

Binocular depth perception and the cerebral cortex

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Abstract | Our ability to coordinate the use of our left and right eyes and to make use of subtle differences between the images received by each eye allows us to perceive stereoscopic depth, which is important for the visual perception of three-dimensional space. Binocular neurons in the visual cortex combine signals from the left and right eyes. Probing the roles of binocular neurons in different perceptual tasks has advanced our understanding of the stages within the visual cortex that lead to binocular depth perception.

Tuning function

A set of measurements that summarize the selectivity of a sensory neuron for some particular aspect of the stimulus, such as orientation, visual motion or binocular disparity.

Disparity selectivity

The selectivity of a visual neuron for binocular disparity, usually summarized in the form of a tuning function.

Magnocellular pathway

Distinct pathway from retina to cortex that has synaptic relays in the lateral geniculate nucleus, which arrive in layers that consist of large cell bodies. Magnocellular neurons do not transmit colour information and have fast responses.

Binocular depth perception is one of the most demanding visual tasks that we carry out. The horizontal separation of the eyes in the head means that each eye obtains an image of the world from a slightly different viewpoint. The differences between these images, called binocular disparities, present significant challenges that the brain's visual system must overcome in order to make use of them. Binocular vision must be highly accurate: the CNS needs to be able to register a difference between the two eyes that is smaller than the width of a single cone photoreceptor. To extract these fine differences, individual features in the left eye's image must be matched with the correct partner features in the right eye. This kind of problem is faced by the brain in many other circumstances. For example, object recognition requires that sensory input be matched against what is in the memory. Understanding how the binocular system tackles its particular computational problems may therefore lead to insights that are relevant in other contexts.

Much recent progress has been made towards identifying the cortical neurons that carry signals specifically related to binocular depth perception¹. Early in the visual pathways of the macaque monkey it is common for neurons to respond more strongly to some binocular disparities than to others²⁻⁵: the neuron's selectivity can be described by a tuning function for disparity. The responses of these neurons are dominated by the content of the physical stimulus, so that firing primarily signals the presence of the preferred binocular disparity. Further along the pathway, the responses of neurons reflect characteristic features of the way in which depth is perceived.

After briefly reviewing disparity selectivity, I move on to consider criteria for whether a neuron is involved in binocular depth perception. Next, I consider evidence

about the involvement of specific groups of neurons in perceptual judgements. I discuss the hypothesis that distinct processes in binocular vision may be associated with the classically defined dorsal and ventral visual processing streams. Finally, I describe clinical conditions arising from abnormal development of the binocular visual system and consider the implications of the recent findings regarding stereoscopic vision for understanding these conditions.

Similarities across visual areas

Almost all regions of the visual cortex contain neurons that respond to binocular disparity; however, studies have failed to identify a cortical site pre-eminently dedicated to binocular depth perception. Nevertheless, various suggestions about specializations within the visual cortex have been made.

The magnocellular and parvocellular pathways are thought to associate with the dorsal and ventral cortical visual pathways respectively. Magnocellular neurons in the lateral geniculate nucleus (LGN) and neurons in dorsal cortical areas respond better to fast-moving stimuli, whereas parvocellular neurons in the LGN and neurons in ventral areas are thought to be more responsive to colour. However, there is clear contradictory evidence: for example, magnocellular and parvocellular LGN neurons converge in the primary visual cortex and some parvocellular neurons project into dorsal visual areas⁶⁻¹¹.

One hypothesis is that stereopsis is a unique attribute of the magnocellular and dorsal processing stream¹². However, there are equally strong advocates of a crucial role for the parvocellular and ventral system^{13,14}. Yet another view is that the dorsal pathway takes care of coarse stereopsis, whereas the ventral pathway deals with fine stereopsis^{13,14}. Several single-unit recording studies that

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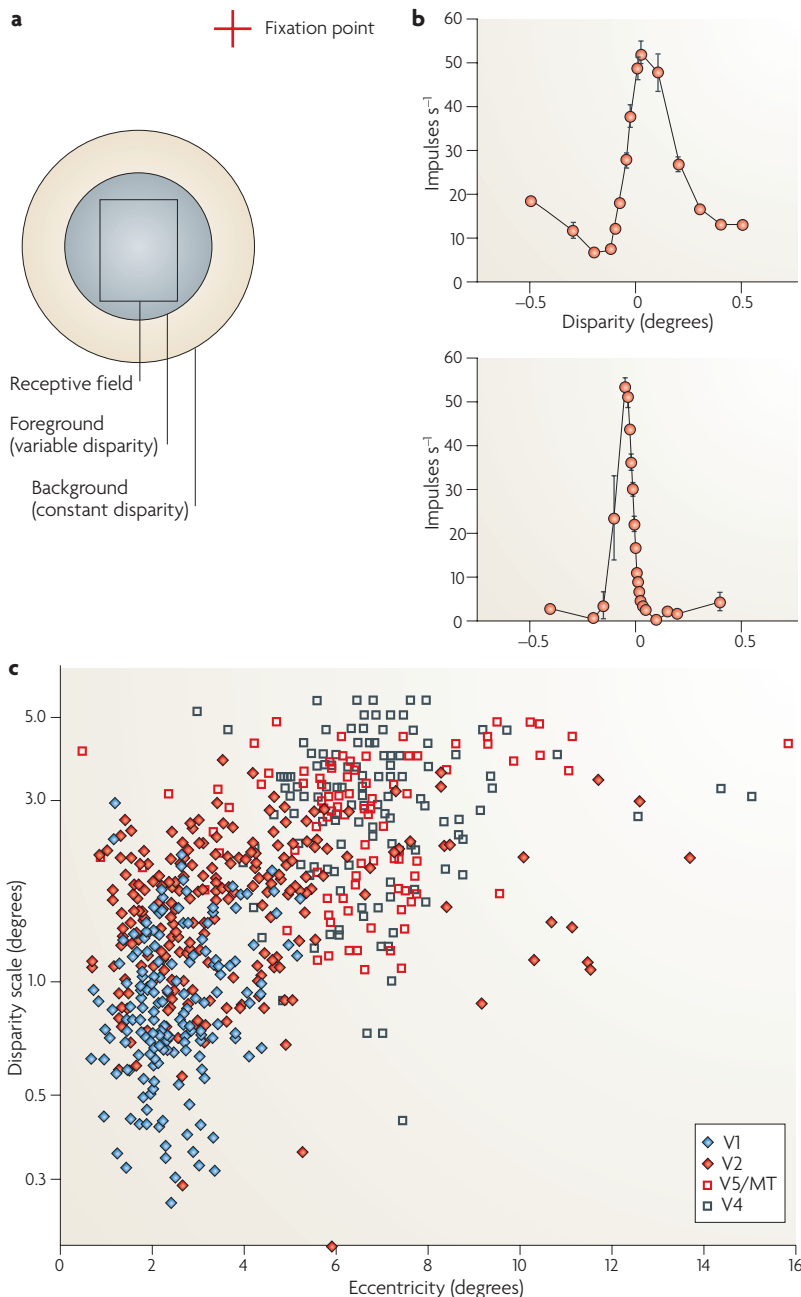


