

# Seeing in three dimensions: the neurophysiology of stereopsis

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**From the pair of 2-D images formed on the retinas, the brain is capable of synthesizing a rich 3-D representation of our visual surroundings. The horizontal separation of the two eyes gives rise to small positional differences, called binocular disparities, between corresponding features in the two retinal images. These disparities provide a powerful source of information about 3-D scene structure, and alone are sufficient for depth perception. How do visual cortical areas of the brain extract and process these small retinal disparities, and how is this information transformed into non-retinal coordinates useful for guiding action? Although neurons selective for binocular disparity have been found in several visual areas, the brain circuits that give rise to stereoscopic vision are not very well understood. I review recent electrophysiological studies that address four issues: the encoding of disparity at the first stages of binocular processing, the organization of disparity-selective neurons into topographic maps, the contributions of specific visual areas to different stereoscopic tasks, and the integration of binocular disparity and viewing-distance information to yield egocentric distance. Some of these studies combine traditional electrophysiology with psychophysical and computational approaches, and this convergence promises substantial future gains in our understanding of stereoscopic vision.**

We perceive our surroundings vividly in three dimensions, even though the image formed on the retina of each eye is simply a two-dimensional projection of 3-D space. Our sensation of depth is based upon many visual cues, some monocular and some binocular. Occlusion, relative size, perspective, shading, blur, and relative motion are among the monocular cues that provide useful depth information. Some of these, such as relative motion<sup>1</sup>, can provide a highly quantitative impression of depth, whereas most others provide only coarse depth information. For many species with frontally located eyes, *binocular disparity* provides a powerful and highly quantitative cue to depth. Binocular disparity refers to small positional differences between corresponding image features in the two eyes, and arises because the two eyes are separated horizontally (see Box 1). Depth perception based upon binocular disparities is known as *stereopsis*.

Behavioral and psychophysical studies of stereopsis have a long history, with important contributions from Wheatstone<sup>2</sup>, Julesz<sup>3</sup> and others, as reviewed elsewhere<sup>4</sup>. Studies of the neurophysiological basis of stereopsis began in the 1960s with the work of Barlow *et al.* and Pettigrew *et al.*, who pub-

lished the first reports of disparity-selective neurons in the primary visual cortex (V1, or area 17) of anesthetized cats<sup>5,6</sup>. These authors demonstrated that different neurons signal distinct ranges of binocular disparities, and they proposed that a population of neurons could encode a range of object positions in depth. Poggio and colleagues<sup>7,8</sup> later studied disparity selectivity in alert, fixating monkeys, and they established four basic classes of neurons. Tuned-excitatory neurons respond optimally to objects at or very near the horopter (zero disparity), whereas tuned-inhibitory cells respond at all disparities except those near zero. Near cells respond best to objects that lie in front of the horopter (crossed disparity), whereas far cells have a preference for objects lying behind the horopter (uncrossed disparity). Although these categories may not be discrete<sup>9,10</sup>, this classification scheme has nevertheless provided a useful vocabulary for the field.

Recent years have seen substantial progress in understanding the neural basis of stereoscopic vision, but many important questions remain. We now know that disparity-selective neurons can be found in a number of visual cortical areas in primates, including V1, V2, V3, MT, MST and

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## Box 1. Geometry of binocular viewing

Because the two eyes are separated horizontally, each eye views the world from a slightly different vantage point. Thus, rays of light from a point in 3-D space generally do not project to corresponding anatomical locations on the two retinas. The difference in position between corresponding images features on the two retinas is referred to as 'binocular disparity'. In general, the pattern of binocular disparities across the visual field depends on many factors, including the 3-D structure of the world, gaze angle, viewing distance and eye alignment. For a detailed treatment of all of these factors, the interested reader is referred to the text by Howard and Rogers (Ref. a). Here, I provide a basic treatment of horizontal and vertical retinal disparities that should be sufficient for the purposes of this review.

### Horizontal disparity

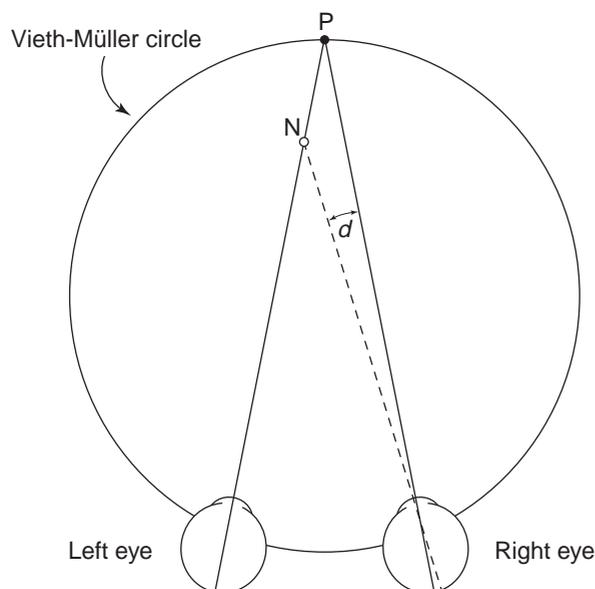
Horizontal disparities are directly related to the locations of objects in depth, and are known to be a sufficient cue for stereopsis (Ref. b). Figure I illustrates the definition of horizontal disparity. If an observer fixates on point P, then the images of P will fall on corresponding points in the two eyes (in this case the two foveae). More generally, the Vieth-Müller circle describes the locus of points in space that produce images at geometrically corresponding points on the two retinas. Thus, by definition, any point on the Vieth-Müller circle will have zero horizontal disparity. In contrast, the images of the nearby point, N, fall on non-corresponding points, with the right eye's image shifted laterally. The angle,  $d$ , gives the horizontal disparity associated with point N. For symmetric convergence, depth and horizontal disparity are related by the following simplified expression (valid if  $D \gg \delta$ ):

$$d \approx I \delta / D^2$$

where  $I$  is the interocular separation,  $\delta$  is the depth of a point in space relative to the plane of fixation, and  $D$  is the viewing distance. Note that horizontal disparity is proportional to depth and inversely proportional to the square of viewing distance.

