A specialization for relative disparity in V2

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Stereoscopic depth perception relies on binocular disparities, or small geometric differences between the retinal images of each eye. The most reliable binocular depth judgments are those that are based on relative disparities between two simultaneously visible features in a scene. Many cortical areas contain neurons that are sensitive to disparity, but it is unclear whether any areas show a specific sensitivity to relative disparity. We recorded from neurons in the early cortical visual area V2 of the awake macaque during presentation of random-dot patterns. The depth of a central region ('center'), and that of an annular surrounding region ('surround'), were manipulated independently in these stimuli. Some cells were fully selective for the resulting relative disparities. Most showed partial selectivity, which nonetheless indicated a sensitivity for the depth relationship between center and surround. Both types of neural response could support psychophysical judgments of relative depth.

A striking psychophysical feature of human stereopsis (stereo vision) is that depth perception depends on relative, not absolute, disparity. The absolute disparity of a single point is the horizontal difference in the retinal location of its image with respect to the left and right foveas. The difference in the absolute disparities of two visible features in the external visual field is termed 'relative disparity'. When a large disparity change is applied uniformly across the visual scene (thus changing absolute, but not relative, disparity), people do not perceive a change in depth[1–3]. Whereas absolute disparities change with vergence eye movements (equal but opposite rotations of the two eyes), relative disparities are unaffected by vergence. Perhaps for this reason, fine stereo judgments require the use of relative disparities in both humans[4] and monkeys[5].

These observations suggest the existence of some neural activity, from which psychophysical judgments of relative depth are derived, that explicitly signals relative disparities. Single neurons can, in principle, display this sort of selectivity. Such neurons would show a disparity preference which depends upon two different regions in the visual field (**Fig. 1a**). Neurons that perfectly encode relative disparity would show shifts in preference for one region that are equal in magnitude and direction to the imposed disparity change in the other region. A more indirect method of signaling relative disparity (**Fig. 1b**) occurs when the degree of sensitivity to relative disparity varies over the neuron's working range of absolute disparity. Here, relative disparity is accurately encoded over only a narrow range of absolute disparities. Outside that range, responses are intermediate between selectivity for absolute and selectivity for relative disparity. Such intermediate responses share a critical feature with responses fully selective for relative disparity: the sensitivities for the two disparities are interdependent, so that the preferred value of one disparity depends on the value of the other. We refer to such responses (and others, such as those shown in **Fig. 1b**) as 'sensitive to' but not 'selective for' relative disparity. These two cases are in contrast to a much simpler pattern (**Fig. 1c**), where the response profile is the sum of two separate sensitivities, one for each of the two absolute disparities. These sensitivities do not interact at all: for each absolute disparity, its preferred value is the same regardless of the other's. Although the greatest response is elicited by a particular combination of disparities in the center and surround, this neuron does not show specialization for relative disparity (as neurons in **Fig. 1a** and **Fig. 1b** do).

As yet, encoding of relative disparity has not been demonstrated in any brain area. The firing rates of neurons in primate visual area V1 are determined only by absolute disparity[6]. Disparity-sensitive responses in extrastriate visual areas such as MT and MSTl (in medial-temporal cortex) are more complex[7,8] than those in V1. In MT and MST1, disparities outside the receptive field (RF) modulate responses to stimuli within the RF. This way, a neuron's optimal surround disparity is frequently different from its optimal center disparity. Although these results are consistent with a sensitivity to relative disparity, they could also occur if the center and surround regions are differentially sensitive to absolute disparity (as shown in **Fig. 1c**). Responses of this kind need not reflect a specific signal for the relative disparity between center and surround. Thus it remains unclear which, if any, cortical areas might support relative depth judgments.

