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Representation of binocular surfaces by cortical neurons

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Useful representations of the three-dimensional (3D) world go beyond assigning depth to individual points, building maps of surfaces and shapes. Studies in a wide range of extrastriate cortical areas have shown that single neurons show selective responses to 3D surfaces. The extent to which this advances the representation beyond that provided by the earliest binocular signals requires careful evaluation. We conclude that current data are not sufficient to identify distinctive contributions from different cortical areas to the binocular representation of 3D surfaces.

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Review

Binocular disparities (which arise because the two eyes have different vantage points) provide one of the most important visual sources of information about the distance to objects in the three-dimensional (3D) world. Although we know much about how cortical neurons are able to measure the disparity of small patches (reviewed in [1]), such local measures alone are of limited value — further processing is required to make explicit key features of the world around us. (Just as the map of point brightness on the retina requires further processing for 2D vision.) Specifically, representing extended surfaces and 3D shapes is the important task (e.g. when swinging between branches). The first section describes recent studies exploring the representation of surfaces and shapes in extrastriate cortex. The second section describes neuronal responses in the striate cortex that may also play a role.

Extrastriate cortex

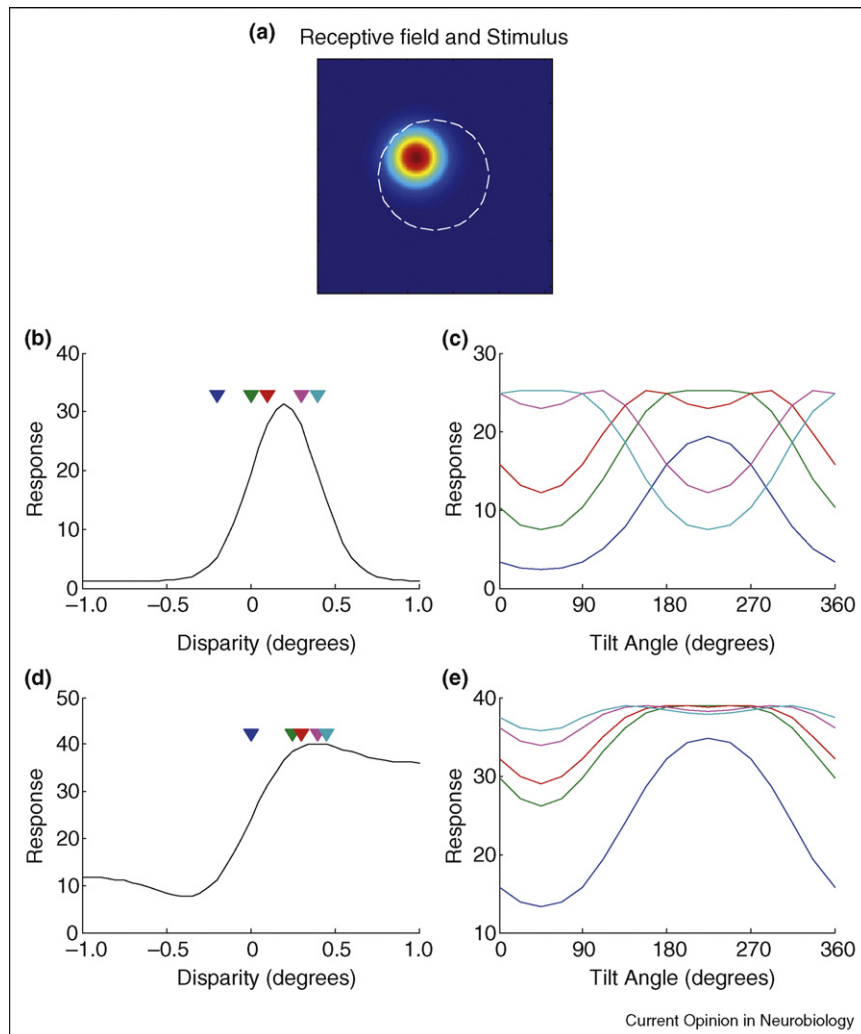
Two parameters are required to describe surface orientation. The most widely used nomenclature is that of

Stevens [2], where ‘Slant’ refers to the magnitude of the deviation from frontoparallel, and ‘Tilt’ describes the axis around which the rotation is applied. Thus for binocular stimuli, slant describes the magnitude of the disparity gradient, while tilt gives the direction of the gradient. Several studies in several extrastriate visual areas have reported that, given a nonzero slant, neurons fire in a way that is selective for the axis of tilt.