Figure 1 | Recording from binocular neurons. Binocular neurons in the visual cortex receive inputs from the left and right eyes. The way in which these inputs are combined can be probed with random-dot figures (BOX 2), which give rise to a perception of depth. **a** | A monkey can be trained to fix its gaze on a target, while random-dot patterns showing different binocular depths are presented over the receptive field of a visual neuron. **b** | The activation of the neurons depends on the binocular depth in the random-dot figure: the examples here are from the primary visual cortex and plot firing rate against binocular disparity. Each tuning curve can be described by a Gabor function (mathematically, the product of a Gaussian function and a sine wave). The frequency of the sine wave has been established as a suitable descriptor of the tuning function (data from two different V1 neurons are shown)^{15,115}. **c** | Plot of the reciprocal of this frequency, called here 'disparity scale', on the abscissa against the visual eccentricity of the receptive field. Data are shown from four visual cortical areas: V1 (REFS 15, 115), V2 (O. M. Thomas, B. G. Cumming and A.J.P., unpublished observations), V4 (REF. 16) and V5/MT¹⁸. There is no obvious difference in the disparity range that is processed in the ventral visual area V4 in comparison with the dorsal visual area V5/MT. Cortical areas V1 and V2 contribute to both the dorsal and ventral streams, so their disparity range provides a baseline for comparison. Modified, with permission, from REF. 1 © (2001) Annual Reviews.

address this question have now been carried out in the macaque monkey^{1,15–18}. Each study used closely similar methodology to measure and analyse the disparity selectivity of the neurons.

FIGURE 1 plots results from the primary visual cortical area (V1 or striate cortex) and three extrastriate cortical areas: the secondary visual area V2, the ventral extrastriate area V4 and the dorsal extrastriate area (V5 or middle temporal area, MT). There was no obvious relationship between the range of disparity sensitivity and the location of a neuron in the dorsal or ventral streams. One interesting feature is the indication that individual neurons of cortical area V2 show a more extended range of disparity processing than neurons in V1. One issue is that the neurons from the four cortical regions examined do not have receptive fields that cover the same range of visual eccentricities.

It is also thought that signals about binocular depth may travel via specific compartments of V1 and V2. These compartments are marked by histological features^{2,13,19,20}, primarily based on staining for a mitochondrial enzyme, cytochrome oxidase. However, the illustrated data in these articles did not provide suitable histological results to enable the identification of specific compartments of visual areas.

The simplest hypothesis consistent with the data is that the disparity range of all these cortical sites derives from binocular interactions that are set up in V1. This is also consistent with a human functional MRI (fMRI) study that examined several dorsal visual areas²¹: there was no evidence for a generally coarser representation of depth in the dorsal visual areas.

It is tempting to declare that we should simply pursue more vigorously the goal of seeking sites in the cortex that uniquely represent binocular depth. For example, V3A has been offered as a candidate²². However, an understanding of the cortical processing of binocular depth must respect some general principles about the goals of neuroscience. A valid specification of the function of a brain region does not simply rest on describing the information that it holds. We also need to understand from where and in what format the region receives information, and to where and for the support of which tasks it sends information. No sensory signal would be of any practical value if it remained locked within a single cortical site, without any means of affecting behaviour. Thus, the goal of seeking a label to characterize the function of a particular brain region inevitably diverts attention from the bigger picture.

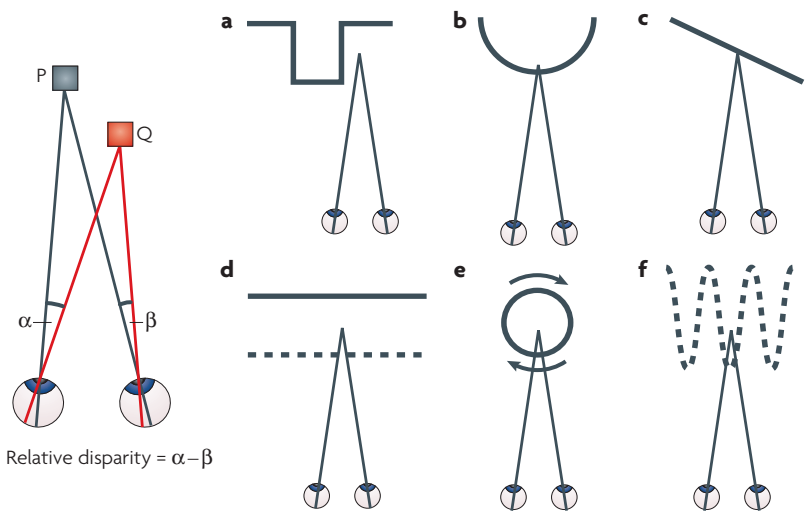
Neuronal correlates of depth perception

The data described above provide little insight into some of the important perceptual phenomena arising from stereoscopic vision. Here I review three examples, the study of which has led to a marked revision of our views on the organization of binocular stereopsis in the early visual pathways.

Absolute and relative disparity. When the eyes are looking towards a pair of visible points at different distances from the observer, the absolute disparity of one of these points

Box 1 | **Absolute and relative disparity**

There are two types of signal for the stereo disparity systems in the brain: absolute and relative disparity. Suppose that both eyes are looking at a particular location in space (P, left panel): the image of P falls on the fovea of each eye. When a visual feature (Q) is at a different depth, the image of Q falls at different positions on the left and right retinæ with respect to the foveae. To look at Q directly, the eyes have to rotate by different angles. This difference of angles is called the absolute disparity of Q.