Previous studies indicate that neurons in V2 are important for processing binocular depth[9–12]. Here, we examined the responses to relative disparity from cells in this cortical area in awake, behaving monkeys. The stimulus was a dynamic random-dot stereogram[13] (RDS) consisting of a central patch and a surrounding annulus. The patch was sized and positioned to cover the minimum response field of the neuron (see Methods). Neuronal responses were measured as a function of the

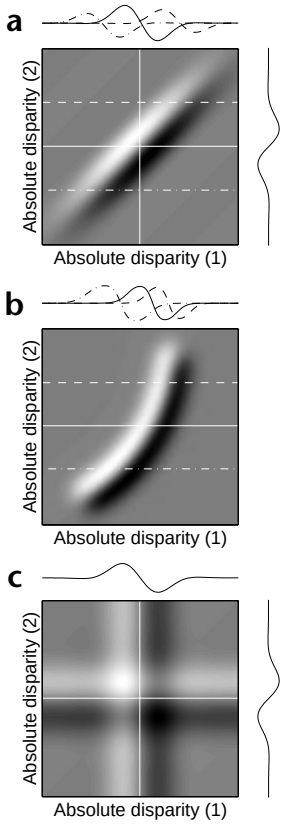


Fig. 1. Possible neuronal responses to a stimulus with regions (1 and 2) whose absolute disparities are varied independently. Firing rate is indicated by the grayscale intensity from black (lower rate) to white (higher rate). (**a**) A neuron tuned to relative disparity between 2 regions shows a pronounced diagonal structure. Cross-sections (solid, dashed and dotted lines) taken at 3 different values of the disparity imposed in 1 region of the receptive field (region 2) show systematic shifts in the preferred value in region 1. (**b**) Relative disparity is encoded in a more complicated way: responses to relative disparity predominate only over a limited range of absolute disparities. Elsewhere, the neuron's response is dominated by the disparity in region 1. (**c**) Neurons that are sensitive to both absolute disparities, but show no specific selectivity to relative disparity. Here, the sensitivity profile is just the sum of separate sensitivities to the 2 disparities. Measurements made only on single horizontal and vertical cross-sections[8] cannot distinguish this case from that shown in (**a**): the resulting tuning curves are identical.

absolute disparity of the center patch[10] at two or three different surround disparities. Hence, the relative disparity between center and surround was manipulated independently of the absolute disparity of the center (see **Fig. 2**). We found that a proportion of V2 neurons are sensitive to the relative disparity between these two regions. These sorts of responses could directly support judgements of binocular stereoscopic depth in a way that V1 neurons cannot.

Results

We recorded from a total of 165 isolated neurons (in two animals), of which 68 showed selectivity to the disparity of the center for at least two surround disparities. The full protocol (a minimum of four repetitions at each of seven appropriate disparities for each surround condition) was completed for 62 of these neurons. We found neurons showing a clear sensitivity to relative disparity (**Fig. 2b**): as the surround disparity was altered, the preferred center disparity changed. In this example, the tuning curves recorded at surround disparities of 0.00° and +0.45° (**Fig. 2d**) showed a shift in the peaks of these curves such that the response to a given disparity difference between center and surround was nearly constant. These data could not be explained by supposing that part of the surround stimulus fell on the RF of a neuron that was fundamentally selective for absolute disparity. Under these circumstances, the magnitude of the responses would change for all center disparities, without a change in the value of the center disparity that produced the strongest response. The change in location of the peak of the tuning curve is the essential feature that indicates sensitivity to relative disparity.

If a neuron were to perfectly encode relative disparity, the size and direction of the shift should match the change in surround disparity (as shown in **Fig. 2d**). The shift for this neuron over a different range of surround disparities (**Fig. 2c**) was in an appropriate direction, but of a smaller magnitude than that required for full selectivity to relative disparity. To quantify the magnitude of the shifts, pairs of Gabor functions were fit to disparity tuning data for pairs of surround disparities. The pair of tuning curves were constrained to the same shape, differing only by an offset along the disparity axis. The shift between curves was expressed as a fraction of the change in surround disparity. This