However, slanted surfaces necessarily produce changes in disparity. These alone will stimulate neurons that are disparity selective, even if that selectivity is uniform over the receptive field. To attempt to overcome this problem, a common practice is to demonstrate that tilt preference shows invariance over changes in mean disparity. Simple simulations show that even this property must be interpreted with care. Figure 1 shows that if the mean disparities are confined to one side of a symmetrical tuning curve, the preferred tilt appears invariant. When disparities span the peak of the tuning curve, this invariance is no longer present. However, for asymmetric disparity tuning curves, the interaction between mean disparity and tilt is harder to interpret. Figure 1d shows an odd-symmetric disparity tuning curve. Here the artifactual tilt selectivity is preserved over a range of mean disparities, including some that span the peak.

The most thorough analysis to use this approach [3••] studied neurons in area MT, and included quantitative measures of all the important properties: first, receptive field location and size; second, disparity selectivity for frontoparallel planes; and third, tilt selectivity, repeated with several mean disparities spanning the peak in the measured disparity selectivity. Figure 2 shows data for an example neuron from that study, which exhibits clear tilt selectivity that is well preserved when disparity is altered. However, the data have some similarities with the simulations shown in Figure 1d (this is not accidental — the simulation was built with this data set in mind). The simulation uses a similar disparity tuning curve, and has the RF displaced slightly up and left from the stimulus center — in the same direction as the example data. This combination produces much of the tilt selectivity seen in the data. Nonetheless, the influence of mean disparity on the neuronal responses is smaller than in our simulation, so it seems that the neuron does indeed have some true tilt selectivity (selectivity that could not be produced by disparity selectivity that is uniform), as do the other examples in this study. However, given the simulations in Figure 1, the quantification of the strength of tilt selectivity requires complex analyses. Even the ‘tilt discrimination index’ (TDI) used by [3••], which pools

Figure 1



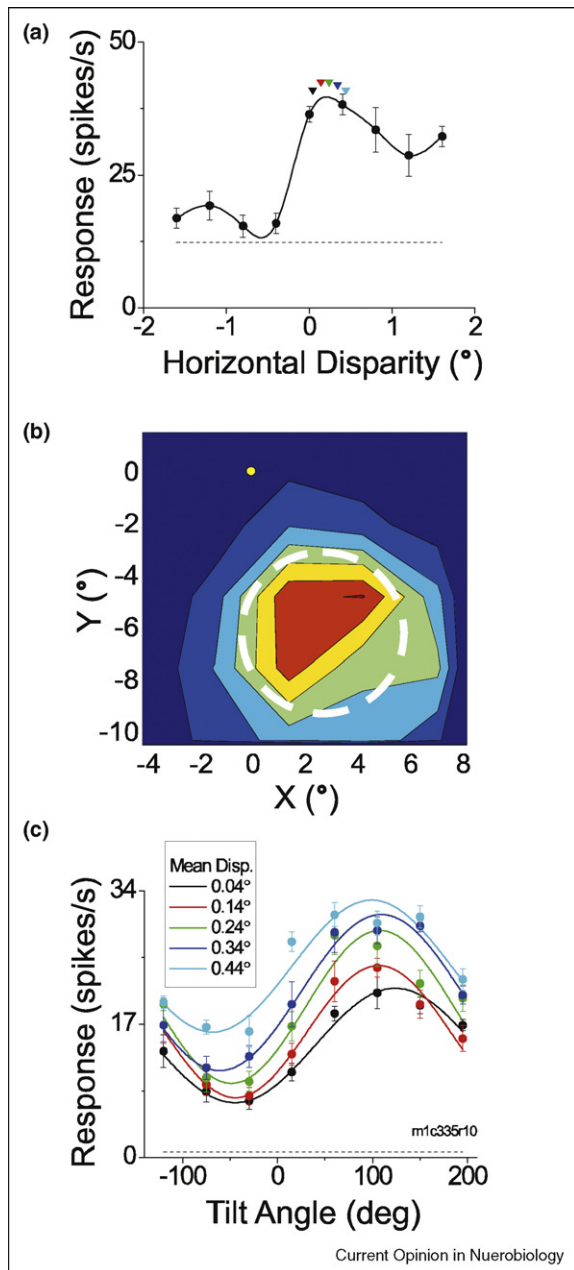
Uniform disparity selectivity can produce the appearance of tilt selectivity. **(a)** A spatial weighting function (the receptive field) of a model neuron, and the location of the stimulus. **(b)** A symmetrical disparity tuning function, which describes the response at every point in the receptive field (scaled by the RF). **(c)** The resulting responses to tilt. Line color indicates the mean disparity, matching the triangles shown in **(b)**. Comparing responses to different disparities can reveal that the apparent selectivity to tilt is an artifact. If responses are compared across two mean disparities that are symmetrical about the peak of the disparity tuning curve (compare green and cyan curves), there is a reversal in the apparent tilt preference. If the two mean disparities lie on the same side of the peak (compare green and blue curves) the preferred tilt angle does not change. If the point on the surface about which rotations are applied lies exactly at the center of a circularly symmetric receptive field, the response is not affected by tilt. **(d)** A disparity tuning curve that is not symmetrical. **(e)** The resulting responses to disparity and tilt. Note that the selectivity for tilt is no longer necessarily reversed by using mean disparities either side of the peak, so even a measure that collapses across all disparity values will still show tilt selectivity.