Relative disparity is another way of measuring the relationship between P and Q.

$$\text{Relative disparity} = \alpha - \beta$$

Regardless of where the eyes

are pointing, the angular separation of P and Q as seen by the left eye (α) is bigger than the separation seen by the right eye (β). The difference in angular separations ($\alpha - \beta$) is called the relative disparity between P and Q. Relative disparity requires two simultaneously visible features to define it. The relative disparity between two visual targets is a sensitive way of measuring the spatial relationship between them in three-dimensional space.

There are multiple possibilities for choosing two visible features for creating sensitivity to relative disparity. The right panels show the depth profiles of some stimuli that all have the same relative disparity. All have been used to probe the response of single neurons or functional MRI signals to relative disparity. Ventral visual areas appear to be more specialized for the processing of three-dimensional shape (a,b), whereas the dorsal areas are more specialized for the processing of extended surfaces (c) and their segregation into depth planes (d, transparent depth planes; e, rotating transparent cylinders). Panel f shows a sinusoidal variation of depth as a function of spatial position.

Parvocellular pathway

Distinct pathway from retina to cortex that has synaptic relays in the lateral geniculate nucleus, which arrive in layers that consist of small cell bodies. Parvocellular neurons carry information about colour and fine spatial detail, and have slower responses.

Stereopsis

The sense of depth that is generated when the brain combines information from the left and right eyes.

Coarse stereopsis

Binocular depth perception outside the range for stereoscopic acuity, processing disparities greater than 0.3 degrees in the human fovea.

Fine stereopsis

Binocular depth perception responsible for stereoscopic acuity and normally taken as processing disparities within the range of 0.3 degrees in the human fovea. This range is larger at greater visual eccentricities.

Single-unit recording

An experimental method of studying the nervous system in which the electrical impulses from single nerve cells are measured and analysed.

Visual eccentricity

The location of an object in visual space with respect to the line of sight from the eye, usually measured in degrees of angle between the line of sight and a line projecting from the eye to the object. It also refers to the location of a visual receptive field projected out into visual space.

Fovea

The most central region of the retina, which contains a high concentration of cone photoreceptors and forms a slight depression in the retinal surface. It projects into visual space to a region about 5 degrees across, equivalent to an object 8.7cm in diameter viewed from 1m away.

may be defined as the angular difference in the projections of that point onto the left and right eyes with reference to each eye's fovea. The relative disparity between two points is the difference between their absolute disparities. Taking this difference eliminates the fovea as a reference point and the relative disparity can also be calculated as the difference between the angle subtended by the pair of visible points at the left eye and the angle between those points at the right eye (BOX 1), a formulation that avoids reference to any retinal landmark.

If neurons are tuned for absolute disparity, they detect disparity in terms of a coordinate system organized around retinal landmarks: the coordinate frame for measuring disparity moves with the eyes²³. These neurons are well suited for providing the sensory component of a control loop that directs convergence eye movements²⁴. However, it has become clear that the human stereoscopic system relies more on relative disparity when assessing the perceived depth of objects²⁵. Strikingly, there are conditions under which human observers are essentially blind to large changes in absolute disparity²⁶⁻²⁹. Under these conditions, not only does the stereoscopic depth perception system retain exquisite sensitivity to relative disparity, but the unseen changes in absolute disparity can drive convergence eye movements^{27,28,30}.

Several research groups have explored monkey cortical visual areas with microelectrodes to search for single neurons that encode relative disparity. V1 neurons

show no sensitivity to relative disparity (TABLE 1) when probed using a visual stimulus with a centre-surround configuration in which the centre has one absolute disparity and the surround has another²³ (presenting a relative disparity between the centre and the surround). At least some V2 neurons show consistent tuning for relative disparity across a range of absolute disparities³¹ if the centre covers the receptive field of the neuron and the surround is beyond it. Some V2 neurons are also sensitive to the presence of a step-change in disparity within their receptive field³². This may indicate an alternative form of selectivity for relative disparity, or these receptive fields may have the capacity to segregate one region from another^{19,33,34} on the basis that each region contains a different absolute disparity³². Overall, this evidence indicates that there is a significant transformation of information between V1 and V2. The importance of V2 is emphasized by an early study showing that lesions of V2 are as detrimental as lesions of V1 in binocular tasks involving judging the relative depth of two vertical lines³⁵. Deep in the ventral stream in areas of the inferotemporal cortex, signals about relative disparity are more complex. Here there are neurons that are specifically sensitive to the three-dimensional shape of curved objects defined stereoscopically³⁶.

fMRI in humans and macaques has also been used to search for responses to relative depth^{22,37}, using stimuli that should favour either a response to absolute disparity or to relative disparity²². A stimulus that was

Extrastriate cortex

A belt of visually responsive areas of cortex surrounding the primary visual cortex.

Random-dot stereograms

A pair of images, one for each eye, composed of picture elements that are randomly either black or white. When combined, stereopsis reveals a previously hidden figure, which the brain detects by matching up the picture elements presented independently to each eye.

Correlation detection

A measurement that provides a simple summary of the similarity between two sets of data. In this context, the two data sets are the neural signals arising from small patches of retina at closely similar locations in the left and right eyes.

Saccadic eye movement

The transfer of gaze from one location to another by rapid, coordinated movement of the eyes.

Simple cell

Neuron of the primary visual cortex, the visual receptive field of which is orientation selective and can be divided into spatially distinct regions that are mutually antagonistic and in which light either enhances or suppresses action potentials from the neuron.

Complex cell

Neuron of the primary visual cortex, the visual receptive field of which is orientation selective but, unlike simple cells, cannot be divided into spatially distinct regions.

arguably richer in relative disparity information produced stronger activation in areas V3, V3A and the caudal intraparietal region in the macaque and V3A, V7, V4D-topo and the caudal parietal disparity region in humans²². A potentially more sensitive approach is a habituation paradigm, in which the blood-oxygen-level-dependent response to relative disparity is measured under two different conditions³⁷. In one block, neurons sensitive to relative disparity are adapted by repeated presentation of the same relative disparity, which causes their response to decline; during the comparison block they are exposed to a wide range of different relative disparities and the cortical response is expected to decline less steeply. The same strategy was used to assess the cortical response to absolute disparity. Although the study³⁷ did not succeed in fully separating the influence of relative and absolute disparity, the outcome was that dorsal visual areas responded primarily to absolute disparity whereas ventral visual areas exhibited roughly equal sensitivity to absolute and relative disparity.