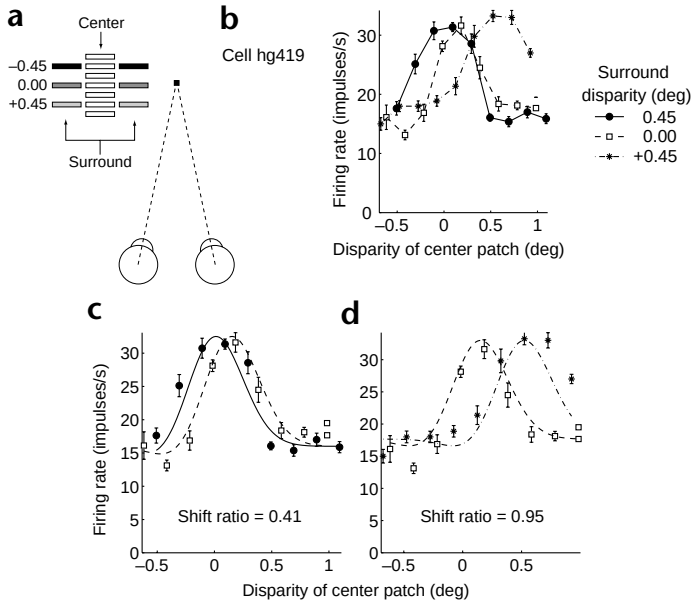
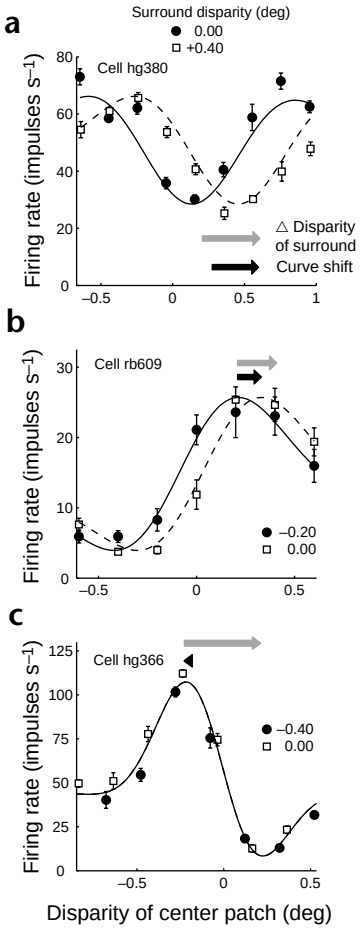


Fig. 2. The cyclopean stimulus configuration and the responses of a disparity-tuned neuron (**a** and **b**, respectively). Tuning curves for the disparity of the center patch (shown as an open box) are plotted at 3 different disparities of the surround (filled box). All stimulus conditions were randomly interleaved. (**c**, **d**) Analysis of the data in (**b**). A neuron selective to relative disparity will display tuning curves shifted by the change in surround disparity. The curves fitted to the data differ only in their position on the disparity axis. This difference is expressed as a shift ratio on a scale from 0 (tuning for absolute disparity) to 1 (tuning for relative disparity). In (**c**) and (**d**), the shift has the direction expected for relative disparity selectivity.

Fig. 3. The responses of 3 further neurons recorded at 2 different surround disparities. This data has been corrected for any changes in vergence during recording. The shifts expected of neurons tuned to relative disparity are shown by the gray arrows; the shifts measured experimentally are shown by solid black arrows. (**a**, **b**) Cells show shifts in the direction expected for relative disparity selectivity; the cell in (**a**) has a shift that approaches unity (0.8). (**c**) This cell showed no significant shift; its responses are consistent with selectivity for absolute disparity.



'shift ratio' should have a value of zero for absolute disparity–selective cells and a value of one (unity) for relative disparity–selective cells.

Sensitivity to relative disparity could arise spuriously if the animal's vergence angle changed with the surround disparity—this eye movement alone would alter the absolute disparity of the center patch. Hence, if the animal were to systematically converge at the depth of the surround, the relative disparity between center and surround would always equal the absolute disparity of the center. To remove this potential artifact, the vergence position was always monitored and the measured vergence was incorporated into the calculation of the shift ratio (see Methods).

