode a slightly larger range of disparities than do position shifts (by 60% in cats and 25% in monkeys). However, this comparison is somewhat difficult to interpret:

1. Position shifts are measured in terms of visual angle; phase shifts are expressed in units of phase angle. This can be converted numerically into units of visual angle by scaling with the spatial period of the RF, but care is required in interpreting these numbers. Phase shifts outside the range $\pm\pi/2$ are simply inverted versions of phase shifts within the range $\pm\pi/2$, so it is not clear how much additional information they convey about disparity (SJD Prince, BG Cumming, AJ Parker, submitted for publication).

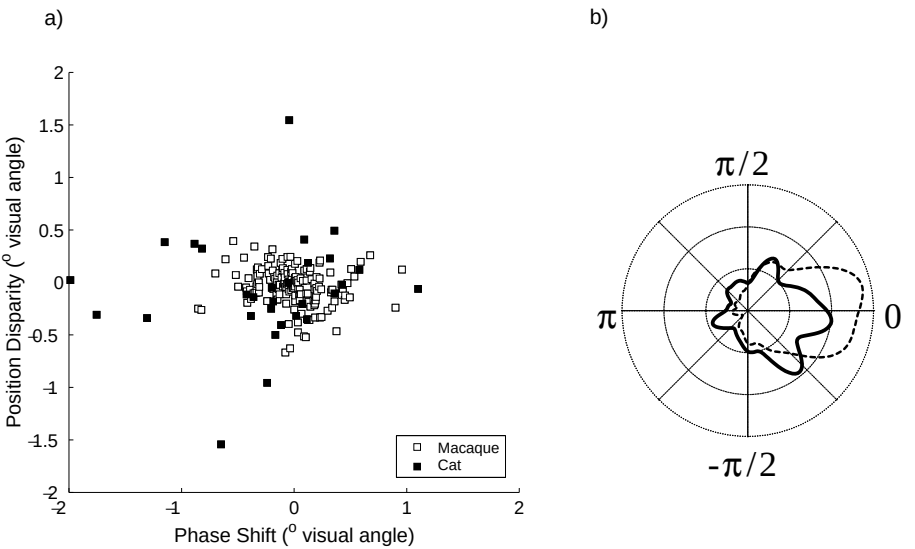

Figure 6 (*a*) Relative magnitudes of phase and position shifts in simple cells from cats (solid symbols, data from Anzai et al 1999a) and all cell types from monkeys (open symbols, data from SJD Prince, BG Cumming, AJ Parker, submitted for publication). Phase disparities have been converted into equivalent position disparities. The range of phase disparities is larger than position disparities. The pattern of results is broadly similar in the two species. (*b*) Compares the probability distributions for phase differences in monkeys (solid line Prince et al 2000a) and cats (dashed line, data combined from DeAngelis et al 1991, Anzai et al 1999a,c). These are plotted as polar probability density functions: The distance of each point from the origin indicates the probability of finding a fitted phase equal to the point's polar angle. The distribution is similar in the two animals, both showing a bias towards even-symmetric tuning (phase shifts near zero).

2. Position shifts are inherently two-dimensional (Anzai et al 1997), whereas phase shifts are one-dimensional. As shown in Figure 4, position shifts can encode useful information about disparities parallel to the RF orientation, but phase shifts cannot.

Given these difficulties and the modest difference in reported magnitudes, it seems likely that both phase and position mechanisms contribute importantly to disparity encoding, and this is similar in monkeys and cats. It is unclear what advantage is derived from employing both coding mechanisms, although Erwin & Miller (1999) offer one possible explanation.

The very existence of significant phase differences between the RF structure in the two eyes (in both cats and monkeys) has important implications. It argues strongly against the view that disparity selectivity depends on monocular responses to distinctive "trigger features," since cells with phase differences are responding to different features in the two eyes. Also, phase disparities enforce a "size-disparity correlation"—neurons can only encode disparities up to $\pm 1/2$ of the preferred spatial period. This limitation is computationally useful, since it restricts the number of false matches (e.g. Marr & Poggio 1979). It is interesting that even position shifts tend not to exceed this half cycle limit (SJD Prince, BG Cumming, AJ Parker, submitted for publication). Some aspects of psychophysical performance also show a size-disparity correlation (discussed in Prince & Eagle 2000, Smallman & Macleod 1994): This may be a reflection of the underlying physiological substrate (DeAngelis et al 1995).

Classes of Disparity Tuning

Phase disparities also provide a rationale for understanding the different shapes of disparity tuning curves that are observed (Nomura et al 1990). Poggio et al (1988) and Poggio (1995) distinguish three classes of disparity tuning curve (Poggio 1995):

1. "Tuned excitatory" (TE) neurons respond maximally to zero or near-zero disparities and show a roughly symmetrical response profile. These are subdivided into tuned zero (T0, maximal response to zero disparity), tuned near (TN) (maximal response to small crossed disparities), and tuned far (TF) (maximal response to small uncrossed disparities). The shape of these disparity tuning curves can be explained by supposing that the phase disparity is near zero.
2. Tuned inhibitory (TI) neurons are similar to TE cells, but inverted, showing maximal suppression for near zero disparities. This can be explained by a phase disparity near π.
3. Near and far neurons have asymmetrical response profiles (or more correctly, odd-symmetric), responding only to crossed (near cells) or uncrossed (far cells) disparities. The typical description of these cells also includes that their responses are "extended rather than tuned" (Poggio 1995)—there is a broad range of disparities over which the responses

change little. This particular feature is less easily reconciled with a simple phase disparity. Phase disparities near $\pi/2$ or $-\pi/2$ produce odd-symmetric curves that are just as tuned as even-symmetric curves. However, all the published examples of near/far cells showing these extended responses have used bar stimuli. With such stimuli, it is hard to exclude a contribution from monocular changes in the stimulus (see section on Measuring Disparity Selectivity). Our experience is that when a sufficiently large range of disparities is explored using random dot stimuli, no clear "plateau" is observed in the tuning of near/far cells, and they are well described by odd-symmetric Gabor functions.

Viewed from the perspective of phase disparities, it seems more natural to view these tuning curves as points on a continuum (as suggested by LeVay & Voigt 1988; Freeman & Ohzawa 1990) rather than as distinct classes. Prince et al (SJD Prince, BG Cumming, AJ Parker, submitted for publication) examined the distributions of both phase and position disparities in a large population of disparity-selective cells from monkeys and found no evidence of distinct classes (see Figure 5).