At first sight, it may seem straightforward to pursue these results at the level of single neurons, searching further into the rest of the extrastriate cortex, looking for higher concentrations of neurons selective for relative disparity³⁸. Indeed, it has been suggested that relative and absolute disparity might be a key parameter separating the dorsal and ventral pathways³⁷. However, further consideration suggests that there is a richer and more complex relationship between dorsal and ventral pathways. A key issue is that relative disparity is not a simple attribute of a single stimulus (BOX 1). Experimenters have used stimuli with widely different spatial configurations that all present numerically the same relative disparity. Further complexities arise in the case of the fMRI adaptation study³⁷, in which there was no single measure of the relative disparity between all the visible features in the stimulus. The apparent sensitivity of a cortical region or a single neuron to relative disparity may therefore depend on how these relative disparities are spatially disposed within the stimulus.

Recent studies in V5/MT highlight these issues. Some V5/MT neurons show sensitivity to relative disparity, when the cue presented is a single plane that is tilted with respect to the observer and has a relative disparity between the nearer and further edges of the plane³⁹. However, in the same region, neurons show no sensitivity to relative disparity when a centre-surround configuration is used⁴⁰. Furthermore, V5/MT neurons are highly sensitive to the introduction of a relative disparity in a rotating transparent cylinder stimulus^{41–44}, again suggesting a fundamental responsiveness to relative disparity, as the same disparity introduced as an absolute disparity would probably be below threshold⁴⁵. This complex story shows that the spatial layout for presentation of relative disparities is vitally important. It also demonstrates that it is impossible to apply a label such as ‘relative disparity’ to a particular brain region without being more specific about the kind of relative disparity referred to. Finally, even if the use of such labels were justifiable, the label is only a placeholder until a better understanding of the function of this brain region is achieved.

Binocular anticorrelation. Binocularly anticorrelated stimuli present visual features of opposite contrast sign to the left and right eyes (BOX 2): each bright feature in one eye is paired with a dark feature in the other eye. These patterns are a valuable tool in dissecting different stages in the binocular visual pathways. The perceptual effect of anticorrelation is dramatic. In random-dot stereograms, the appearance of stereoscopic depth is destroyed when the patterns are anticorrelated^{46–50}, with the result that a centre region cannot be visually segregated from its surround.

Many binocular neurons in the visual pathways respond selectively to anticorrelated stimuli by showing an inverted tuning curve for binocular disparity^{51–53}. Disparities that produce the strongest excitation with correlated stimuli produce the weakest response with anticorrelated stimuli and vice versa (FIG. 2a). This is evidence that the fundamental computation carried out by these binocular neurons is a form of correlation detection (BOX 2). There is evidence too that correlation detection is an important computation in human vision: an early stage of disparity detection, which shows an inverted response under anticorrelation, can be revealed psychophysically⁵⁴. There are also certain conditions in which human observers report perceptually reversed depth with anticorrelated figures. However, this requires the anticorrelated figure to be situated against a binocularly correlated background^{46,55,56}, so this stimulus differs from that used in the neurophysiological studies⁵¹.

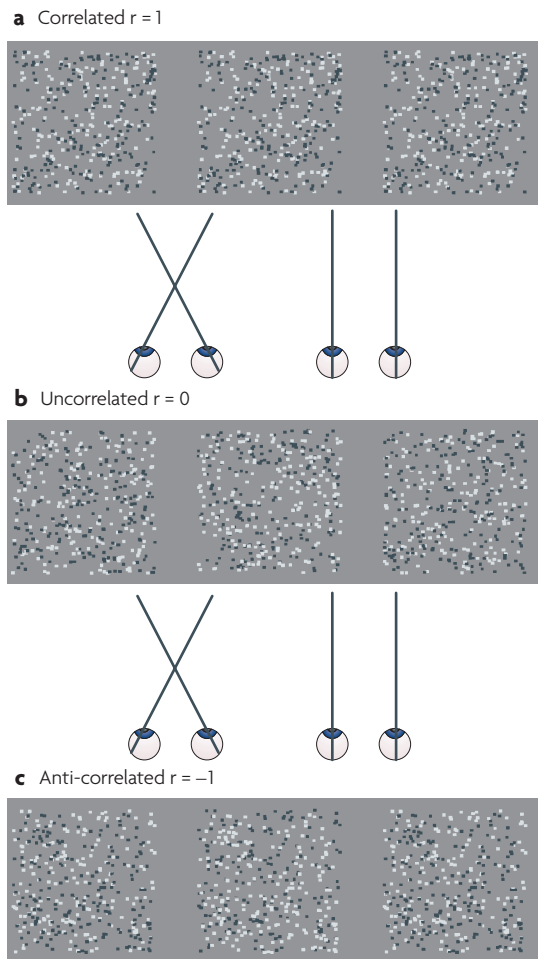
Certain types of eye movement also show an inverted response to binocular disparity when the stimulus is anticorrelated^{52,57} (FIG. 2b). During a saccadic eye movement, if the new fixation point for the eyes is surrounded by a field of random dots, the binocular disparity of which changes just as the eyes land on the fixation point, there is a brief, involuntary change of binocular alignment. If the disparity change moves visual features towards the observer’s head, then the corrective eye movement makes the eyes converge. If the disparity change moves visual features away from the observer’s head, then the eyes diverge. When an anticorrelated stimulus is used, the opposite pattern of corrective vergence adjustments is found.

The mechanism for generating the inverted responses to binocular anticorrelation has been modelled for V1 neurons as a linear summation of the signals arriving from the left and right eyes followed by a nonlinear output (BOX 3). The linear summation takes place in several subunits: the receptive field of each subunit is organized like that of a simple cell. The spatial receptive fields of some subunits have an even-symmetric structure, whereas other subunits have an odd-symmetric structure. The outputs of these subunits are squared and pooled to give a prediction of the activity of a disparity-selective binocular complex cell^{51,58}. This model is incomplete but has a number of features that can explain the responses of V1 neurons to binocular anticorrelation. For example, the inverted tuning curve follows from the initial linear summation of inputs from the left and right eyes.