The neuron shown above (**Fig. 2**) displays shift ratios of 0.95 and 0.41, corresponding to, respectively, an almost perfect encoding of relative disparity and a representation between absolute and relative selectivity. Thus this neuron is sensitive to relative disparity over the whole range of disparities tested, but is selective for relative disparity only over a limited range (as in **Fig. 1b**). Results from three other disparity-sensitive neurons are shown with the accompanying fits (**Fig. 3**). The shape of the tuning curve is unaffected by the surround disparity, but in two cases (**Fig. 3a** and **Fig. 3b**), changes in surround disparity displace the tuning curve along the disparity axis. This displacement can indicate a near-perfect representation of relative disparity, where the size and direction of the shift corresponds closely to the change of surround disparity (**Fig. 3a**; shift ratio 0.80). Some neurons showed sensitivity, but only a partial selectivity, to relative disparity (**Fig. 3b**; shift ratio 0.60), or an insensitivity to relative disparity (**Fig. 3c**; shift ratio –0.07).

For 24 neurons in which three surround conditions (zero, crossed, and uncrossed) were tested, two independent shift ratios were calculated. These two shift ratios were positively correlated ($r = 0.48$, $P < 0.01$). Thus, neurons that signal relative disparity do so over a range of absolute disparities. A notable feature of this data is that the size of the shift depends on the choice of the surround disparity (as shown in **Fig. 2**). In this example, a change in surround disparity from 0° to +0.45° (**Fig. 2d**) produced a larger shift than a change from 0° to –0.45° (**Fig. 2c**). Note that the 'preferred absolute disparity', defined as the preferred center disparity when the surround disparity is zero, was also positive. The larger shift ratio occurred when the surround disparity was closer to the preferred absolute disparity. This phenomenon was systematic (**Fig. 4**): the shift ratio in cases where the surround disparity moved toward the preferred disparity tended to be larger than the shift ratio in cases where the surround disparity moved away from the preferred disparity ($P < 0.01$, paired t-test). Neurons with shift ratios of unity can directly signal the relative disparity of the stimulus. For those cells with non-unity shift ratios, the firing rate also depends on the absolute disparity of the stimulus, so any estimate of the relative disparity based purely on the firing rate of such a cell becomes less precise as the shift ratio departs further and further from unity. This trend (**Fig. 4**) corresponds to a more accurate representation of relative dis-

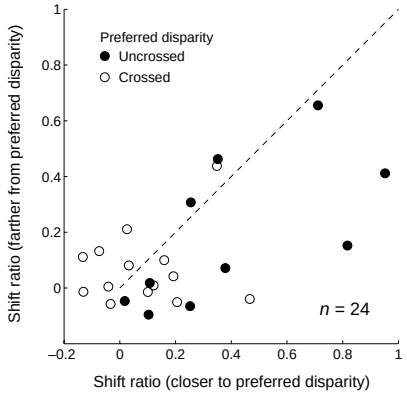


Fig. 4. Pair-wise comparison of shift ratios measured at different surround disparities, for a set of neurons. For each neuron, the tuning was measured with 3 surround disparities—crossed, zero and uncrossed. The preferred absolute center disparity was defined as the peak in the tuning curve when the surround disparity was zero. If this peak was at a crossed disparity (open symbols), then the shift ratio incorporating a crossed surround disparity was plotted on the abscissa. If the peak was at an uncrossed disparity (solid symbols), the shift ratio incorporating an uncrossed surround disparity was plotted on the abscissa. Although the shift ratios are correlated (rank correlation, $r = 0.48$, $P < 0.001$), they tend to lie beneath the identity line: larger shifts occur when the surround disparities are nearer to the preferred center disparity.

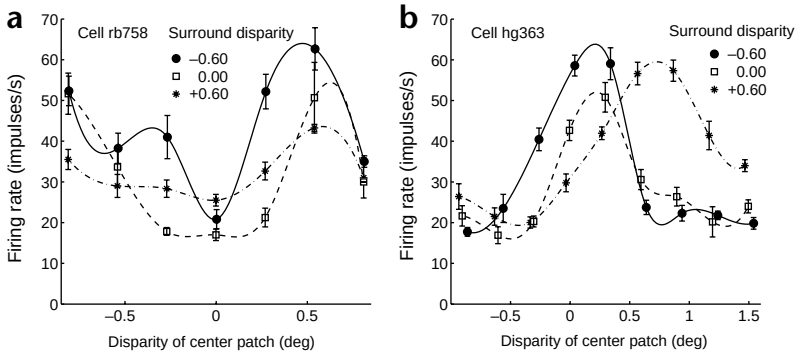


Fig. 5. Two neurons in which changes in surround disparity altered the shape of the disparity tuning curve. (**a**) The main effect of changing the surround disparity is to alter the magnitude of the response to the preferred center disparity. (**b**) There is a shift in preferred center disparity with surround disparity, but there is also a reduction in response magnitude associated with a surround disparity of zero.