### Vertical disparity

When an object is located closer to one eye than the other, the object's image will be slightly larger on the retina to which it is closer. This magnification dif-



**Fig. I. Horizontal disparity.** A top-down view of an observer who is looking straight ahead and fixating on point P. The plane of the image corresponds to a horizontal cross-section through the observer's head and eyes. The images of a nearby point, N, will have a horizontal binocular disparity denoted by the angle  $d$ . The large (Vieth-Müller) circle is the locus of points in space that have zero horizontal disparity.

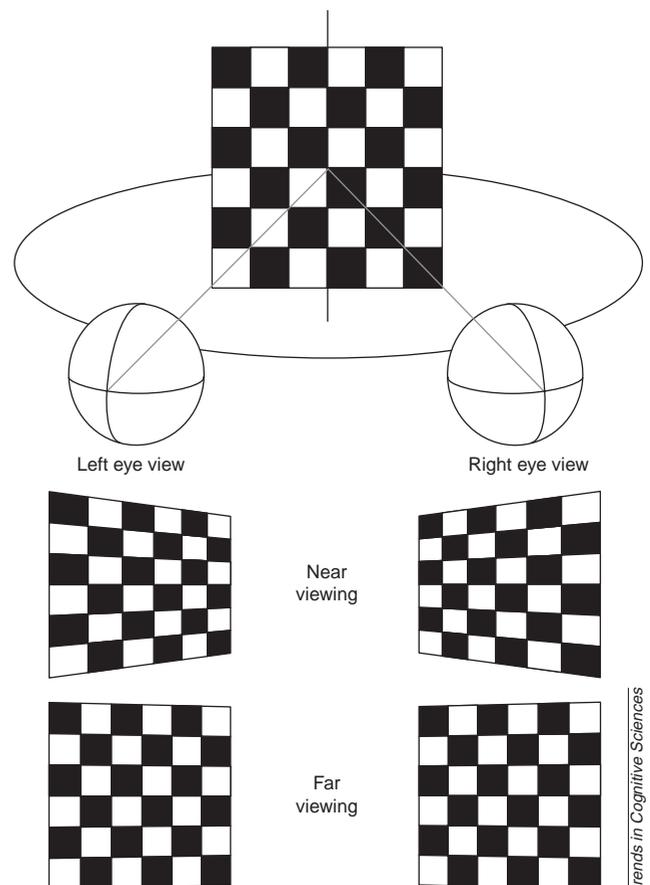
ference gives rise to vertical disparities, as illustrated in Fig. II. In this diagram, an observer views a fronto-parallel surface containing a checkerboard pattern. When the viewing distance is relatively near, there are opposite gradients of vertical subtense in the two eyes' views, due to the differential perspective of the two eyes. Thus, there is a horizontal gradient of vertical disparity between the two images. For symmetric convergence, the relationship between vertical disparity, visual field location and viewing distance is given by the equation:

$$v \approx I x y / D$$

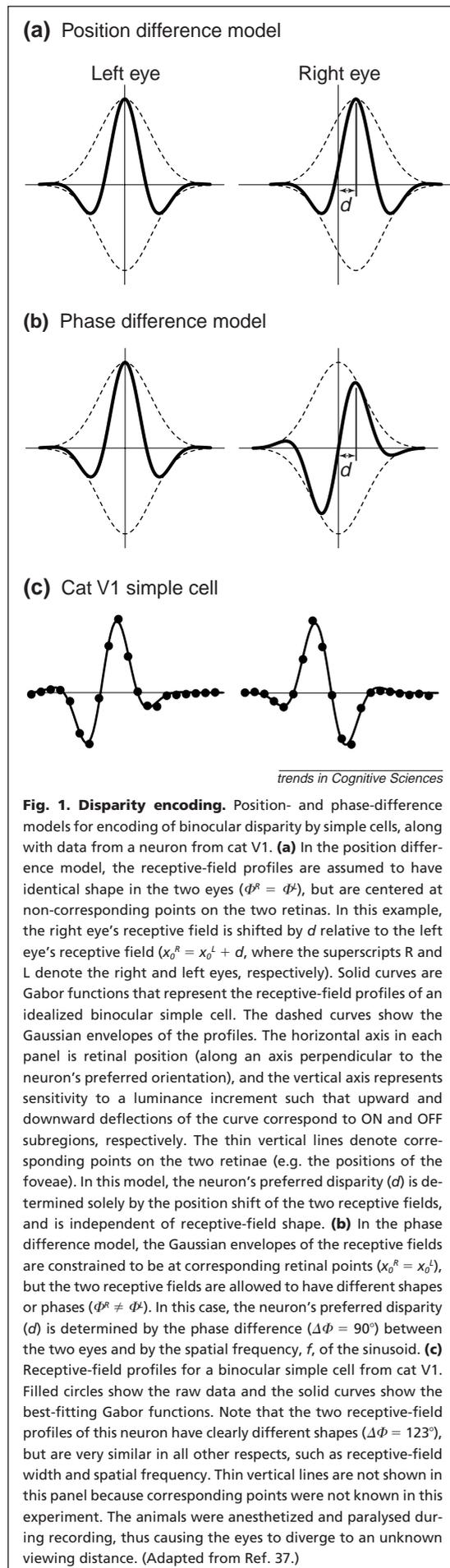
where  $v$  is the vertical disparity,  $I$  is the interocular separation,  $x$  and  $y$  are the horizontal (azimuth) and vertical (elevation) angles to the point in space, and  $D$  is the viewing distance. Note that vertical disparity will be zero for points along the vertical meridian ( $x = 0$ ) or in the horizontal plane of regard ( $y = 0$ ). Also, note that vertical disparity is inversely proportional to viewing distance. Thus, if one knows the vertical disparity at a point in space ( $x, y$ ), the viewing distance could be determined (Refs c,d).

### References

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**Fig. II. Vertical disparity.** An observer views a fronto-parallel surface in symmetric convergence. The middle and bottom rows of the figure illustrate the left and right eye views for near and far viewing distances, respectively. Note that there are opposite gradients of vertical subtense in the two eyes' views, and that these gradients are larger for near viewing than far viewing. In this illustration, the gradients have been exaggerated for visual effect. Also, the left and right eye views have not been inverted (as they would normally be by the lens).