Depth Perception and Disparity-Selective Neurons in V1

It appears that we have a good understanding of the mechanism by which V1 neurons signal disparity. Here we consider how well these neuronal properties can account for the perceptual properties of stereopsis. In this context, we consider (*a*) the stereo correspondence problem, (*b*) the distinction between relative and absolute disparities, (*c*) the statistical reliability of neuronal signals and psychophysical judgements, and (*d*) the relationship between disparity and depth.

The Correspondence Problem If a single random dot pattern is convolved with monocular filters in each eye, there will usually be several disparities that elicit similar responses in both eyes. The pattern will activate binocular filters tuned to different disparities, but only one of these is perceived. In order to discard the "false" matches, the correspondence problem must be solved. (This need not entail considering matches dot by dot. The number of false matches depends on the monocular filters that are applied.)

It is of course possible that V1 neurons are more sophisticated than the energy model and distinguish false matches from correct matches. In order to test this possibility, it is necessary to place false matches in the neuronal receptive field. Most experiments with RDS have used dynamic RDS—each frame of the display contains a fresh pattern of dots, but the disparity relationships remain constant. Unfortunately, the disparities at which false matches occur depend on both the monocular filters and on the particular dot pattern used. Therefore, if one dot pattern contains a false match at some disparity, the dot pattern displayed on the next frame will in general not contain a false match at the same disparity. For this reason, averaged across many RDS frames, even the energy model responds maximally to the correct matches (Qian 1994, Fleet et al 1996, Cumming & Parker 1997).

One stimulus manipulation that clearly differentiates the properties of the energy model from those of visual perception is to reverse the contrast of the image in one eye. Each bright feature on one retina is then paired geometrically with a dark feature on the other retina, and vice versa. Such stereograms are called anticorrelated because the correlation coefficient between luminance values in the two images is a negative one. Ohzawa et al (1990) and Livingstone & Tsao (1999) examined the responses with bar stimuli and (as described above) found an inversion of the disparity tuning. This is exactly what one would expect from the energy model, since its response reflects binocular correlation (see legend to Figure 3). Cumming & Parker (1997) found very similar results using anticorrelated RDS in awake monkeys (for a comparison, see Ohzawa 1998). In both cases, the effects of anticorrelation on neuronal activity are quite different from the perceptual effects. With bar stimuli, human observers perceive depth in the geometrically correct direction (Helmholtz 1909, Cogan et al 1995, Cumming et al 1998). In anticorrelated RDS of the type used by Cumming & Parker (1997), no depth is perceived (Julesz 1971, Cogan et al 1993, Cumming et al 1998). In this case observers appear unable to access the information about disparity contained in the firing rate of single V1 neurons. Both types of anticorrelated stimulus activate disparity-selective neurons without observers perceiving a stimulus at the equivalent depth. Thus, the psychophysical matching process appears to discard these responses as false matches. The neural responses are not associated only with psychophysically matched disparities. This dissociation between neuronal firing and perceived depth does not imply that the perception of depth is completely independent of activity in V1 neurons. They may perform an initial analysis of binocular correlation that extrastriate areas use to solve the correspondence problem.

In one quantitative respect, the neuronal responses to anticorrelation deviate from the predictions of the energy model: Although the disparity tuning curves are generally inverted by anticorrelation, the magnitude of the disparity-induced modulation is often smaller for anticorrelated stimuli than for their correlated counterparts (Cumming & Parker 1997, Ohzawa et al 1997). The energy model predicts that these magnitudes will be the same. It remains to be seen whether major changes in the model are required to accommodate this observation.

A different examination of the role of V1 in stereo correspondence was presented by Cumming & Parker (2000). They used circular patches of sinusoidal luminance gratings. For two disparities differing by the spatial period of the grating, the stimulus within the RF is identical, although the perceived depth is different. Consider a grating at a crossed disparity equal to one grating period. Within the RF, each bar of one monocular grating superimposes on the next bar of the other monocular grating. Thus, within the RF it is identical to a grating at zero disparity. Nonetheless, what is perceived is a patch of grating standing in front of the fixation point. The perceptual effects were demonstrated psychophysically in the animals from whom neurons were recorded, and a similar psychophysical result had been reported in humans using rows of dots (Mitchison 1988, McKee & Mitchison 1988). Cumming & Parker (2000) found that for the vast majority of V1 neurons,

the response was determined by the local disparities within the RF, regardless of the perceived depth. This reinforces the view that additional processing is required beyond striate cortex to account for how depth is perceived in stereograms.

Relative and Absolute Disparities The mechanisms discussed so far signal the disparity of a feature in retinal coordinates (how far the two images fall from corresponding retinal locations). This is called the absolute disparity. The difference between the absolute disparities of two features is called their relative disparity. A major advantage of relative disparities is that they are unaffected by vergence eye movements, whereas changes in vergence alter the values of absolute disparities. Cumming & Parker (1999) controlled vergence movements in a feedback loop to manipulate absolute disparities independent of relative disparities. The results showed clearly that neurons in monkey V1 signal absolute, not relative, disparity. In contrast, a number of psychophysical studies have suggested that stereopsis relies primarily on relative disparities. Stereoacuity, when measured using a single isolated feature (absolute disparity threshold), is fivefold poorer than when relative disparities are provided by a simultaneously visible reference stimulus (Westheimer 1979). When an absolute disparity is applied uniformly to a large display, substantial changes in disparity are not detected (Erkelens & Collewijn 1985a,b; Regan et al 1986).

Neuronal and Psychophysical Sensitivity Both the experiments on stereo correspondence and those on relative disparity indicate that signals that determine depth perception are different from those carried by single V1 neurons. Further elaboration of stereo signals probably occurs outside V1, and this may produce signals that could be used more directly for depth perception. If these signals were derived from V1 neurons, then the precision with which V1 neurons are able to signal disparity imposes limits on the precision of subsequent processing and psychophysical performance. This was examined explicitly by Prince et al (2000), who measured the smallest disparity change that single V1 neurons could detect with a given reliability (the neurometric threshold). The performance of the animals was measured with the same stimuli (psychometric thresholds). Many neuronal thresholds were as low as the psychometric thresholds, which indicates that a modest degree of pooling from V1 responses is sufficient to account for observed stereoacuity. Note that this result applied when the animals' task was a relative disparity judgment. When the animals were forced to rely on absolute disparities alone, the psychometric thresholds were generally larger (poorer performance) than the neurometric thresholds. Under these circumstances, the animals were not able to discriminate between stimuli even when information available in single V1 neurons made the discrimination possible.