parities (shift ratios closer to unity) when the preferred relative disparity is nearer to zero. This may be a physiological parallel to the psychophysical observation that it is easiest to discriminate one relative disparity from another when they lie around zero relative disparity[4,14].

The preceding analysis was applied exclusively to cases where the shape of the tuning curve was unaffected by the surround disparity. Some cells (as in **Fig. 5**) were omitted on this basis (see Methods). In some neurons, the surround disparity strongly influenced firing response, but did not produce relative disparity sensitivity (see cell in **Fig. 5a**). Despite the lack of a relative disparity signal, this neuron does have the properties reported for neurons in MSTl[8]—the surround disparity that produces the greatest activation (–0.6°) is different from the preferred center disparity (0.6°). Thus, modulation of the center response by a change in the disparity of the surround does not guarantee sensitivity for relative disparity.

A change in the shape of the tuning curve can also be associated with a shift in preferred center disparity, indicating a sensitivity to relative disparity (**Fig. 5b**). For both of these tuning curves, the single Gabor + shift model (see Methods) was a poor description of the data (the fits accounted for < 80% of the disparity-related variance). An alternative analysis was performed to include these cases. Spline curves (smooth polynomials constrained to pass through each data point) were fit independently to each tuning curve, and the peak was taken as a measure of the preferred disparity. This method has the advantage that it is completely model free (allowing more neurons to be included), but it does not permit cell-by-cell testing for the statistical significance of shifts. For cells to which both measures could be applied, the two estimates of the peak shift were well correlated ($r = 0.84$, $n = 75$). The distribution of shift ratios was similar for both measures (**Fig. 6**). Both distributions show a clear bias towards positive values ($P < 0.01$, Wilcoxon test), indicating a sensitivity to relative disparity. This is distinctively different from the results of similar experiments in V1 (ref. 6; replotted in **Fig. 6a**).

Nevertheless, many V2 neurons showed shift ratios near zero: for 43 out of 75 comparisons (from 51 cells), there was no significant shift in preferred absolute disparity ($P \geq 0.01$). These V2 neurons seemed to respond to the absolute disparity of the center, as V1 neurons do. The remaining 32 cases showed a significant shift in the preferred absolute disparity ($P < 0.01$). Almost all of these shifts (29 of 32) are positive, which is the correct direction for relative disparity sensitivity. Moreover, several shift ratios are near 1.0; these responses are dominated by the relative disparity between center and surround.

Discussion

We examined the representation of relative disparity in area V2 of awake monkeys. Unlike neurons in V1, a proportion of V2 neurons were sensitive to the relative disparity between different regions of a random-dot stereogram. For these cells, a change in the disparity of one region elicited a change in the preferred disparity of the other. In a few cases, this corresponded to an accurate encoding of relative disparity, which is the sort of representation that could directly support judgments of relative binocular depth. Other neurons showed responses intermediate between absolute and relative disparity selectivity. Like those that accurately encode relative disparity, responses of this type show an interdependence between the disparity sensitivities to the two regions of a stereogram. This indicates a sensitivity to relative disparity, even though it