results across different mean disparities, can be substantial in the absence of true tilt selectivity.

Some invariance of slant/tilt preferences over changes in mean disparity has been demonstrated in areas MT [3^{••}], V4 [4], CIP [5], and IT [6,7]. Although only the study in MT used measures of disparity selectivity to guide the choice of disparities tested, all these studies show example cells for which the slant/tilt selectivity was better preserved than the simulation in Figure 1d. The lack of quantitative measures of disparity tuning in the other

studies makes it difficult to draw conclusions from the population measures. Nonetheless, most of these studies used a wide enough range of disparities that disparity selectivity alone is unlikely to explain all the results. It seems that all of these areas contain some neurons that can signal 3D surface orientation. The difficulties with quantification at the population level prevent meaningful comparisons between areas given existing data. One possible basis for such a comparison could compare observed responses with those predicted from the measured RF and disparity selectivity. To date, only

Figure 2



Responses of an MT neuron to tilt in a random dot stereograms, reproduced from [3**], with permission. **(a)** The disparity selectivity measured with uniform disparity. **(b)** The measured receptive field. **(c)** Responses to different tilt angles, each color corresponding to a tuning curve performed at a different mean disparity (colors match the triangles showing the disparity in A).

the study by [3**] gathered all the data required for such an analysis.

Since asymmetric disparity tuning is common across extrastriate cortex [1,8,9], controls other than varying the mean stimulus disparity may be better. One alterna-

tive is to vary the location of stimulus center (the point about which 3D rotations are applied). If a stimulus placed to one side of the receptive field center produces one artifactual pattern of tilt selectivity, then placing the stimulus symmetrically on the other side of the RF center should produce the opposite pattern of tilt selectivity, provided that the RF shape is symmetrical. If receptive fields are more nearly symmetrical than disparity tuning functions, this is a better control. Recording in the inferotemporal cortex (TE) with a variety of 3D shapes, Janssen *et al.* [7] found that responses to preferred shapes remained higher than those to nonpreferred shapes across a range of stimulus locations. When using complex shapes, varying stimulus position is a much better control than varying mean disparity. Since the latter does not change disparity gradients, local responses to the gradient alone may explain what appear to be responses to complex shapes (e.g. [10]).