IT (Refs 7,8,11–17). However, the roles that these different areas play in stereopsis remain poorly defined, as discussed below. My goal here is not to review in detail the physiological properties of binocular neurons in different areas, as this has been done recently<sup>18</sup>. Instead, I offer a critical review of a few key issues where substantial progress has recently been made and/or where important questions remain outstanding. These issues highlight some of the benefits to be derived from combining physiological, psychophysical and computational approaches to the study of visual perception.

### Encoding of binocular disparity

In the visual system, neural signals from retinal ganglion cells pass first through the lateral geniculate nucleus (LGN) of the thalamus before arriving in visual cortex. Although the responses of some LGN neurons to visual stimuli in one eye are suppressed or facilitated by the presence of stimuli in the other eye<sup>19–23</sup>, there appears to be no direct evidence for disparity selectivity in the LGN. Instead, disparity selectivity seems to emerge for the first time in primary visual cortex (V1), where signals from the two eyes converge upon single neurons<sup>5,6</sup>. How is binocular disparity initially encoded by V1 neurons, and what implications does this encoding scheme have for stereoscopic perception?

#### Position versus phase encoding

Most of the geniculate input to V1 impinges on *simple* cells, which are most numerous in cortical layers 4 and 6 (Refs 24,25). Thus, one can make the argument that V1 simple cells constitute the first stage of disparity processing in the brain. Simple cells are orientation-selective and have receptive fields containing adjacent subregions that alternately prefer either bright or dark stimuli (i.e. ON and OFF subregions)<sup>26,27</sup>. These receptive-field profiles have been found to be well-described by a Gabor function<sup>27–29</sup> [ $G(x)$ ] (see Fig. 1a), which is the product of a Gaussian (a bell-shaped sensitivity profile) and a sinusoid:

$$G(x) = k \times \exp(-(2(x-x_0)/w)^2) \times \cos(2\pi f(x-x_0) + \Phi)$$

where  $x_0$  and  $w$  correspond to the center position and width of the Gaussian envelope,  $f$  and  $\Phi$  denote the spatial frequency and phase of the sinusoid, and  $k$  is an arbitrary scaling factor.

If simple cells have this general receptive-field structure when tested through either eye, there are two basic ways that they could encode a range of binocular disparities: via positional differences between the two eyes, or via phase differences. In the position difference model (Fig. 1a), the receptive-field profiles are assumed to have identical shape in the two eyes, but are centered at non-corresponding points on the two retinas. In the phase difference model (Fig. 1b), the receptive fields are centered at corresponding retinal points, but the two receptive fields are allowed to have different shapes or phases<sup>30,31</sup>. As we shall see below, these two encoding schemes make very different predictions regarding the perceptual limits of stereoscopic vision.

What is the physiological evidence for these contrasting models of disparity encoding? Hubel and Wiesel<sup>26</sup> originally reported that 'the spatial arrangements of excitatory and inhibitory regions were the same' for the two receptive fields of binocular simple cells. This conclusion was supported by

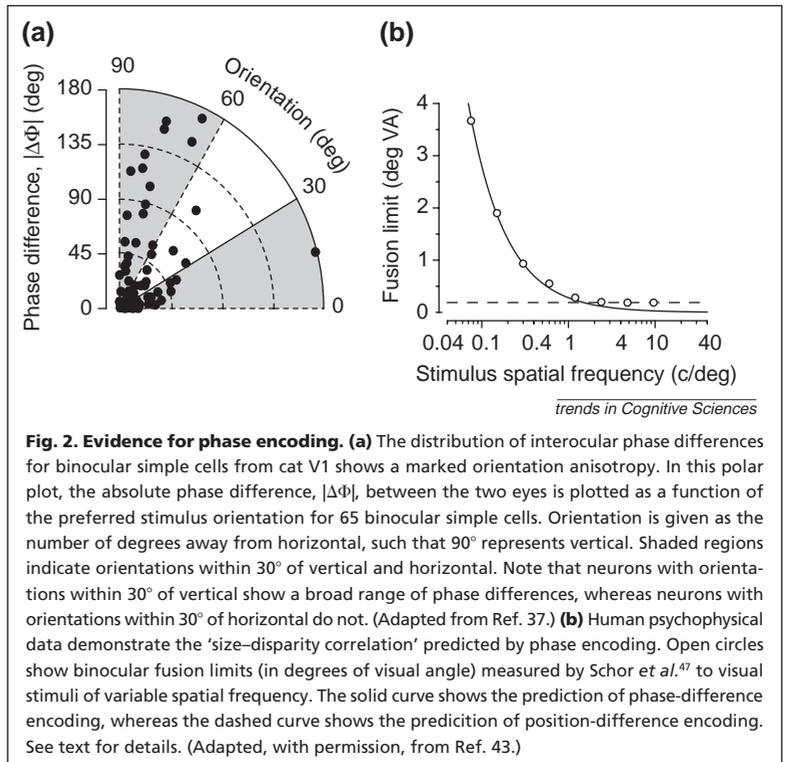
Maske *et al.*<sup>32</sup>, who reported that RF profiles for the two eyes were ‘remarkably similar’, although their data were not subjected to a rigorous quantitative analysis. In fact, a close inspection of their data (Ref. 32, Figs 2a, 2c, 4) reveals clear evidence of phase differences between the two receptive fields.

Wagner and Frost<sup>33</sup> have reported that binocular neurons in the visual Wulst of the barn owl exhibit a ‘characteristic disparity’ in their responses to dichoptic sine-wave stimuli of variable spatial frequency, which implies that these neurons have only a positional difference between the two receptive fields. In a modeling study, however, Zhu and Qian<sup>34</sup> have argued that the data analysis methods used by Wagner and Frost were not sufficient to distinguish between the phase- and position-difference models. In addition, as acknowledged in a subsequent paper<sup>35</sup>, most of the data of presented by Wagner and Frost were from multi-unit recordings, which seriously complicates their interpretation. Any substantial heterogeneity in disparity tuning among nearby single units would render the results of their experiment inconclusive.