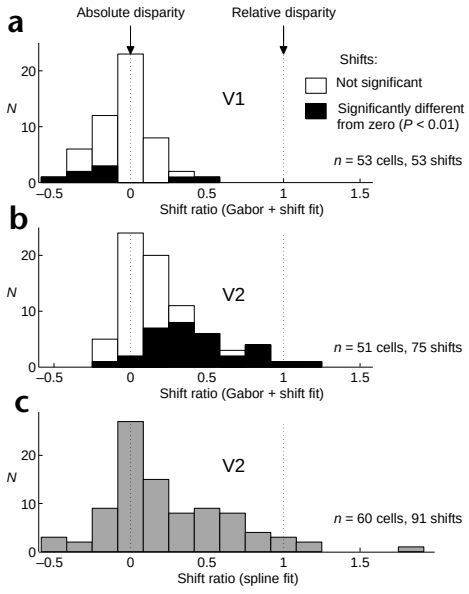


Fig. 6. Summary of shift ratios. Data are compared for V1 (**a**; from ref. 6) and V2 (**b**, **c**). (**a**) Shift ratios are symmetrically arranged around zero, and few shifts are significantly different from zero. The responses of V1 cells are consistent with a pure sensitivity to absolute disparity. (**b**) Results for V2 neurons that showed no change in tuning curve shape (75 shift ratios are shown from 51 neurons). The vast majority (58) are positive shifts, indicating sensitivity to relative disparity. Many shifts (32) are significantly different from zero ($P < 0.01$), and 29 of these are positive. A proportion of cells have shift ratios approaching 1.0, indicating a pure representation of relative disparity. (**c**) Shift ratios of V2 neurons calculated from spline fits. Spline fits include cells even in cases where changes in surround disparity caused changes in tuning curve shape, so there are 91 shift ratios from 60 cells. The results are similar to those seen in (**b**).

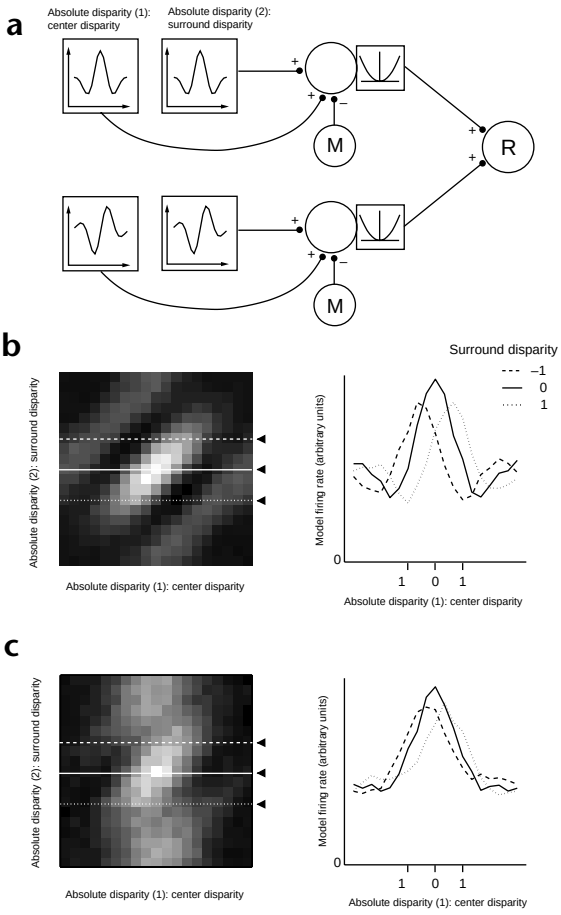


Fig. 7. A simple model of how responses to relative disparity might be generated from inputs that are sensitive only to absolute disparity. (**a**) Model construction is analogous to that of the disparity energy model. Inputs exclusively sensitive to absolute disparity, similar to those found in V1, are summed and squared. This output nonlinearity increases the response when there is an appropriate relative disparity between the center and surround. Such responses are summed (neuron R) to produce a consistent selectivity for relative disparity. One difference between this model and the energy model is that we subtracted the output from monocular filters (M). If this monocular term is not subtracted, the response is more strongly influenced by absolute disparity. (**b**) The responses of this model to all combinations of center and surround disparities. Left, the response strength is shown by grayscale intensity; right, these responses are shown in the same manner as for neuronal results. Responses are a consistent function of relative disparity, irrespective of the absolute disparity. (**c**) The size of the shifts is reduced if the stimulus center impinges upon the model's receptive field surround. Responses shown are those generated when the stimulus center overlapped with two-thirds of the receptive field surround.

does not constitute full selectivity. Both of these forms of interdependent response are a specialization for relative disparity that distinguishes V2 from the striate cortex.