Box 2 | **Binocular anticorrelation: what does it mean?**

A device that receives two inputs and measures how well these inputs match one another can be modelled as a detector of correlation between the two inputs. The correlation coefficient indicates the quality of the match by means of a number that varies from 1 (a perfect match) through 0 (no relationship between inputs, such as two independent random variables) to -1 (completely opposite signals in the two inputs). If you have stereoscopic vision, you can arrange for one image to be presented to your left and another to your right eye by diverging or converging your eyes. This will allow you to see the effect of binocular correlation and anticorrelation. The icons of eye position in the figure illustrate how to use the images for fusion with convergence (left and middle dot patterns) or divergence (middle and right dot patterns).

A random-dot stereogram is made up of dots assigned as bright or dark according to a sequence of binary random numbers. If the dot patterns presented to the left and right eyes are based on the same, identical sequence of random numbers, then the correlation between the left and right eyes is $+1$: a circle defined by a depth difference should be seen (a). If the dot patterns are based on independent sequences of random numbers, then the correlation between left and right eyes is 0 on average and the stereogram is binocularly uncorrelated: no circle is defined (b). If the dot patterns are based on the same, identical sequence but for every bright dot in the left eye there is a dark dot in the right eye, and for every dark dot in the left eye there is a bright dot in the right eye, then the correlation between the left and right eyes is -1 and the stereogram is anticorrelated: a circle is present in principle, but is invisible (c). Anticorrelation of random-dot stereograms prevents the perception of stereoscopic depth^{47,49,50}. In the neurophysiological and perceptual studies, the dots forming the stereogram were dynamically updated, but the stimuli are otherwise similar to those shown here. Note that the two outer random-dot fields in panel c (anticorrelated) are each intended for binocular comparison with the middle random-dot field. Inadvertent fusion of the two outermost random-dot fields here will lead to the presentation of a binocularly correlated random-dot figure as in panel a.



However, other aspects of the neuronal responses require amendment of the model⁵⁹. First, in most neurons, the size of the inverted response to binocular anticorrelation is smaller than the response to binocularly correlated stimuli. Second, the disparity-tuning curves for correlated and anticorrelated responses are not always related by a simple inversion. Third, the response of some neurons to binocularly correlated patterns is predominantly a suppression of their firing, below the response level generated by visual stimulation of one eye alone, at some values of binocular disparity. These tuned-inhibitory neurons often have enhanced firing when the same disparities are presented with binocular anticorrelation. These observations mean that a simple change in the output nonlinearity of the binocular energy model cannot account for the response to binocularly anticorrelated stimuli. One model that can successfully account for the range of observed responses to binocular anticorrelation includes an intermediate nonlinear stage prior to binocular combination, equivalent to a monocular

simple cell with linear summation followed by a static threshold nonlinearity^{59,60}.

The response to binocular anticorrelation has been summarized by comparing the amplitude of variation in firing rate as a function of disparity for correlated and anticorrelated random-dot stereograms (FIG. 2; TABLE 1). In V1, the reduced amplitude of the anticorrelated response means that the average value of this ratio is 0.52 (REF. 51). Of course, this means that the V1 neurons are firing substantially in response to stereograms with anticorrelated centre and surround regions. One might expect that individuals would respond to this consistent disparity signal by reporting the perception of stereoscopic depth. As this is not the case, it seems that activation of V1 alone is insufficient for the perception of stereo depth, suggesting that other cortical sites may be better candidates for a direct association with stereo depth perception. At those sites, the response to anticorrelated stereograms should be eliminated (or greatly reduced below that of V1). Data are available from several extrastriate cortical sites (FIG. 3; TABLE 1). Responses to binocular anticorrelation

Energy model

A computational model of visual neuronal processing that consists of a quadrature pair of linear filters followed by the nonlinear operation of squaring and combination across those filters.