Using a sensitive technique for mapping receptive fields, Freeman and colleagues showed that V1 simple cells in the cat do exhibit interocular phase differences<sup>30,36–38</sup>. Data from one such neuron is shown in Fig. 1c. In addition, DeAngelis *et al.* showed that neurons selective for vertical orientations exhibit a broader range of phase differences than neurons tuned to horizontal orientations<sup>36,37</sup> (Fig. 2a). Thus, this population of neurons would signal a much larger range of horizontal than vertical disparities. Such an observation might be expected, given that most natural images contain a much larger range of horizontal disparities than vertical disparities (due to horizontal separation of the eyes). Indeed, in their original report on this subject, Barlow *et al.* showed that V1 neurons in cats exhibited a larger range of preferred disparities along the horizontal dimension than along the vertical dimension<sup>5</sup>. In contrast, subsequent studies generally failed to find any horizontal–vertical anisotropy in the distribution of receptive-field *position* differences between the two eyes<sup>9,39–42</sup>.

Although the results of DeAngelis *et al.* show clearly that phase differences do exist, their data do not rule out a contribution of position differences to disparity encoding<sup>36,37</sup>. This issue has recently been re-examined by Anzai *et al.*<sup>43,44</sup>. By mapping the left- and right-eye receptive fields simultaneously for pairs of V1 simple cells, Anzai *et al.* measured the interocular phase difference for each neuron, as well as the relative interocular position difference between the two neurons. Their results show that both phase and position disparities do exist, thus supporting hybrid position/phase models of disparity encoding<sup>34,45</sup>. However, at all but the highest spatial frequencies tested, phase disparities seem to predominate. An important caveat, however, is that they measured *relative* interocular position differences, from which they inferred the distribution of absolute position differences by assuming that these are randomly distributed amongst neurons within a local region of cortex. If neurons are, in fact, clustered according to their interocular position differences, then Anzai *et al.* would have underestimated the contribution of position differences to disparity tuning.

As alluded to above, the phase and position models make different predictions for how the perceptual limits of stereopsis



should depend on the spatial frequency content of the visual image. In the phase model, the range of disparities encoded by a population of neurons is inversely proportional to spatial frequency. This is because phase differences are limited to a range of  $\pm 180^\circ$ , and because a particular phase difference corresponds to a large preferred disparity (in degrees of visual angle) when the spatial frequency is low, but a small preferred disparity when the spatial frequency is high<sup>36</sup>. In contrast, for the position model, the range of disparities that can be encoded does not necessarily depend on spatial frequency.

Indeed, many human psychophysical studies show that the limits of stereoscopic depth perception are inversely related to spatial frequency; this is the so-called ‘size–disparity’ correlation<sup>46–51</sup> (but see Refs 52,53 for dissenting opinions). Data from one such study<sup>47</sup> are shown in Fig. 2b, along with predictions of the phase- and position-difference models. Note that the psychophysical fusion limits measured by Schor *et al.* (open circles) follow the prediction of phase encoding (solid line) quite faithfully up to a spatial frequency of about 2 cycles/deg. Insofar as cat V1 physiology can be compared to human psychophysics, the balance of evidence therefore suggests that phase encoding of disparity is an important mechanism, at least for lower spatial frequencies. It is unfortunate that similar physiological data are not available from primates. Ideally, one would like to measure left and right eye receptive-field profiles for binocular neurons in the alert fixating monkey, so that one could obtain both interocular phase differences and absolute position differences for individual neurons. The main barrier to achieving this is sufficient measurement and control of small eye movements that occur during fixation, which may be significantly large relative to the scale of V1 receptive fields. One could also measure psychophysical depth limits in the same animals and compare these with the physiological data. Toward this end, Livingstone and Tsao<sup>54</sup> have recently reported measurements

of binocular receptive fields for V1 neurons from alert monkeys, but their data do not directly address the position versus phase encoding issue.

#### *Absolute versus relative disparity encoding*

Most physiological studies of disparity encoding have at least tacitly assumed that V1 neurons are selective for the absolute disparity of visual features on the retina (i.e. relative to the foveae), rather than the relative disparity between two or more visual features (e.g. one object in the RF and one outside the RF). In contrast, psychophysical studies demonstrate that humans are often most sensitive to the relative disparities between multiple visual targets<sup>4,55</sup>. Recently, the issue of whether V1 neurons encode absolute or relative disparity has been addressed in an elegant study by Cumming and Parker<sup>56</sup>. Using a disparity feedback loop to manipulate absolute disparities while monkeys performed a vergence tracking task, they showed that the responses of most V1 neurons are entirely consistent with encoding of absolute disparity, and they found no V1 neurons whose responses were entirely consistent with encoding relative disparity.

Given that stereoscopic perception is heavily dependent on relative disparities, one would expect to find neurons selective for relative disparity at some level in the visual system. Although relatively little is known about this, a recent preliminary report<sup>57</sup> suggests that some neurons in V2 may signal the relative disparity between their classical receptive fields and the surrounding regions. The disparity tuning curves for these neurons shift when the disparity of the surround is varied. Another recent study of neurons in the lateral portion of area MST also suggests that some neurons respond to the relative disparity between their classical receptive field and the surrounding regions, although center and surround disparities were not varied independently in that study<sup>58</sup>. Together, these studies suggest that there is a general trend for neurons to respond more often to relative disparities as one ascends the visual pathways.

#### **Cortical maps of binocular disparity**

Columnar architecture is a common feature of the organization of cerebral cortex. In many cortical areas, neurons within a vertical column (normal to the cortical surface) have similar functional properties. Moreover, these properties usually vary systematically across the surface of cortex as one moves from column to column, thus forming a topographic map. Topographic maps exist in many cortical regions, including visual, auditory, and somatosensory areas, as well as primary motor areas<sup>59</sup>. These maps have provided important clues about the function of the corresponding brain areas. By this logic, one might expect to find a topographic map of binocular disparity in visual areas that are important for stereopsis. Until recently, however, there has been a dearth of compelling evidence for such a map.