This is the first unambiguous demonstration of neural sensitivity to relative disparity anywhere in the brain. Extrastriate visual areas other than V2 may also signal relative disparity, but this will require further experimental investigation. V1 is the only brain area in which is it clear that there are no relative disparity signals[6]. Much deeper within the visual processing stream, in the inferotemporal (IT) cortex, there are binocular neurons with specific responses to curved binocular depth surfaces[15,16] . The gap between V1 and IT responses might be bridged by V2 units that signal relative disparity.

An apparent sensitivity to relative disparity could be generated by neurons that are truly selective to absolute disparity (similar to those found in V1) if the eyes were to converge systematically at the depth plane of either the center or the surround. In this situation, the absolute and relative disparity covary. Our neuronal data was collected while we simultaneously recorded the position of both eyes, and our measure of relative disparity selectivity takes any vergence eye movements into account. A recent study[11] has examined the responses of V2 neurons to a RDS consisting of two distinct regions, each with a separately manipulated disparity. In two of the five neurons recorded, the preferred disparity for a given region depended on the disparity of the other; this finding is consistent with relative disparity sensitivity and with our results, although the investigators did not adjust neuronal responses for changes in eye position that the animals might have made.

How might the V2 responses reported here be generated from known properties of V1 neurons? To simulate this information processing stage, we constructed a model using computations analogous to the energy model[17–20], where units with similar disparity selectivity but different phases are combined to yield a phase-invariant response. Construction proceeds in two stages. First, we combined pairs of neurons sensitive to absolute disparity (one from the receptive field center, one from the surround) by summing their responses followed by an output non-linearity (half-squaring). Like the analogous stage in the energy model (binocular simple cells), the output nonlinearity is a critical feature: it has the effect that the output is greatest when the two inputs have similar magnitudes, which occurs when there is an appropriate relative disparity between the center and surround. The second stage sums the output from a number of such subunits, each with an identical sensitivity to relative disparity. The responses of this model to combinations of center–surround disparity (**Fig. 7**) are similar to the neuronal responses reported above. This output, analogous to that of the energy model, displays a constant relative disparity selectivity over a range of absolute disparities. There are undoubtedly other ways to model the same result, but it is clear that V2 neurons need only receive input from appropriate V1 neurons to produce selectivity for relative disparity.

Several shift ratios were significantly ($P < 0.01$) different from zero, yet clearly less than 1. Such responses do not correspond to a perfect encoding of either absolute or relative disparity. These responses may reflect an initial stage in the development of relative disparity selectivity. Another possibility arises from the structure of the present model. Although the model is truly tuned to relative disparity, it generates shift ratios smaller than 1 if the spatial layout of the stimulus is not properly matched to the model's receptive field. The shift ratio is reduced when the stimulus center impinges upon the surround of the receptive field (**Fig. 7c**). Thus overestimates of the size of the center region during the experimental protocol would lead to shift ratios smaller than 1. Many cells with shift ratios <1 may have shown shift ratios closer to 1 for other spatial configurations.

Specialized responses to relative disparity are presumably elicited by specific geometrical configurations of the binocular depths of surfaces. Although the present study has explored a limited range of stimulus configurations, it is clear even at this

stage that signals in V2 could directly support binocular depth judgments in a way that signals from V1 cannot. These V2 cells display a stimulus specificity that is more exact than a simple modulation of the neuronal response by stimuli outside the classical receptive field[7,8]. Although it is likely that further relative disparity processing takes place, perhaps in other extrastriate visual areas, the specialization of some V2 neurons suggests that they form part of a pathway specifically responsible for processing binocular stereoscopic depth.

Methods

Ethical review. All procedures were carried out under the auspices of the UK Home Office Project and personal licenses held by the authors and laboratory. The use and care of animals was approved by the UK Home Office.