Disparity and Depth There are many unresolved questions concerning how a map of angular disparities might be converted into a representation of the three-dimensional world. Are all possible relative disparities encoded? Are they

converted into a depth map with some fixed coordinate frame? Most of these complex questions have not been addressed at the neurophysiological level. One exception is the effect of viewing distance. The disparity produced by a fixed depth difference depends on viewing distance. A few studies (Trotter et al 1992, 1996; Gonzalez & Perez 1998a) have reported that disparity-selective neurons in V1 alter their response to a fixed stimulus disparity when the viewing distance is changed. The change in viewing distance requires a change in vergence angle, but as these studies did not measure vergence, it is possible that inaccuracies in vergence resulted in changes in horizontal disparity. Also, changes in viewing distance induce changes in vertical disparity (Mayhew & Longuet-Higgins 1982), which should also affect response rates. (Disparity tuning curves performed at different viewing distances correspond to different cross sections through the surfaces shown in Figure 4.) At present it is not possible to be sure that effects like those observed by Trotter et al are not the result of changes in the vertical and horizontal disparities of the retinal stimulus.

Conclusion

The major features of disparity-selective responses in cat and monkey V1 are captured by a relatively simple model (the energy model of Ohzawa et al 1990). The model is certainly a simplification—it is likely that real complex cells receive input from more than four subunits. Nonetheless, this simple model has been very successful—only two failures have been noted to date: (*a*) a poor correlation betwen monocular spatial frequency tuning and the spatial scale of the disparity tuning function, and (*b*) a failure to explain the reduced amplitude of responses to anticorrelated stimuli.

Although the mechanism of disparity-selectivity in V1 seems to be well understood, there are several substantial differences between the properties of stereopsis and the properties of V1 neurons. Conversely, disparity-selective V1 neurons seem well suited to the control of vergence eye movements: Anticorrelated RDS elicit reversed vergence movements (Masson et al 1997); vergence depends on absolute rather than relative disparity; and maintaining alignment of the eyes requires signals about horizontal and vertical disparities. It is even possible that vergence control is the primary role of these V1 neurons—there is no definitive evidence that stereopsis is mediated by disparity-selective V1 neurons—but it seems more likely that V1 serves as an initial stage in stereo processing. Extrastriate areas may then make explicit the signals that support depth perception (discarding false matches and representing relative disparity). We now turn our attention to the role of these areas.

EXTRASTRIATE CORTEX

Considerably less is known about stereoscopic processing outside V1 than within V1. Disparity-selective neurons can be found in many different areas of the brain

(for a review see Gonzalez & Perez 1998b). In cats, disparity-selective neurons have been reported to occur in extrastriate areas 18, 19, and 21, in the superior colliculus, and in the accessory optic system (Ferster 1981; LeVay & Voigt 1988; Guillemot et al 1993a,b; Pettigrew & Dreher 1987; Wang & Dreher 1996; Vickery & Morley 1999; Berman et al 1975; Bacon et al 1998; Grasse 1994). In monkeys, disparity-selective neurons can be found in extrastriate areas V2, V3, V3A, VP, MT, MST (both subdivisions), and IT (Hubel & Wiesel 1970, Poggio & Fisher 1977, Poggio et al 1988, Burkhalter & van Essen 1986, Felleman & van Essen 1987, Maunsell & van Essen 1983, Roy et al 1992, Janssen et al 1999, Uka et al 2000), as well as in some visuomotor regions of parietal and frontal cortex (Gnadt & Mays 1995, Ferraina et al 2000).

To understand why binocular disparity is repeatedly represented in different areas, it is useful to identify ways in which disparity processing differs from V1. This requires more than just measurements of disparity tuning to simple stimuli: It is essential to record and/or manipulate the activity of disparity-selective neurons in cortical areas during a variety of stereoscopic tasks. In this section, we consider how the representation of binocular disparity in extrastriate cortex differs from that in V1, and we review emerging evidence for more direct links between neuronal activity and perception.

Columnar Architecture for Disparity

Columnar architecture is a common feature of the organization of cerebral cortex. In many cortical areas, neurons within a column normal to the cortical surface have similar functional properties, and these properties usually vary systematically from column to column, thus forming a topographic map (Mountcastle 1997). Thus, one might expect to find a map of binocular disparity in areas that are important for stereopsis. DeAngelis & Newsome (1999) provide compelling evidence for a map of binocular disparity in visual area MT. Using RDS, they showed that disparity selectivity often occurred in discrete patches (typically 0.5–1 mm in extent) that were interspersed among similar-sized patches of cortex with weak disparity tuning. Within the disparity tuned patches, preferred disparities changed smoothly across the surface of MT, but there was little change in disparity selectivity along penetrations normal to the cortical surface. This suggests strongly that there are disparity columns in MT, in addition to the well-known columns for direction of motion (Albright et al 1984). A similar methodology applied in monkey V1 by Prince et al (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication) also found evidence for a clustering of disparity selectivity, although this was much weaker than in MT (see Figure 7). Earlier investigations in V1 using bar stimuli yielded conflicting results: Blakemore (1970) qualitatively described "constant depth" columns, whereas LeVay & Voigt (1988) reported a weak clustering of disparity preference.