If observed selectivity for 3D surface orientation cannot be explained by uniform disparity selectivity, it follows that the receptive field contains two or more regions with different disparity selectivity. Nguyenkim and DeAngelis [3**] made measures of disparity selectivity in small subregions of the RF and showed that these explained the tilt selectivity well. All of the tilt selectivity described above could be probably be explained simply by combining two subunits with different receptive field positions and different selectivity for absolute disparity. These results may therefore reflect the same mechanism described in other studies that found different disparity selectivity in different parts of the receptive field. This has been reported in MSTl [11] and as early as V2 [12,13]. Thus, in every extrastriate area in which the question has been investigated, from V2 to IT and the intraparietal sulcus, there are neurons in which disparity selectivity seems not to be uniform over the receptive field. No study has conclusively demonstrated responses that require more than the sum of two regions with different selectivity for absolute disparity.

As a result, current data do not differentiate the responses of neurons selective for 3D structure in different extrastriate areas. A few studies have explored neuronal responses to disparity-defined shapes that are not simply planes, but have curvature in depth. The studies by Janssen *et al.* [7,14] incorporated controls to exclude explanations on the basis of uniform disparity tuning. They show dramatic examples of neurons that are strongly activated by curved binocular surfaces, while planar approximations spanning the same disparity range caused far weaker activation. It seems improbable that such responses could be explained by a mechanism as simple as the sum of two disparity selective subunits, but without quantitative simulations it is unclear what mechanism provides the simplest account of these interesting data. A clear understanding of this may be important

before comparing responses in TE with responses in other cortical areas to curved stereoscopic surfaces.

Striate cortex

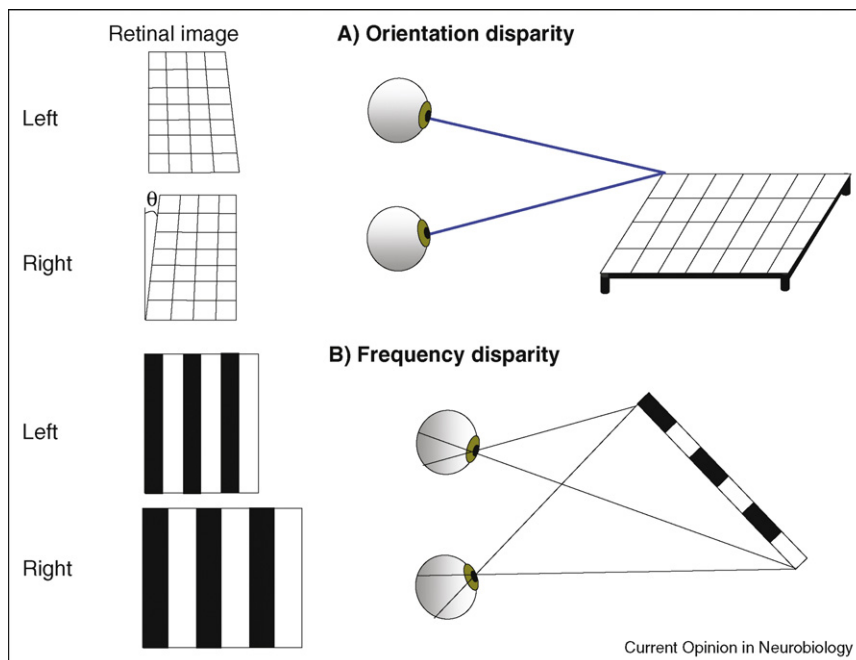
The only region of the cortex where attempts to show selectivity for surface orientation have failed is the striate cortex, though no published study has used methods equivalent to those described above. Nienborg *et al.* [15] used sinusoidal modulations of disparity in random dot stereograms. If neurons fire more strongly to slanted planes than to planes of uniform disparity, stronger modulations in firing rate for intermediate spatial frequencies of modulation should be produced (the lower the frequency, the more uniform the disparity over the RF). Very few V1 neurons showed any reduction in modulation of activity at low spatial frequencies.

However, a second mechanism may make an important contribution to the representation of 3D surfaces, on the basis of differences between the orientation and spatial frequency of images between the eyes. As illustrated in Figure 3A, vertical lines on a plane that is slanted around a horizontal axis project to lines that are not vertical in the retinal image. The rotation away from vertical is in the opposite direction in the two eyes, producing an 'orientation disparity', that can be used to detect the surface slant. In principle this can be done completely independent of the disparities measured at individual locations.