Unit recording and stimulus presentation. Extracellular single-unit recordings were made in V2 of 2 alert monkeys (*Macacca mulatta*). Scleral search coils were implanted in both eyes under general anesthesia[21], together with a head holder and a recording chamber. Animals were then trained to maintain binocular fixation. Tungsten-in-glass microelectrodes were introduced transdurally each day into the primary visual cortex and advanced through white matter to reach the secondary visual cortex on the posterior bank of the lunate sulcus. Spike waveforms and eye-position traces were recorded to disk using the DataWave Discovery package (DataWave Technologies, Minneapolis, Minnesota). Mean firing rate was used to assess the unit response, summing all spikes that occurred from a time 50 ms after the first video frame of the stimulus was presented until 50 ms after the last video frame was presented. Dynamic random-dot stimuli, with a new dot pattern every 72-Hz video frame, were generated on a Silicon Graphics (Mountain View, California) workstation, and displayed on two EIZO Flexscan monitors (Ishikawa, Japan) through a haploscope. The dot width was usually 0.20 degrees, the dot density was 25% and the stimulus duration was 2 s. The dots were generated such that half were black and half were white, presented on a mid-gray background. The stereogram consisted of a surround annulus and a circular central region; the absolute disparity of both regions was varied from trial to trial, in a pseudo-random sequence. Before RDS testing, we presented flashing black and white bars at the neuron's preferred orientation (the method of minimum response fields[22]) to determine the receptive field (RF). We marked minimum response field boundaries where the bars, when moved slowly into the RF, first reliably elicited a response. The borders were used to ensure that the central region of the stereogram completely covered the minimum response field at all disparities[6]. The strength of the surround inhibition elicited by bars and gratings was not measured.

Analysis. A total of 165 neurons were recorded from 2 animals: 111 from monkey Hg and 54 from monkey Rb. We carried out a one-way analysis of variance on each of the disparity tuning functions (at different surround disparities) constructed for each cell, and neurons were included if at least 2 functions showed a significant effect of disparity ($P < 0.05$). Sixty-eight cells satisfied this criterion, of which 62 yielded sufficient data (a minimum of 4 repetitions at each of 7 appropriate disparities for each surround condition) to perform the following analysis. For each neuron, the mean firing rate as a function of disparity was fitted to a Gabor function:

$$f(d) = A\exp(-(d-D)^2/2\sigma^2)\cos(2\pi\omega(d-D)+\phi)+B$$

by nonlinear regression, where A, ω and ϕ are the amplitude, spatial frequency and phase, respectively, of the cosine component; σ is the standard deviation of the Gaussian; D is a position offset; and B is the baseline firing rate.

To quantify shifts in the tuning function, we performed a pair-wise comparison of the results for different surround disparities. Two data sets were fit simultaneously. Although the fitting procedure allowed all parameters to vary, they were (except D) also constrained to be the same for the 2 curves. The shift (S) between these 2 curves was taken to be $D_1 - D_2$, where D_n is the value of D for a single curve. The statistical significance of the shift was assessed by comparing this fit with a fit to all the data with a single Gabor. The residual variances around these 2 fits were compared with a sequential F-test[23] to determine whether the shift term produced a significant improvement. The shift ratio is:

$$(S-V)/(B-V)$$

where B is the change in the surround disparity between the 2 conditions and V is the mean change in vergence computed across all center disparities. Note that as the change in vergence approaches the change in surround disparity, $(B–V)$ approaches zero and it becomes impossible to distinguish relative disparity and absolute disparity. Larger shift ratios are not associated with larger changes in vergence angle (rank correlation, $r = –0.07$, $P = 0.88$).

We excluded 10 cells (of 62) for which the Gabor + shift model accounted for less than 80% of the total variance (these cells showed a change in the shape of the tuning curve as a function of surround disparity). Changes in amplitude (such as those shown in **Fig. 5**) are poorly fit because A is not allowed to vary with the surround disparity. If the data is fit with Gabors where all the parameters can vary with the surround disparity, then these account for a very high proportion of variance (median 0.97). We also excluded 1 unit because a large vergence change occurred in response to the surround disparity (exceeding one-third of the difference between surround disparities). The remaining 51 neurons (24 from monkey Rb, 27 from monkey Hg) were subjected to a quantitative comparison of absolute and relative disparity encoding.

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Competing interests statement

The authors declare that they have no competing financial interests.

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