Blakemore<sup>60</sup> initially proposed that cat V1 contains 'constant depth' columns, as well as 'constant direction' columns. In a constant depth column, all neurons were reported to have similar receptive-field position disparities; in a constant direction column, the receptive fields for one eye would all fall along a line of sight, whereas receptive fields for the other eye would be scattered. Although these results were suggestive

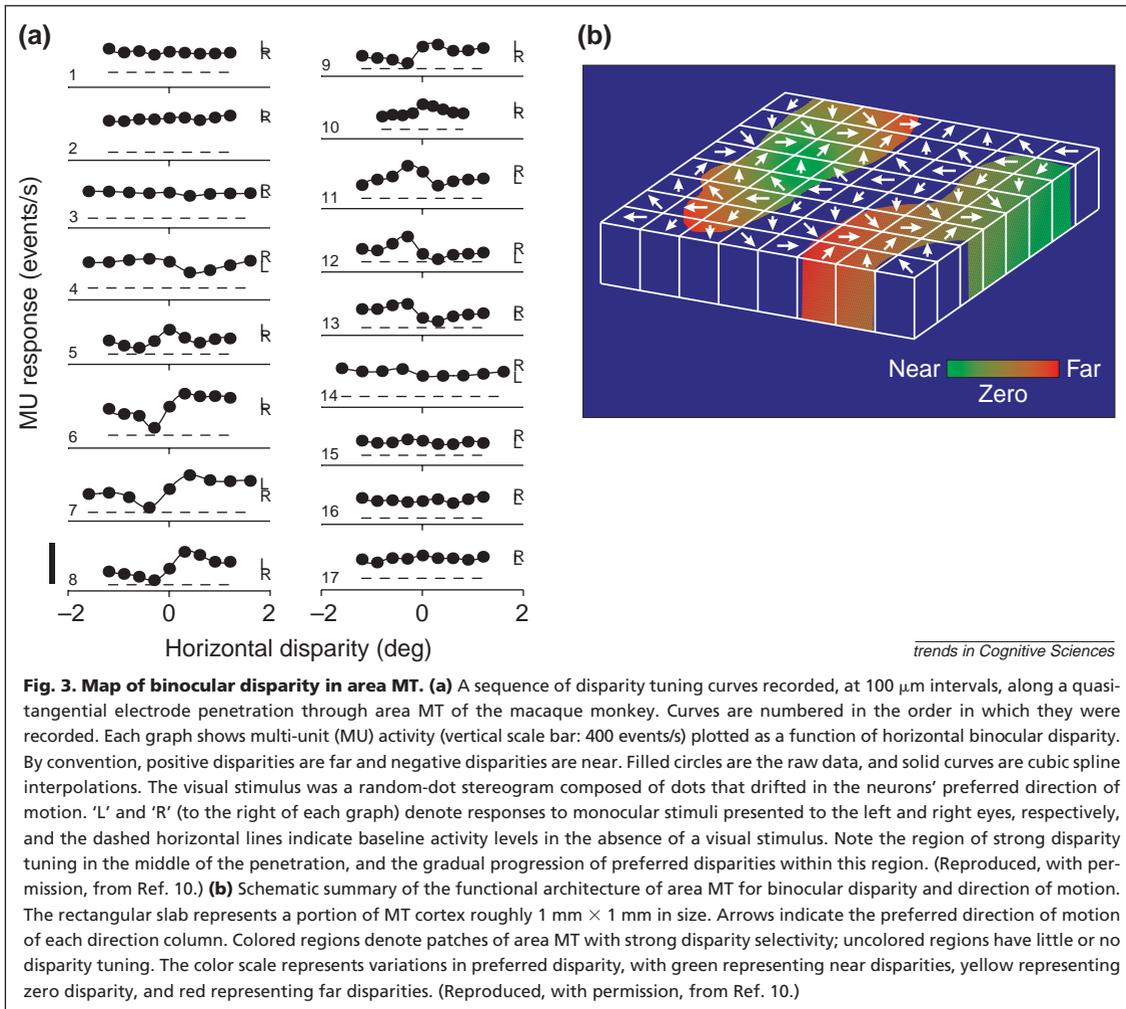
of disparity columns, the lack of direct measurements of disparity tuning, the small number of measurements made along many penetrations, and the lack of quantitative receptive-field mapping methods left the issue unresolved.

Also working on the anesthetized cat, LeVay and Voigt<sup>9</sup> later showed that nearby V1 neurons have slightly more similar disparity preferences than would be expected by chance (assuming a random distribution of neurons). Thus, there appears to be some modest clustering of neurons by disparity in cat striate cortex, but this clustering is far weaker than that for orientation selectivity or ocular dominance<sup>9</sup>. One problem with this study is that many neurons were recorded near the V1/V2 (area 17/18) border and could not be confidently assigned to either area. Thus, if the organization for disparity were markedly different in V1 and V2, these differences could have diluted any effect that might have been observed for V1 or V2 separately. To my knowledge, there are no published data bearing on the issue of whether V1 contains disparity columns in primates.

In monkey V2, Hubel and Wiesel<sup>11</sup> initially reported that disparity-selective neurons were found in groups and were segregated from neurons that lacked disparity tuning. Moreover, they suggested (without showing data) that nearby neurons had similar disparity preferences. These general observations have been confirmed by more recent studies and have been linked to the stripe-like pattern of staining for cytochrome oxidase (CO) in V2. Specifically, a few studies<sup>61–63</sup> have reported that disparity-selective neurons are preferentially found in the 'thick' CO stripes of V2. Hubel and Livingstone also reported that neurons are clustered by disparity preference along electrode penetrations through V2, although their data were not analyzed quantitatively<sup>61</sup>. A similar claim was put forward by Clarke *et al.* for V2 of the sheep<sup>64</sup>. Finally, in a recent preliminary report, Burkitt *et al.*<sup>65</sup> showed using optical imaging that there appears to be an orderly map of disparity within the thick stripes of V2. Taken together, these studies indicate that there is a topographic map of disparity in V2, at least within the thick CO stripes.

Recently, DeAngelis and Newsome<sup>10</sup> have provided evidence for a map of binocular disparity in visual area MT, a higher-level extrastriate area that receives much of its input from the thick stripes of V2 (Refs 66–68). Disparity selectivity was found to occur in discrete patches (typically 0.5–1 mm in extent) that were interspersed among similar-sized patches of cortex that lacked disparity tuning. Within the disparity-tuned patches, preferred disparities changed smoothly across the surface of MT (see Fig 3a). In addition, DeAngelis and Newsome found little change in disparity selectivity along penetrations normal to the cortical surface, indicating that there are disparity columns in MT. The organization of disparity selectivity in MT is schematized in Fig. 3b, overlaid upon the well-documented architecture for direction of motion (arrows)<sup>69</sup>.