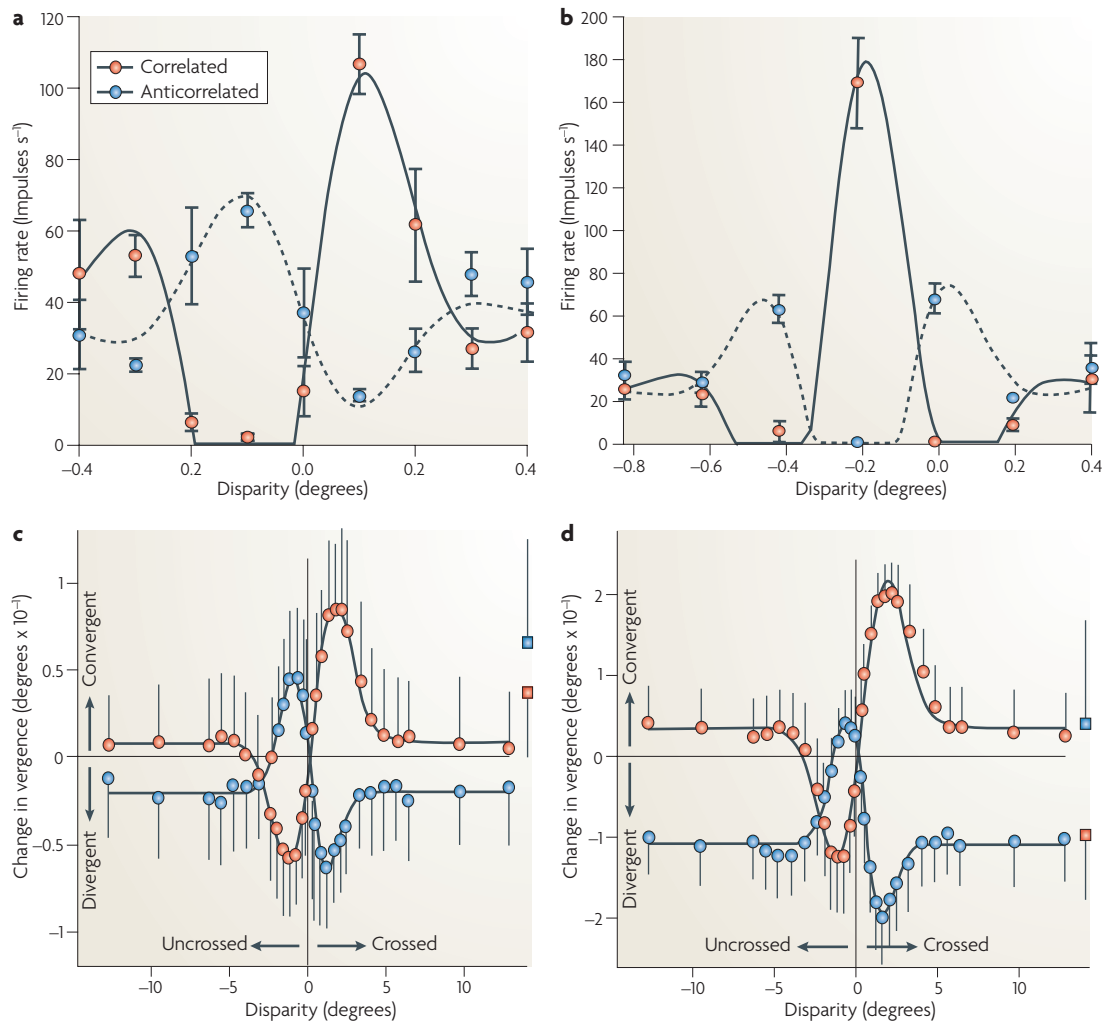


Figure 2 | Responses to binocular anticorrelation. The graphs show responses to binocularly anticorrelated random-dot stereograms, revealing inverted responses to binocular disparity (BOX 2). Responses of visual cortical neurons from the monkey V1 (REF. 51), odd symmetric (a) and even symmetric (b). Rapid corrective vergence eye-movements⁵⁷ in humans (c) and monkeys (d). A comparison of humans and monkeys shows that their eye movements are similar. An inversion of the tuning curve when comparing binocular correlation against anticorrelation indicates that the underlying computation is similar to a region-based cross-correlator. Reproduced, with permission, from *Nature* REFS 51,57 © (1997) Macmillan Publishers Ltd.

in V2 are similar to those in V1 (REF. 61), although it has not been possible to determine whether neurons with different responses to anticorrelation have different locations in the architecture of thick and thin stripes^{19,20}. In the dorsal stream, the responses of V5/MT and the medial superior temporal area (MST) to binocular anticorrelation are essentially as strong as V1 (REFS 52,53,55). However, in the ventral stream, area V4 shows a modest reduction to 0.39 in the response to anticorrelated stimuli¹⁷, and area TE in the inferior temporal cortex shows essentially a complete abolition of the response to anticorrelation⁶².

The last result points to a crucial role for the ventral stream in explaining the different perceptual responses to correlated and anticorrelated stereograms. By contrast, the responses of the dorsal stream seem better placed to explain the responses of the eye movement system. Indeed, the pooled responses of a population of

MST neurons provide a sufficient explanation for the amplitude and disparity tuning of the rapid corrective vergence movements⁵², and some MST neurons appear to carry signals related to the motor components of vergence⁶³. At first this seems to reflect a simple division of perception and action⁶⁴. However, as will be described later, there is also evidence for a role for the dorsal pathways in perceptual judgements.

Ambiguity in stereo matching. When looking at a simple picture consisting of a set of 2 or more vertically spaced bars, human individuals report that they see the expected number of bars, all in the depth plane of the picture^{47,65}. Superficially, this is simple. There are a number of bars, each having the same zero disparity as the binocular fixation point. The bars correctly appear to be in the picture plane. However, since each eye receives an image of identical bars, the binocular visual system

Box 3 | How neurons may compute relative disparity

A mechanism selective for relative disparity must have different responses to a particular depth, depending upon the context in which that depth is presented. This property can be described by the original energy model for absolute disparity⁵⁸ or visual motion¹¹⁴. The economy of this proposal is attractive. Exactly the same cortical circuitry that performs useful computation of absolute disparity at the first level can be reused at a second level to extract relative disparity.

The essence of the energy model is that if we have a single quantity L that depends linearly on two variables (x and y) then the energy model computes $H = [L(x + y)]^2$, with the result that H is sensitive to the interaction between x and y , since: $H = [L(x) + L(y)]^2 = L^2(x) + 2L(x)y + L^2(y)$

The important interaction between x and y is given by the term $2L(x)y$. The quantities represented by x and y are completely open. For the motion energy model¹¹⁴ they are spatial position and time. In the original disparity energy model⁵⁸ they are horizontal image coordinates in the left and right eyes. This disparity energy model measures absolute, not relative, disparity. To calculate relative disparity, we need the interaction between two detectors of absolute disparity. Thus, applying an energy model once more to the outputs of two detectors of absolute disparity uses the same type of neural wiring to generate the novel property of relative disparity³¹.

The multiplicative interaction between x and y gives relative disparity, a constant difference between two absolute disparities. The interactions provided by the energy model provide for a consistent selectivity to relative disparity over a range of different absolute disparities. Sensitivity to the interaction of x and y is optimized by taking the outputs of pairs of neurons sensitive to absolute disparity: one pair has even-symmetric tuning functions for absolute disparity, the other pair has odd-symmetric functions. Taking pairs of functions with even and odd symmetry means that all possible spatial distributions of the disparities within the visual scene are efficiently detected. The pairs of functions do not need to have pure even and odd symmetry, if they form a quadrature pair.

Even-symmetric function

A mathematical function for which $F(-x) = F(x)$, where $x > 0$.

Odd-symmetric function

A mathematical function for which $F(-x) = -F(x)$, where $x > 0$.

Quadrature pair

Pair of functions which have an identical Fourier amplitude spectrum in the frequency domain, but have a Fourier phase spectrum that differs by 90 degrees at all frequencies.

must sort out which bar as seen by the left eye belongs with which bar as seen by the right eye. A brain region that responds whenever there is a match between the bars will generate so-called 'false matches'⁴⁷. In addition to the fact that this does not occur, the false matches also have the interesting property that their disparity with respect to the binocular fixation point is such that if they were seen, they would signal a different binocular depth in front of or behind the picture plane.

This generates an important test of the kind of binocular processing that occurs at a particular cortical site⁶⁵. In V1, neurons fire just as strongly for false binocular matches as for genuine ones⁶⁶. Given the evidence so far, one would expect that this outcome would be different in extrastriate visual areas. Indeed, in V2, a number of neurons show stronger firing for correct visual matches^{61,67}.

Different computations, different streams

The discussion of the contributions of the dorsal and ventral streams to the processing of binocular depth has rejected the idea that stereoscopic depth is processed in just the dorsal stream or that there is a simple division of coarse stereopsis in the dorsal stream and fine stereopsis in the ventral stream. Some commentators have pursued this argument to its extreme and rejected any specializations for binocular depth within these streams⁶⁸. However, recent evidence points to a new hypothesis: the two streams carry out fundamentally different types of stereo computation. This reflects the specialization of each stream for certain visual tasks, with the result that

each stream makes a distinctive contribution to processing binocular depth information (FIG. 3; TABLE 1).