Similarly, planes rotated about a vertical axis give rise to a spatial frequency disparity (Figure 3B). The observation that binocular neurons in striate cortex sometimes show differences in preferred orientation [16,17] and spatial frequency [18,19] between the eyes (but measured monocularly) provides a potential physiological substrate for detecting such disparities. Bridge and Cumming [20] measured responses to binocular gratings, varying orientation separately in the two eyes. The only neurons that showed selectivity for the binocular orientation difference were also disparity selective, and their responses to binocular gratings with orientation differences were closely related to their disparity selectivity. Thus, though V1 neurons do not encode orientation disparity separately from position disparity, the different preferred orientations in the two eyes do have an impact on the binocular responses of these neurons.

In the case of binocular responses to spatial frequency differences, an even more rigorous investigation was performed by Sanada and Ohzawa [21]. They used reverse correlation measures to show that many cells exhibit changes in preferred disparity across the receptive field. (The method involves a rapid sequence of flashed bars, at all combinations of positions in both the eyes.) They were able to calculate the spatial frequency difference between the eyes necessary to produce this feature in the energy model, despite the fact that the stimulus

Figure 3



Geometry of orientation disparity and spatial frequency disparity. **(A)** The eyes looking down on a table. If the left edge of the table points directly at the left eye, this will project to a vertical line on the left retina, but a line that is rotated away from vertical in the right eye. The difference in orientation (θ) is the orientation disparity of the line. **(B)** A plan view of two eyes viewing a vertical square-wave grating slanted around a vertical axis. The surface is foreshortened to a greater extent in the left eye's view, so the spatial frequency of the retinal image is higher.

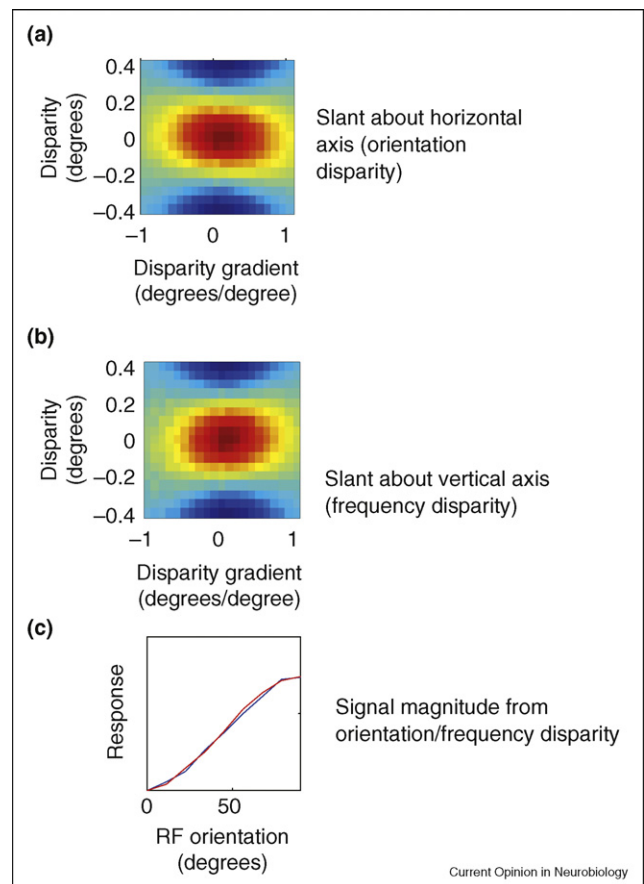
(flashed bars) had no spatial frequency difference between the eyes. Measures of spatial frequency selectivity in the two eyes (using monocularly presented gratings) produced independent estimates of spatial frequency difference between the RFs in each eye, which correlated with the difference inferred from the reverse correlation stimulus.