There is also a clustering of disparity-selective neurons in the thick stripes of V2 (Hubel & Livingstone 1987, Peterhans & von der Heydt 1993, Roe & Ts'o

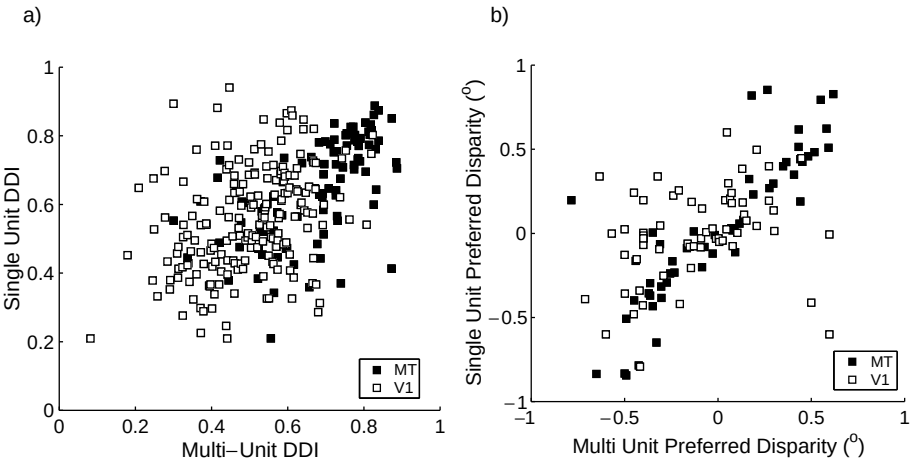

Figure 7 Clustering of disparity preference in areas V1 (open symbols) (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication) and MT (solid symbols, DeAngelis & Newsome 1999), assessed by comparing properties of isolated single units (SU) with multi-unit (MU) recordings at the same site. (*a*) Plots the modulation of firing rate induced by disparity for MU and SU data. This is measured using the disparity discrimination index (DDI) (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication). $\text{DDI} = (\text{Max} - \text{Min})/(\text{Max} - \text{Min} + 2\text{SD})$, where SD is an estimate of the standard deviation of firing calculated across all disparities. Although there is a significant correlation in both V1 and MT, the latter is stronger. It is also clear that both MU and SU responses are generally more strongly tuned for disparity in MT than in V1. (*b*) Plots the disparity that produces maximal activation for MU and SU (some data points from MT fall outside the range plotted here). Again there is a significant correlation for both areas, but the correlation is much stronger in MT ($r = 0.91$) than in V1 ($r = 0.30$).

1995). No quantitative electrophysiological studies have demonstrated an orderly map of disparity across adjacent columns, although this was reported in a recent optical imaging study (Burkitt et al 1998). Although all of these studies have used bar stimuli in anesthetized animals, the results are sufficient to suggest that there is a topographic map of disparity within the thick stripes of V2. Less is known about columnar architecture for disparity in ventral stream areas; however, Uka et al (2000) have recently reported modest clustering for disparity in inferotemporal cortex.

Can Extrastriate Responses to Disparity be Derived from V1?

Two differences between the shapes of disparity tuning curves in striate and extrastriate cortex have frequently been noted (see for example Poggio 1995). First, neurons in extrastriate cortex tend to be more coarsely tuned to disparity than neurons in V1 and have peak responses at larger disparities. Second, while the majority of V1 neurons show symmetrical tuning (like the T0 cell in Figure 5), in

extrastriate areas odd-symmetric tuning (near and far cells) predominates. Both of these observations suggest that the outputs of disparity-selective neurons in V1 must be combined in specific ways to generate extrastriate neuronal responses.

If neurons in extrastriate cortex have coarser disparity tuning than V1 neurons, it indicates that there is a range of large disparities that have no effect on the firing of V1 neurons, but do alter the firing of neurons in extrastriate cortex. This implies that the extrastriate responses are not derived from disparity-selective neurons in V1, but are constructed de novo. However, it is important to consider the effect of stimulus eccentricity. Most disparity-selective neurons studied in V1 have had parafoveal RFs, whereas studies in extrastriate cortex typically involve more eccentric stimulation. No study has compared disparity tuning to the same stimuli at matched eccentricities across brain areas. Figure 8 therefore compares

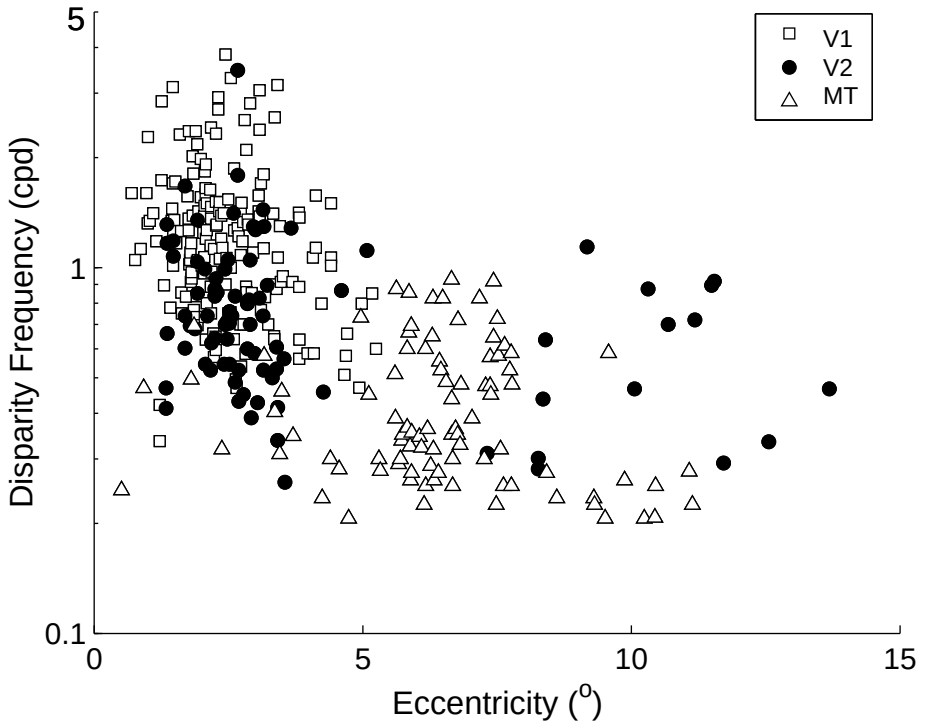

Figure 8 The spatial scale of disparity tuning, as a function of eccentricity, compared across cortical areas. "Disparity frequency" plots the peak frequency in the continuous Fourier transform of the disparity tuning curve. Narrow tuning curves have high peak frequencies, broad tuning curves have low frequencies. Although disparity tuning curves recorded in MT are generally coarser than those in V1, this may largely reflect the eccentricity at which they were recorded. Data taken from Prince et al (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication), DeAngelis & Newsome (1999), and Thomas et al (OM Thomas, BG Cumming, AJ Parker, submitted for publication).

the responses of V1,V2, and MT neurons to disparity in RDS. The spatial scale of each disparity tuning curve is estimated from the dominant spatial frequency in the Fourier transform of the tuning curve (SJD Prince, AD Pointon, BG Cumming, AJ Parker, submitted for publication), and this is plotted as a function of stimulus eccentricity. At matched eccentricities, there is a sustantial overlap between the data of different areas, although there is a tendency for the extrastriate neurons to show coarser tunning.