The above discussion suggests that areas V2 and MT are likely to be important processing stages for the elaboration of disparity signals. Both MT and the thick stripes of V2 belong to the 'dorsal' processing stream, which is thought to analyze spatial relationships and determine object locations in space<sup>70</sup>. Thus, these areas might be directly involved in computing depth, a function for which topographic maps of



disparity would be quite useful. It will be interesting to see if other visual areas, particularly those within the 'ventral' stream, also contain maps of disparity. It could be that disparity selectivity in the ventral stream serves different functions, such as scene segmentation and object recognition, for which it is not necessary to organize disparity-selective neurons in maps. As there are no published studies of disparity selectivity in area V4 and only limited data from inferotemporal cortex<sup>17</sup>, this speculation will have to await further studies. Indeed, an important goal moving forward must be to better define the roles that different visual areas play in stereoscopic vision, a topic to which we now turn.

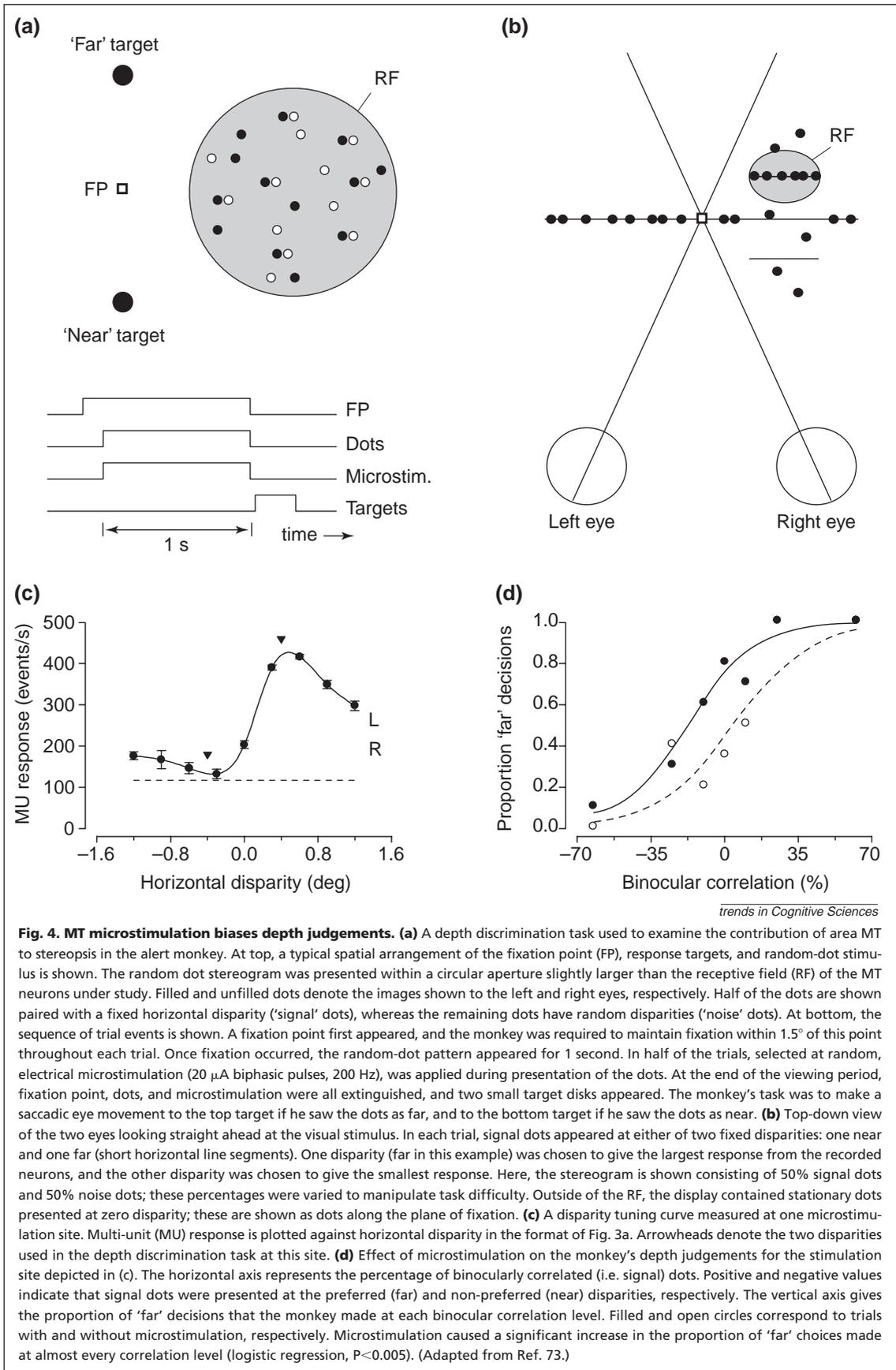
#### Linking neurons to behavior

As mentioned in the introduction, disparity selective neurons have been found in a number of visual cortical areas<sup>18</sup>. Which of these areas are involved in depth perception, and what aspects of depth perception do they serve? These are perhaps the most important questions to ask, and also the most difficult to answer. Although the presence of disparity-selective neurons may indicate a role for all of these areas in stereopsis, this is not necessarily the case. Disparity-tuned neurons are useful for a variety of visual processes, such as figure-ground segregation, feature linking, eye alignment, and guidance of vergence eye movements. Thus, simply measuring the disparity tuning of neurons may give little insight into the functional roles that they play. To move beyond this limi-

tation, it is necessary to record and/or manipulate neural responses while subjects perform a variety of stereo vision tasks. Although little has been accomplished in this regard overall, recent experiments in the alert, behaving monkey preparation have taken important steps in this direction.

Parker and colleagues have recently recorded from single neurons in V1 while monkeys performed a fine-grain disparity discrimination task<sup>71,72</sup>. Monkeys were trained to discriminate the depth of a random dot pattern placed over their receptive fields from the depth of a surrounding annulus of random dots. Thus, the task involved detecting the relative disparity between center and surround stimuli. The ability of neurons to discriminate relative depth was much poorer, on average, than the monkey's ability. Importantly, however, the best V1 neurons had sensitivities comparable to that of the animal. Thus, at least a subgroup of V1 neurons could account for performance on this task. It will be interesting to know how neural sensitivity on this task changes at higher levels in the visual pathway and to understand the computations by which neural sensitivity might be enhanced and refined in subsequent stages (e.g. by pooling responses of neurons across space).