The dorsal stream appears to make a simple computation of stereo depth, largely relying on a direct computation of the binocular correlation between the left and right eyes' images⁵². The presence of an inverted, disparity-tuned response to binocular anticorrelation is evidence that the fundamental computation is a correlator, or something similar⁵³. In the dorsal stream, relative disparity is processed, but this is only manifest in the processing of spatially extended surfaces, contributing to indicating the gradient of extended surfaces and the segregation in depth of one surface from another^{69,70}. This suggests that binocular depth in the dorsal stream helps the individual to orient in the visual world and to navigate.

A typical pattern of fixation behaviour in a moving human individual is to maintain gaze on a point in the visual world whilst walking forwards. When the trajectory of movement is not along the line of sight, the eye must rotate to maintain the point on the fovea. This brings about an orderly relationship between the pattern of optic flow on the retina and the binocular depth of the objects with respect to the fixation point. Objects further than the fixation point move with the observer's own motion, whereas objects nearer than fixation point do the opposite. Some neurons in the dorsomedial portion of area MST are selective for a link between optic flow on the retina and binocular depth, in that these neurons change their direction preference according to the binocular depth of the stimulus^{70,71}.

By contrast, according to this hypothesis, in the ventral stream, the computation carried out by the nervous system is more sophisticated. The ventral stream is also sensitive to relative disparity. However, there appears to be a full resolution of the binocular matching problem⁶², and the neurons in this stream appear to be specifically sensitive to the relative depth between different features located at nearby positions in the visual world^{38,72}. Thus, the dorsal and ventral streams require different spatial configurations of the stimulus to reveal their distinctive forms of sensitivity to relative disparity. Further down the ventral stream, in the inferotemporal cortex, neurons acquire sensitivity to the shape and curvature of three-dimensional surfaces^{36,73}, consistent with a role in analysing the three-dimensional shape of objects. Signals from stereoscopic depth must be integrated with other signals (motion, texture, shading, perspective) about three-dimensional objects^{74–76}, but more work is needed before we understand this process at the physiological level.

The firing rates of most neurons in the dorsal and ventral streams are influenced by both relative and absolute disparity. This raises a concern that no-one has so far discovered a cortical site with a pure response to relative disparity. The firing of all neurons recorded is influenced by absolute disparity or viewing distance as well, so these neuronal responses are at best only partially correlated with relative disparity. The literature on gaze control shows that responses that are only partially correlated with shifts of gaze angle are a suitable basis for an

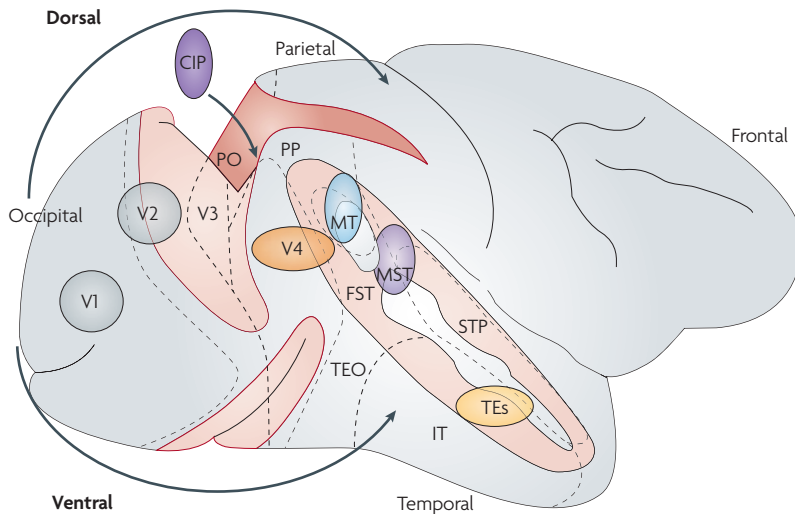


Figure 3 | Stereo vision in dorsal and ventral pathways. The dorsal and ventral visual pathways make different contributions to the analysis and perception of stereoscopic depth. Two experimental paradigms shown in TABLE 1 have been pursued in a number of cortical areas in such a way that comparisons can be made across these areas. The figure shows a diagrammatic picture of the macaque monkey cortical areas, in which the main flow of visual information through the dorsal and ventral visual pathways is identified by arrows. The cortical areas that have been investigated are listed in TABLE 1. The ventral visual areas are highlighted with horizontal ellipses of red/orange tints, and the dorsal visual areas are highlighted with vertical ellipses of blue/purple tints. The early visual areas V1 and V2 are highlighted with neutral grey circles. CIP, caudal intraparietal area; FST, fundal superior temporal area; IT, inferior temporal cortex; MST, medial superior temporal area; MT, medial temporal area; PO, parieto-occipital area; PP, posterior parietal cortex; STP, superior temporal polysensory area; TE_s, a collection of areas in the anterior inferior temporal cortex. Modified, with permission, from REF. 116 © (1999) Elsevier Science.

evidence that derives from the recording of neuronal properties. However, following permanent lesions, the nervous system may rearrange itself so that the lesion's effect is not evident at the behavioural level. Here I discuss two alternative techniques that link the activity of neurons with perceptual judgements about stereo depth. This evidence also highlights the role of single neurons and their connections, rather than the importance of brain regions that is emphasized in most classic lesion studies.

The first approach is fundamentally correlative, but highlights the contribution made by the responses of single neurons to individual perceptual decisions: the monkey makes perceptual judgements that depend on stereo disparities (such as a near–far discrimination task) while neuronal activity is recorded. Suppose we have a neuron that responds to near disparities in the stimulus. If this neuron also shows enhanced firing when the monkey makes a perceptual choice in favour of ‘near’ rather than ‘far’ perceived depth at the same value of stimulus disparity, this suggests that the neuron contributes to the perceptual judgement^{80–82}. These relationships have been quantified as choice probability — the extent to which observation of the neuronal response during the task would enable the prediction of the behavioural response. The second approach is even more compelling: the experimenter interferes directly with the neuron's activation, either by making a small, localized injection that reversibly inactivates neurons in a few millimetres of cortex or by artificially stimulating the neurons, typically with electrical microstimulation^{83,84}. The latter is one of the few ways of intervening in a causal yet positive way in neural function⁸². If neurons that prefer near disparities are stimulated, then the animal tends to produce more judgements in favour of near depth, even when it is not rewarded to do so^{40,84}.