The claim that the symmetry of disparity selectivity differs between cortical areas rests largely on the results of classifying neurons manually into the categories proposed by Poggio & Fisher (1977). The few studies that have attempted to measure this property quantitatively have used different measures and different stimuli (LeVay & Voigt 1988, Roy et al 1992) and so are hard to compare. Figure 9 therefore applies the same metric (the phase of a fitted Gabor) to data gathered with RDS from different brain areas. The data used were from area V1 (SJD Prince, BG Cumming, AJ Parker, submitted for publication), V2 (OM Thomas, BG Cumming, AJ Parker, submitted for publiction), MT (DeAngelis & Newsome 1999), and the dorsal part of MST (MSTd) (Takemura et al 1999). The fitted phase of the Gabor measures the symmetry of the tuning curve (see Figure 5).

In accord with earlier claims, V1 shows a preponderance of even symmetry, while other areas do not. V2 and MT contain many neurons with phases intermediate between even and odd symmetry, and MSTd shows a preponderance of odd symmetry. This suggests that the shape of tuning curves for extrastriate neurons is not simply inherited from V1 neurons. It might be that an appropriate combination of even-symmetric inputs (e.g. inhibition from cells with peaks at crossed disparities, excitation from cells with peaks at uncrossed disparities) is used to construct odd-symmetric responses outside V1, but this too requires more than a simple pooling of inputs from V1.

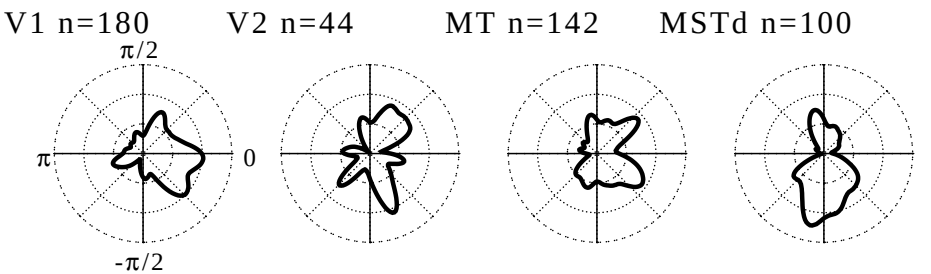

Figure 9 The distribution of phases for Gabor functions fitted to disparity tuning data in different areas of the macaque brain. Fitted phases near zero indicate symmetrical tuning, phases near $\pm\pi/2$ indicate odd symmetry (near and far cell types). There seems to be a systematic progression toward increasing odd symmetry from V1 to MSTd.

Representation of Relative Disparity

As discussed above, stereopsis is strongly dependent on relative disparities between different locations in the visual field, and yet V1 neurons signal only absolute disparities (Cumming & Parker 1999). One possibility is that relative disparity might be explicitly represented at the level of single neurons somewhere in extrastriate cortex. This could be achieved by spatial interactions between the classical RF and the nonclassical surround, which are prevalent in many visual cortical areas (Allman et al 1985). Recent studies have demonstrated center-surround interactions that depend on binocular disparity in area MT (Bradley & Andersen 1998) and in the lateral portion of area MST (Eifuku & Wurtz 1999).

To examine relative disparity encoding more directly, OM Thomas, BG Cumming, AJ Parker (submitted for publication) presented RDS consisting of a center and a surround while recording from V2 neurons. The horizontal disparity of both regions (Figure 10*A*) was varied independently. The center patch was sized to match the classical RF. Figure 10*B* shows the type of interaction that yields relative disparity encoding, with a strong diagonal structure in the response map. As the surround disparity changes, the preferred center disparity changes proportionally so that response remains roughly invariant along diagonal lines of constant relative disparity. Thomas et al measured the response to a range of center disparities at different surround disparities (e.g. horizontal cross sections in Figure 10*B*). If a neuron encodes relative disparity, then its preferred center disparity should shift by an amount equal to the surround disparity.

Figure 11 shows example tuning curves and summarizes the shifts in tuning for populations of neurons from areas V1 and V2. For a handful of V2 neurons, the shift is consistent with relative disparity coding, whereas other V2 neurons show a partial but significant shift in the direction of relative disparity encoding. The remaining V2 neurons, as well as virtually all neurons tested in V1, do not show any significant shift in their disparity preference with changing surround disparity. These latter neurons appear to encode only absolute disparities. These results strongly suggest that some V2 neurons encode relative disparity.

Eifuku & Wurtz (1999) have also suggested that neurons in the lateral portion of area MST encode relative disparity. In this study, the authors measured responses to variable center disparities at a surround disparity of zero and responses to variable surround disparities at a center disparity of zero. This corresponds to horizontal and vertical cross-sections, respectively, through the center of the two-dimensional map (black lines in Figure 10*B,C*). For a number of cells, the tuning curve for surround disparities was roughly the inverse of the tuning curve for center disparities. Although this pattern of results might reflect encoding of relative disparities (Figure 10*B*), these data could also have arisen from a separable interaction between center and surround disparities, as depicted in Figure 10*C*. By a separable interaction, we mean that the response to combinations of center and surround disparities is proportional to the product of the responses to center and surround disparities alone. A separable interaction does not indicate selectivity for