These two studies therefore provide confirmation that binocular orientation and spatial frequency differences are encoded at the earliest stage of binocular coding, the striate cortex. However, they do not support the idea of specific, separate mechanisms. The results of both studies are well described by the binocular energy model [22,23^{*}], in which the binocular response is determined by the cross-correlation between the images after filtering. This will be maximal when the transformation between the left and right images (including displacement, rotation, and scaling) matches the transformation relating left and right receptive fields. The inclusion of changes in orientation and spatial frequency allows such filters to produce maximal responses to surfaces that are not frontoparallel.

The success of the energy model in describing the responses of real neurons allows us to use the model (in the same way as described by Bridge *et al.* [23^{*}]) to evaluate the contribution of differences in orientation and spatial frequency to the encoding of 3D surfaces. In order to detect surface orientation with energy model units exploiting only position disparity, it is necessary to compare the responses of two units with different RF positions. For an RF separation of just 1 sd of the Gaussian envelope, Bridge *et al.* found that position disparity provided signals about surface orientation that were more than double the magnitude of those derived from orientation disparity. This is illustrated in Figure 4a, which shows the responses of one model cell to combinations of slant (disparity gradient) and disparity. Figure 4b shows a similar situation holds for spatial frequency disparity. Both of these model cells had vertically oriented RFs. For neurons with preferred orientation away from vertical, the effect of slant on firing rate is reduced. For any given RF orientation, plots like Figure 4a and b can be used to quantify the information available for discriminating small changes in slant (finding which orientation/frequency disparity produces the largest changes in response as a function of slant). Figure 4c shows that this signal gets weaker as the orientation approaches horizontal (a result of the projection geometry in Figure 3c, see [24,25]). In spite of this, both physiological studies found that the distribution of orientation/frequency disparities in the RF did not depend upon RF orientation.

In summary, the binocular response of disparity selective V1 neurons reflect how well the transformation between left and right images matches the transformation relating

Figure 4



Energy model responses to slanted surfaces. **(a)** The response (given by color) of a model with a small orientation disparity, to combinations of disparity and disparity gradient (slant around a horizontal axis). The axes are scaled so that disparity values are equivalent to slant values, if tilt is calculated by comparing responses in RFs with no orientation disparity, but separated in space. The spatial separation used here is 1 sd of the Gaussian envelope defining the RF (as in [23^{*}]). The horizontal elongation of the response surface illustrates the fact that orientation disparities provide weaker signals about slant than mean disparity. **(b)** The equivalent responses for a neuron with a spatial frequency disparity, for slant about a vertical axis. Comparing model neurons with equal and opposite orientation/frequency disparities quantifies the strength of the signal related to slant that is provided by a given orientation/frequency disparity in the RF. **(c)** The strength of response modulation produced by slant is plotted as a function of receptive field orientation. Blue line shows signal from orientation disparities for slant about a horizontal axis. Red line shows signal from spatial frequency disparities for slant about a vertical axis. Despite the fact that the magnitude of spatial frequency differences produced by a disparity gradient is constant across all nonhorizontal orientations, its effectiveness for detecting slant declines in much the same way as for orientation disparity.

left and right receptive fields. These transformations include differences in orientation and spatial frequency that are sufficient to span the range produced by the 3D orientation of surface patches in most viewing situations. This yields a modest improvement in the ability of a population of neurons to signal surface orientation. For

neurons with near horizontal preferred orientations, the differences in orientation and spatial frequency are of limited use for this function, and yet they are found with the same frequency as in neurons with near vertical orientations. The real significance of orientation/frequency disparities may depend on how signals from V1 are 'read out'. Future studies in extrastriate cortex may clarify this — if neurons showing some specialization for encoding surface orientation (discussed in the section on extrastriate cortex) showed orientation or frequency differences in the direction that matched their preferred surface orientations, this would be powerful evidence that the brain is exploiting these signals from V1.

Conclusion

Disparity selective neurons in striate cortex make a modest contribution to representing 3D shape by means of orientation and spatial frequency disparities. Throughout the extrastriate cortex, neurons show responses that cannot be explained by such homogenous disparity selectivity. Exactly what these inhomogeneities are, and if and how they differ between cortical areas, cannot be evaluated from current data. Understanding these relationships is probably going to require new methods that can probe 3D RF structure in more detail.

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