In another recent study, DeAngelis *et al.* also trained monkeys to perform a depth discrimination task using random dot stereograms<sup>73</sup>. In their task, however, the monkey always discriminated between two fixed, supra-threshold disparities, and task difficulty was manipulated by varying the



fraction of dots that carried the depth signal. The remaining dots were given random disparities to form 'disparity noise' (see Fig. 4a,b). Instead of recording single-unit activity, DeAngelis *et al.* first measured the disparity tuning of multi-

unit activity (see Fig. 4c) at a sequence of recording sites along electrode penetrations through area MT. When they found a series of recording sites (spanning 200–300  $\mu$ m) with consistent disparity tuning, they positioned their electrode in

the middle of the span and applied electrical microstimulation to a cluster of MT neurons while monkeys performed the depth discrimination task. Microstimulation is known to activate neurons within the vicinity of the electrode tip. Thus, if disparity signals in MT contribute to performance of this task, microstimulation should bias the monkeys' judgements of depth. Indeed, this is what DeAngelis *et al.* found (see Fig. 4d), with the direction of the effect being predicted by the multi-unit tuning in 42 out of 43 experiments with significant effects. Microstimulation of sites with a near preference induced a near bias in the monkeys' judgements, and stimulation of far-preferring sites caused a far bias. This result suggests that MT plays an important role in depth perception, at least in the case when weak disparity signals are embedded in noise (such as when an animal tries to locate its prey among dense foliage).

Another set of elegant, recent experiments also suggests that MT plays an important role in depth perception. Both Bradley *et al.*<sup>74</sup> and Parker *et al.*<sup>75</sup> trained monkeys to report the direction of rotation (clockwise versus counterclockwise) of a 3-D cylinder defined by moving random dots. When the 3-D structure of the cylinder is defined by binocular disparity cues (e.g. front surface of the cylinder moves rightward while the rear surface moves leftward), the direction of rotation is unambiguous. MT neurons that are selective for conjunctions of motion and disparity (e.g. rightward and near, or leftward and far) are able to easily distinguish the two directions of rotation in this case. In contrast, when the disparity cues are removed, the percept becomes bistable<sup>76</sup>: for the same visual stimulus, clockwise rotation is seen on some trials and counterclockwise rotation is seen on other trials. Interestingly, Bradley *et al.* showed that the average responses of some MT neurons still distinguish between the two *perceived* directions of rotation<sup>74</sup>, even though the visual stimulus was ambiguous and identical on every trial. Parker *et al.* have taken this a step further by showing that there is a strong trial-by-trial correlation between the responses of MT neurons and the perceptual judgements of cylinder rotation<sup>75</sup>. Interestingly, this trial-by-trial correlation is substantially stronger, on average, than that obtained from MT neurons while monkeys performed a direction discrimination task<sup>77</sup>. This may indicate that individual MT neurons are more directly coupled to judgements of depth than to judgements of motion, or it might reflect the special, bistable nature of the rotating cylinder percept.

The studies described above have begun to elucidate the roles that different visual areas play in stereoscopic depth perception. But these studies are just a beginning, and there are many questions left to answer. For example, it is unclear whether V1 neurons would contribute to the perception of coarse disparities in noise, because this discrimination is likely to require considerable spatial integration and V1 neurons have much smaller receptive fields than MT neurons. Similarly, it is unclear whether MT neurons would contribute to the discrimination of fine relative disparities, given that MT neurons may have considerably broader disparity tuning than V1 neurons<sup>14</sup>. Thus, a comprehensive understanding of stereopsis will involve studying each visual area while monkeys perform a variety of stereo vision tasks. Only then will we gain an understanding of the relative contributions of different visual areas.

### From disparity to distance: the scaling problem

Based on the geometry of binocular viewing (Box 1, Fig. I), it is clear that horizontal disparities provide information about depth relative to the point at which the eyes are fixated. Often, however, we want to know the distance of an object relative to our body (egocentric distance), or the extent of an object in depth independent of its egocentric distance (depth constancy). Both egocentric distance and object depth must be known accurately, for example, if we are to reach out and correctly grasp an object. Horizontal disparity information must be combined with an estimate of viewing distance in order to correctly judge distance and depth. This is referred to as the 'disparity scaling' problem. Many behavioral studies of distance perception and depth constancy indicate that the human visual system does compensate (at least partially) for viewing distance, as reviewed elsewhere<sup>78,79</sup>.

What is the source of our knowledge of viewing distance? In the absence of pictorial depth cues, there are two main candidates: the vergence angle of the eyes, and the pattern of vertical disparities across the visual field. Accurate knowledge of the positions of the two eyes (vergence angle and gaze angle) would specify viewing distance, and could be obtained from the oculomotor system via either proprioceptive feedback or efference copy. Indeed, most classical studies of binocular distance perception have assumed that these oculomotor signals specify the viewing distance<sup>78</sup>. Mayhew and Longuet-Higgins made an important theoretical contribution, however, when they showed that both viewing distance and gaze angle could be determined from the pattern of vertical disparities across the visual field, specifically the horizontal gradient of vertical disparity<sup>80–82</sup> (see Box 1, Fig. II). Thus, in their theory, oculomotor signals would not be needed to specify viewing distance.

The work of Mayhew and Longuet-Higgins touched off considerable debate concerning the relative contributions of vergence angle and vertical disparities to the scaling of horizontal disparities. Some studies have found no effects of vertical disparities on the perceived shape or depth of stereoscopically defined surfaces<sup>83,84</sup>, whereas other studies have found considerable effects of vertical disparities<sup>85,86</sup>. The resolution of this controversy seems to be that vertical disparities only contribute when the field of view is sufficiently large ( $>25\text{--}30^\circ$ ), whereas vergence angle is the main contributor for smaller display sizes<sup>86,87</sup>. But how do these cues act on the responses of visual neurons to implement disparity scaling? We now consider the physiological evidence for effects of both vergence angle and vertical disparities on the tuning of cortical neurons for horizontal disparity.