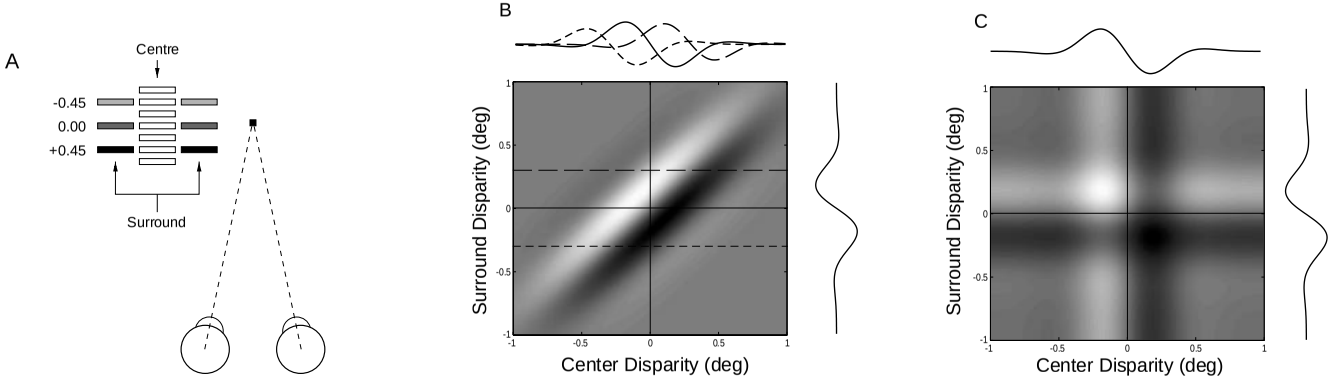

Figure 10 Measurement of relative disparity selectivity. (*a*) A bipartite field of random dots allows the disparity of a central region to be manipulated independently of the disparity of the surround. (*b*) Idealized response pattern for a neuron selective to the relative disparity between center and surround regions. Dark regions denote weak responses; bright regions indicate strong responses. Configurations with a constant disparity difference fall along diagonal lines, hence the strong diagonal structure. The lines at the top of panel (*b*) show horizontal cross sections (disparity tuning curves for the center) taken at different heights (surround disparity). The curves all have the same shape but are translated along the disparity axis relative to one another. Note also that the tuning for surround disparity (right) is the opposite of the tuning to center disparity. (*c*) Response pattern for a neuron that is not selective for relative disparity but has a separable interaction between center and surround disparities. Note that the horizontal and vertical cross sections through zero disparity are identical to those in panel *b*. Thus, these cross sections alone are insufficient to demonstrate relative disparity selectivity.

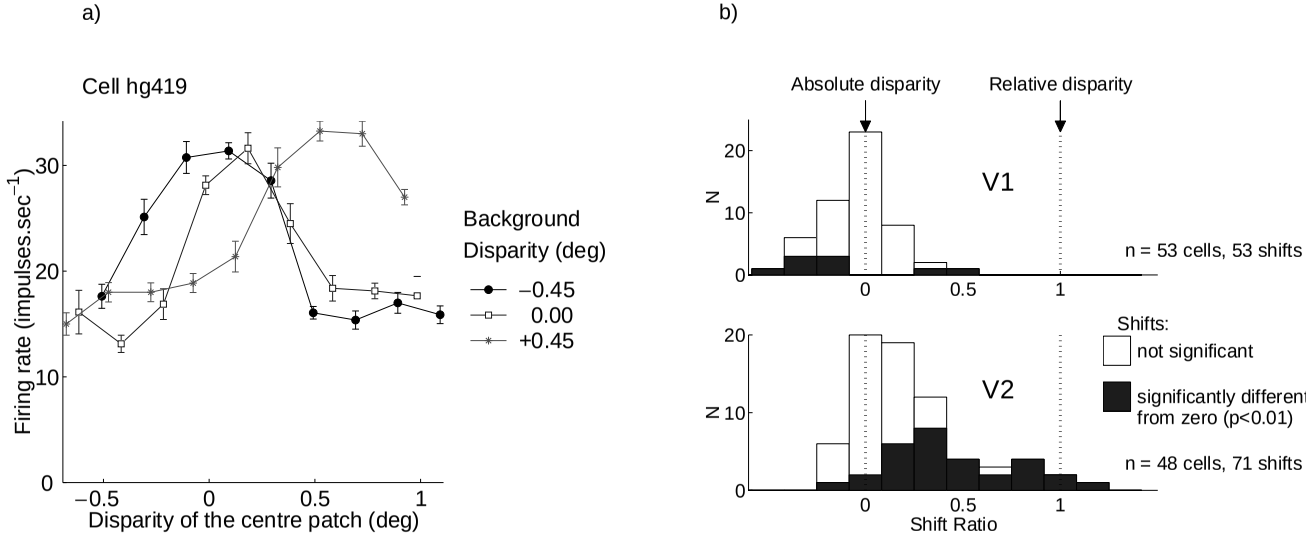

Figure 11 (*a*) The responses of one neuron in V2 to the disparity of a random dot stereogram covering the minimum response field. Surrounding this was a background of random dots, whose disparity was also altered (see key). Change in the background disparity produced systematic shifts in the preferred central disparity, so that the neuron appears to encode the relative disparity between center and surround. (*b*) The magnitude of the shift in preferred disparity, as a fraction of the change in background disparity, measures the extent to which the neuron signals relative disparity (shift ratio 1.0) or absolute disparity (shift 0.0). Unlike neurons from V1 (data from Cumming & Parker 1999), a fraction of neurons in V2 shows some selectivity to relative disparity.

relative disparity, so the results of Eifuku & Wurtz are are not conclusive. Further studies, in which the center-surround disparity space is mapped more finely, will be valuable for understanding the encoding of relative disparities.

The Correspondence Problem

Neurons in V1 respond to binocular matches that are not perceived (i.e. "false" stereo matches). If extrastriate areas combine the outputs of V1 neurons appropriately, they might produce responses more similar to the psychophysical sensations. This might be achieved by combining responses of V1 neurons with different spatial scales (Fleet et al 1996), which could also eliminate the modulation of responses to anticorrelated RDS. Two preliminary reports have examined this, in areas MT (Krug et al 1999) and MSTd (Takemura et al 1999). Both found disparity induced modulations in response to anticorrelated RDS, similar to those already reported in V1 (Cumming & Parker 1997). In this respect at least, disparity-selective responses in MT and MSTd are no closer to psychophysical stereo matching than V1.

Links Between Disparity-Selective Neurons and Perception

Neurons that signal binocular disparity do not necessarily contribute to stereopsis. To establish that a candidate set of neurons contributes to performance of a specific stereoscopic task, additional criteria must be met (Parker & Newsome 1998). First, neuronal activity should be recorded during performance of the task, and it should be shown that the candidate neurons are sufficiently sensitive to mediate task performance (so far only demonstrated for V1 neurons; Prince et al 2000). Second, neuronal activity should be shown to covary with perceptual judgements near psychophysical threshold. Third, artificial manipulation of neuronal activity (either activation or suppression) should be shown to alter performance of the task. Below, we review experiments that begin to address these requirements.

Covariation of Neuronal Firing and Depth Perception If a group of neurons contributes strongly to a three-dimensional percept, then the activity of those neurons should covary with perceptual reports under circumstances in which the visual stimulus is near threshold or ambiguous. Two groups have recently probed for this type of covariation (Bradley et al 1998, Parker et al 2000). Monkeys were trained to report the direction of rotation of a three-dimensional cylinder defined by random dots (Figure 12). When the depth of the cylinder is defined by binocular disparity, direction of rotation is unambiguously perceived. In contrast, when the disparity cues are removed, the percept becomes bistable: For the same visual stimulus, clockwise rotation is seen in some trials and counterclockwise rotation is seen in other trials (Wallach & O'Connell 1953). Bradley et al (1998) recorded from neurons in area MT that are selective for conjunctions of motion and disparity (e.g. rightward and near), and showed that these neurons can encode the direction of rotation of unambiguous cylinders defined with disparity. More importantly, they showed that the average responses of

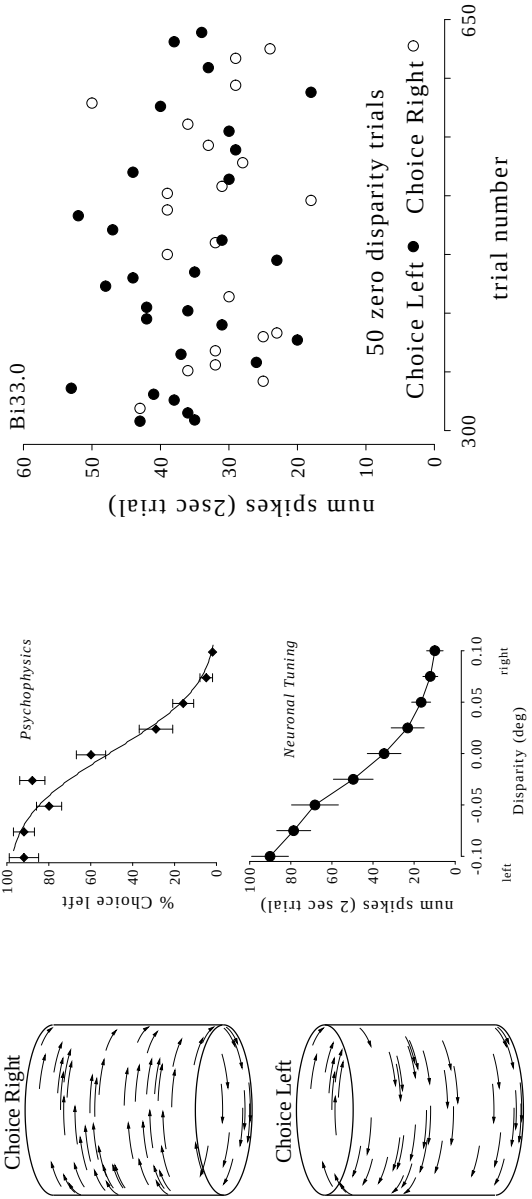

Figure 12 Moving dots portraying a transparent rotating cylinder give rise to an ambiguous percept (*a*). The perceived direction of rotation, which is bistable, depends on whether the leftward moving dots are perceived in the front plane (top) or back plane (bottom). The stimulus can be rendered unambiguous by the addition of disparities defining the depth relationships, and animals report one direction of rotation unambiguously for small disparities (*b*, top). The activity of an example MT neuron, selective for the direction of rotation defined by disparity, is shown in the bottom half of panel *b*. (*c*) The response rates for each trial of the zero disparity stimulus only: Filled symbols indicate those trials where the animal reported leftward rotation at the end of the trial; open symbols indicate rightward choices. Trials associated with "left" choices are associated with higher firing rates. Since this neuron is also selective for leftward rotation defined by disparity, the choice probability is >0.5. For this neuron the choice probability was 0.66, close to the population mean (0.68).

some MT neurons covary with perceived direction of rotation, separate from any disparity-induced modulation. The activity of these neurons appears to reflect the percept and not just the physical stimulus.

Parker et al (2000) extended this observation, analyzing only responses to the ambiguous, zero-disparity stimulus (see Figure 12) and quantifying the covariation with choice probabilities (Britten et al 1996). These define the probability that the behavioral outcome of a trial can be predicted from the firing rate of a single neuron (choice probabilities >0.5 indicate a positive correlation). It is interesting that the average choice probability for the cylinder task (0.68) is substantially higher than the average choice probability (0.56) exhibited by MT neurons during a direction discrimination task (Britten et al 1996). This means that fluctuations in activity of MT neurons are more tightly linked to fluctuations in perceptual reports for the three-dimensional cylinder task. Further investigation of what aspects of the stimulus or task influence the magnitude of the choice probability is required in order to interpret this difference in choice probabilities.

Effects of Lesions Strong trial by trial covariation between firing rate and perceptual reports engenders confidence that the neurons under study contribute to depth perception. However, even these measures are only correlative in nature; thus, choice probabilities do not establish a causal linkage between neuronal activity and perception. Such a link could be established if localized brain lesions produce deficits in stereoscopic vision without degrading other visual capabilities. It is important to ensure that eye movements are unaffected: If a lesion disrupts vergence control then this will be detrimental to stereo tasks. Unfortunately none of the following studies measured or controlled vergence, so the results are inconclusive.

Human Studies. Several studies have examined the effects of cerebral lesions on stereopsis in human patients (Carmon & Bechtoldt 1969, Benton & Hecaen 1970, Rothstein & Sacks 1972, Lehmann & Wächli 1975, Danta et al 1978, Hamsher 1978, Ross 1983, Vaina 1989, Ptito et al 1991). In general, because the lesions are poorly localized, these studies reveal little about the contributions of specific cortical areas to stereopsis. Moreover, equivalent, nonstereoscopic control tasks were generally not performed; thus, it is difficult to be sure that the observed deficits are specific to stereopsis. Nonetheless, a few observations are worth noting.

A few studies have reported that depth perception in RDS ("global" stereopsis) is selectively impaired by lesions to the right cerebral hemisphere (Carmon & Bechtoldt 1969, Benton & Hecaen 1970, Hamsher 1978, Ross 1983, Vaina 1989). In contrast, local stereopsis (stereoacuity measured with isolated stimuli) seems to be equally impaired by left and right hemisphere lesions (Rothstein & Sacks 1972, Lehmann & Wächli 1975, Danta et al 1978, Hamsher 1978). However, only Hamsher (1978) studied global stereopsis and stereoacuity in the same group of patients. The range of disparities used for the two tasks was nearly nonoverlapping, so any interhemispheric difference may be in the range of disparities processed.