### Vergence modulations

Several studies have examined the effects of vergence manipulations on disparity tuning in visual cortex, but these studies do not paint a very consistent picture. Trotter *et al.* trained monkeys to fixate on a moveable monitor at distances of 20, 40 and 80 cm, and they showed that some neurons in monkey V1 change their response amplitude dramatically (but not their preferred disparity) with viewing distance<sup>88,89</sup>. These effects were presumably due to changes in vergence angle, because the display size was relatively small ( $18^\circ \times 14^\circ$ ) and because similar effects were seen in control experiments using

### Outstanding questions

- Although mechanisms of disparity encoding are fairly well understood in cat V1, relatively little is known about primate V1 and extrastriate areas. How do interocular phase and position differences contribute to disparity selectivity in primates, and how does this constrain processing at later stages in the visual pathway?
- Given that V1 appears to compute absolute retinal disparity, how and where are relative disparities encoded in the visual system? What computations do neurons perform to become sensitive to extremely fine relative disparities?
- Most physiological studies of stereopsis have only tested neurons with fronto-parallel surfaces at different depths, whereas many natural surfaces are slanted or curved in depth. The retinal images of these surfaces will contain spatial gradients of binocular disparity. How and where are these disparity gradients encoded in the brain, and how are gradient-selective neurons used to compute surface orientation in 3-D space?
- How are disparity-selective neurons organized in different brain areas? How different is the incidence and organization of disparity-selective neurons between visual areas of the dorsal and ventral processing streams? And what does this suggest about the respective roles of these two streams in stereoscopic vision?
- Which visual areas contribute directly to stereopsis and what types of stereoscopic perception do they support? Where in the brain do single neurons exhibit sufficient sensitivity to account for performance on a variety of stereo vision tasks? And how does pooling the responses of small populations of neurons improve neural sensitivity? How can microstimulation and/or inactivation studies be used to delimit the roles of different areas?
- Where and how in the visual system is knowledge of viewing distance used to compute egocentric depth from horizontal disparities? And what are the contributions of vergence and vertical disparity cues to these computations?

prisms to manipulate the vergence requirement. Although this is a very interesting result, the monkeys' vergence posture was neither measured nor enforced in these studies. Thus, apparent changes in response strength could have resulted from inaccurate or imprecise fixation at different distances<sup>56</sup>. The authors argue against this possibility, however, by pointing out that the weaker responses at some viewing distances were not associated with increased variability in the neural discharge.

Gonzalez and Perez varied vergence angle using mirrors and reported results similar to those of Trotter *et al.*, although substantially less dramatic<sup>90</sup>. Again, however, vergence posture was not measured precisely or enforced directly. More recently, Cumming and Parker have also examined effects of vergence angle on V1 responses<sup>56</sup>. Because the position of each eye was measured with a scleral search coil while monkeys performed a vergence tracking task, vergence angle was known quite accurately. Under these conditions, Cumming and Parker found very little effect of vergence angle on V1 responses. It should be noted, however, that the vergence angles used by Cumming and Parker correspond to a different range of viewing distances (~50–175 cm) than those used in the other studies. Moreover, most of the gain effects seen by Trotter *et al.* were at the nearest viewing distance of 20 cm. Thus, either vergence angle does not appreciably scale horizontal disparities beyond a viewing distance of 50 cm in monkeys, or the responses of V1 neurons do not fully account for depth constancy.

It is worth noting that none of the above studies found neurons that shifted their disparity preference with viewing

distance in a manner appropriate to encode absolute (egocentric) distance. Although gain changes in V1 responses could form a distributed code for absolute distance<sup>88,89</sup>, it remains to be demonstrated that the effects observed by Trotter *et al.* would be sufficient to account for the perceptual effects of changes in viewing distance. Working in extrastriate area MST of the monkey, Roy and Wurtz reported that one neuron (out of 20 tested) shifted its preferred disparity with viewing distance<sup>16</sup>. Unfortunately, this neuron's tuning curve does not exhibit a clear peak or saturation; thus, it is difficult to distinguish a shift from a change in response gain.

#### Vertical disparity modulations

The effects of vertical disparity modulations on cortical responses remain largely untested. Gonzalez *et al.* measured the responses of V1 and V2 neurons in fixating monkeys to both horizontal and vertical disparities, and they reported that neurons selective for one are also selective for the other<sup>91</sup>. In addition, they show a partial display of the joint tuning to horizontal and vertical disparities for one neuron. Working in area MT of anesthetized monkeys, Maunsell and Van Essen measured the joint tuning of several neurons to both horizontal and vertical disparities<sup>14</sup>. The effects of horizontal and vertical disparity appear to be largely separable in their data. Thus, there is no clear evidence to date that vertical disparities cause any change in the range of preferred horizontal disparities, as might be expected if vertical disparities are responsible for scaling horizontal disparities.

It must be noted, however, that both of the above studies only examined interactions between horizontal and vertical disparities *within* the classical receptive field. Because it is the horizontal gradient of vertical disparity across large regions of space that provides robust information about viewing distance<sup>81,85</sup>, vertical disparities outside of the classical receptive field may modulate responses to horizontal disparities within the receptive field. To my knowledge, this general hypothesis has not yet been tested.

Finally, it is worth noting that the disparity-scaling problem might not get solved in visual cortex *per se*. Disparity-selective neurons have been found in subcortical oculomotor areas such as the superior colliculus<sup>92–94</sup> and the accessory optic system<sup>95</sup>, and it remains unclear whether these neurons might help to solve the disparity-scaling problem. Additionally, some regions of posterior parietal cortex are known to contain neurons that are selective for depth<sup>96,97</sup> or 3-D object shape<sup>98</sup>. Sakata *et al.* have reported that some 'visual fixation' neurons modulate their responses quite linearly with viewing distance<sup>99</sup>; thus, these neurons could provide inputs used to scale horizontal disparities. As these responses persist when monkeys fixate a small spot in a dark room, the effects of viewing distance are most likely to be due to changes in vergence angle, although the authors did not control for changes in stimulus size and intensity. Although the disparity-scaling hypothesis has not been tested directly in parietal areas, this may be a promising avenue for future studies.

#### Conclusion

Since the original reports of disparity-selective neurons in the late 1960s<sup>5,6</sup>, most physiological studies of stereopsis have focused on measuring the disparity tuning functions of

cortical neurons. Although much has been learned from these studies, I have argued here that tuning measurements alone may not reveal much about the roles that specific populations of neurons play in stereopsis. More recent studies have begun to tackle these problems by combining traditional electrophysiology with psychophysical and computational approaches, and these efforts are beginning to reveal concrete links between neural activity and stereoscopic depth perception. Looking forward, the convergence of these disciplines holds considerable promise for understanding the neural basis of stereopsis.

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