Vaina (1989) has reported that subjects with right occipital/temporal lesions were able to see depth in RDSs but were unable to identify the shape of regions defined by disparity. In contrast, patients with occipital/parietal lesions failed to see any depth at all in the same stimuli. Thus, Vaina posits that occipital/parietal areas may be necessary for establishing binocular correspondence, whereas occipital/temporal areas are needed for extracting cyclopean form after the correspondence problem is solved.

Animal Studies. A major advantage of animal studies is that surgically induced lesions can be fairly well localized. Cowey & Porter (1979) trained monkeys to discriminate depth in RDSs. They found no deficits following lesions of the central visual field representation in V1 or V2. In contrast, they report substantial deficits following temporal lobe lesions, which appear to include most of inferotemporal cortex as well as substantial portions of prestriate cortex. Although the authors conclude that "global stereopsis is mediated in temporal lobe areas," this conclusion must be treated with care. Lesions of V1 and V2 were restricted to a central region of the visual field smaller than the center portion of the stereograms. Moreover, monkeys were not trained to maintain fixation. Thus, the animals may have simply fixated eccentrically and used portions of V1 and V2 unaffected by the lesions.

Cowey & Wilkinson (1991) tested the stereoacuity of monkeys following similar lesions. Following V1 and V2 lesions, monkeys could still perform the task, but their thresholds were elevated roughly 2- to 10-fold. Because fixation was not enforced, it is unclear whether this residual capacity should be attributed to other brain structures, or whether it resulted from animals fixating eccentrically to perform the task. Lesions of inferotemporal cortex produced only a mild increase in thresholds (1.5- to 2-fold), which suggests that these areas may not be critical for fine stereo judgments.

Schiller (1993) evaluated the effects of V4 and MT lesions on stereopsis in monkeys. Fixation (but not vergence) was tightly controlled, and performance was compared between lesioned and intact portions of the visual field. Neither V4 nor MT lesions, nor the combination of the two, produced any discernible effects on performance in the detection or discrimination tasks used in this study. This is surprising, given that MT and V4 are central stages along the dorsal and ventral processing streams, respectively. This finding might indicate that lower visual areas (e.g. V1, V2, and V3) are sufficient to mediate performance on these tasks, or it might reflect the fact that some of these areas have alternative projections to the temporal and parietal lobes (Felleman & van Essen 1991). However, there are two reasons for interpreting these results cautiously. First, the monkeys were working well above psychophysical threshold; thus, the task conditions did not force the animals to rely on the most sensitive neurons. The effects of lesions might have been much larger near threshold. Second, data are reported only from sessions in which performance had stabilized after the lesions: Transient deficits in stereopsis may have gone unnoticed. As the tasks were not performed at threshold,

disparity-selective neurons in other visual areas may have been able to compensate for the loss of MT and V4.

In cats, unlike monkeys, lesions of V1 spare many visual functions, including grating and vernier acuity (e.g. Berkley & Sprague 1979, Ptito et al 1992). This presumably reflects a more important role of retino-tectal pathways in felines. In this light, it is interesting to note that combined lesions of areas 17 and 18 are reporetd to completely abolish stereopsis in cats (Kaye et al 1981, Ptito et al 1992).

Microstimulation Many of the difficulties with lesion studies (effect of recovery, control of vergence) can be avoided in microstimulation studies, where stimulated and nonstimulated trials are interleaved. Microstimulation studies have previously established that areas MT and MST play a central role in motion perception (Salzman et al 1992, Salzman & Newsome 1994, Celebrini & Newsome 1995).

DeAngelis et al (1998) used microstimulation to probe the role that area MT plays in stereopsis. Monkeys were trained to discriminate between two suprathreshold disparities (e.g. one near, one far) in the presence of disparity noise. The relative proportions of signal and noise dots were varied around psychophysical threshold, and microstimulation was applied during half of the trials. Because of the columnar organization for disparity in MT (DeAngelis & Newsome 1999), electrical stimulation could be applied to a cluster of neurons with similar disparity selectivity. At locations in MT with strong disparity tuning, microstimulation biased the monkey's judgments in favor of the preferred disparity of the stimulated neurons, with no decrement in psychophysical sensitivity. That is, microstimulation of a cluster of far-preferring neurons shifted the monkeys' psychometric function, resulting in more far choices. In contrast, there was generally little or no effect at locations in MT with poor disparity tuning. Thus, injecting an artificial signal into the disparity map within area MT caused a predictable bias in depth judgments. This result establishes the first causal linkage between a population of disparity-selective neurons and stereopsis.

FUTURE DIRECTIONS

The mechanisms by which responses to disparity are produced in striate cortex are now well characterized. These result in signals that differ in many ways from the perception of depth: V1 neurons respond to false matches in the RF and do not signal relative disparities. Rather, V1 seems to measure binocular correlation over a range of vertical and horizontal disparities. These preliminary computations may be exploited in extrastriate cortex for a number of different tasks: stereopsis, vergence control, scene segmentation, and three-dimensional heading judgments.

How each of these more sophisticated judgments is derived from the activity of neurons in striate and extrastriate cortex is largely unknown. Functional imaging

in human subjects is likely to provide valuable insights into which brain areas are specialized for each of these tasks.

It is clear that certain extrastriate areas contain signals that are more closely related and causally linked to the perception of depth. V2 is able to signal relative disparities, and center-surround interactions in MT and MST may achieve similar results. Microstimulation in MT systematically biases depth judgments. These observations raise many further questions, such as how all the possible combinations of relative disparities are represented and how this information is maintained as the eyes move. A few studies have examined the neurophysiological representation of surfaces (Shikata et al 1996, Janssen et al 1999, Taira et al 2000), but much remains to be done in this field.

The quantitative study of responses to disparity in extrastriate cortex, combined with matching psychophysical studies, promises to clarify the ways in which a number of binocular tasks are carried out by the brain. Combining this with the study of how extrastriate responses are derived from those in V1 offers the prospect of a system in which the gap between neuronal mechanisms and perceptual phenomena is significantly narrowed.

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