The first experiment that used one of these paradigms to make a link between stereo depth perception and localized neuronal activation used a stereo task with large binocular disparities (a ‘coarse’ stereo task). Electrical microstimulation in area V5/MT⁸⁴ demonstrated that near and far disparity columns of that cortical area contribute to the formation of the perceptual decision about

effective visuomotor control signal^{77–79}, so this approach may be implemented by the nervous system in the case of relative disparity and three-dimensional shape.

Neuronal signals for perceiving depth

A long-established method for demonstrating a role for cortical areas in perceptual functions has been the use of lesions. Lesions can establish a mandatory role for a brain region in a behavioural function, as opposed to the correlative

Table 1 | **Summary of the involvement of visual cortical areas in binocular depth perception**

Cortical area	Anticorrelated response	Relative disparity
<i>Early visual areas</i>		
V1	Yes ⁵¹	None ²³
V2	Similar to V1 (REF. 61)	Centre–surround ³¹
<i>Ventral areas</i>		
V4	Weaker than V1 (REF. 17)	More than V2, centre–surround ³⁸
TE _s	None ⁶²	Sensitive to surface curvature ⁷³
<i>Dorsal areas</i>		
V5/MT	Similar to V1 (REF. 53)	Surface slant and depth separation ^{39,41,42}
MST	Similar to V1 (REF. 52)	Surface separation in depth ^{69–71}
CIP	Not determined	Surface slant ⁷⁴

CIP, caudal intraparietal area; MST, medial superior temporal area; MT, medial temporal area; TE_s, a collection of areas in the anterior inferior temporal cortex.

Near–far discrimination task
Visual task that requires the individual to judge whether a visual feature (such as a cluster of dots) is nearer or further than the distance to the visual fixation point.

depth (FIG. 4). Later work confirms these observations, but also shows that the same, targeted microstimulation of V5/MT is ineffective when the animal's task requires a fine-scale, relative depth judgement⁴⁰. The same discrepancy is thrown up when neurons in V5/MT are examined for the presence of choice probabilities in these two tasks⁸¹. It has been argued that this observation supports the idea that the dorsal stream carries only information about absolute disparity. However, the coarse task provides both a binocular fixation point and a large background field of dots with zero binocular disparity, against both of which the relative disparities of all other features can be measured. These relative disparities are

large, but they are nonetheless present in the stimulus, so that the perceptual judgement might rely on either absolute or relative disparities.

Experiments discussed earlier have revealed sensitivity to relative disparity in V5/MT in circumstances where relative disparities are used to gain information about the slant³⁹ or segregation-in-depth of extended surfaces^{41–43}. There are individual neurons in V5/MT that are highly sensitive to fine disparity differences in the rotating cylinder paradigm that show firing related to perceptual choice^{42–44,53}, and electrical microstimulation within clusters of these neurons is effective in shifting perceptual choice⁸⁵.

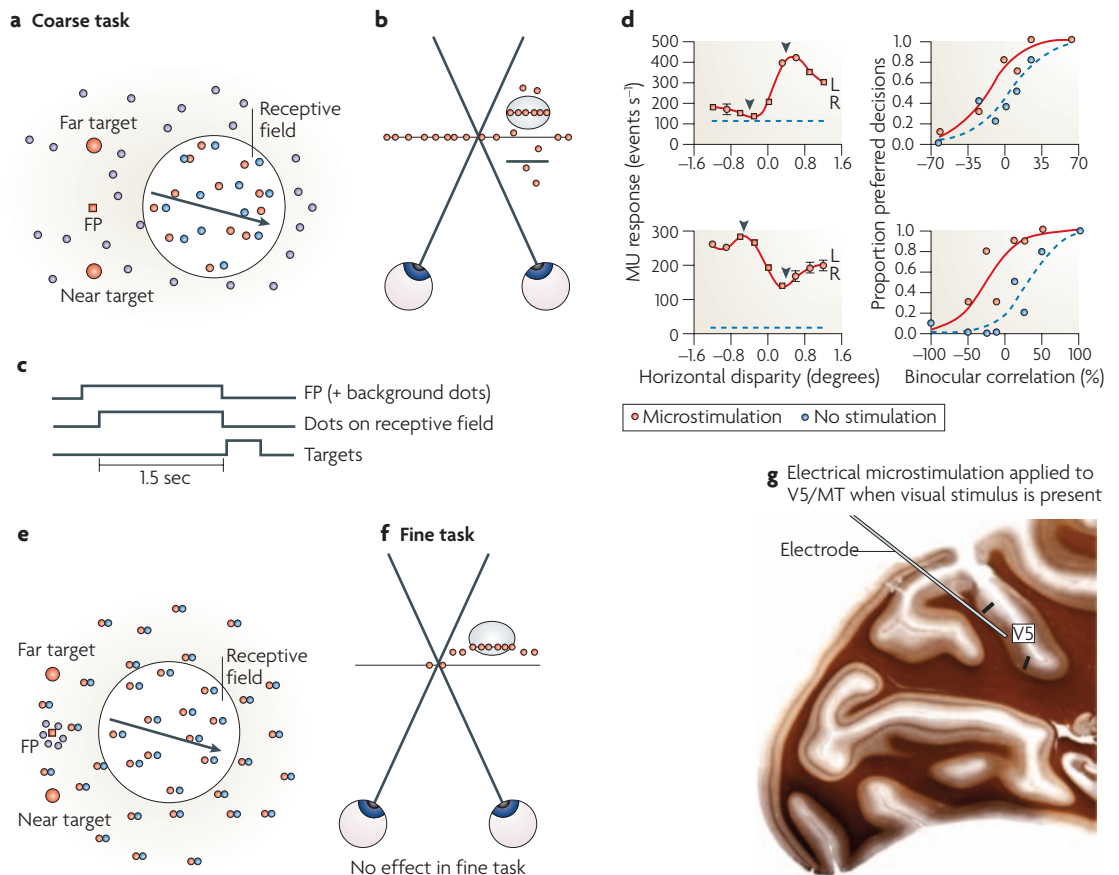


Figure 4 | Intervening in judgements about binocular depth. Electrical microstimulation probes the contribution of small groups of functionally specified, cortical neurons to perceptual tasks. **a,b** | A coarse stereoscopic depth task: the monkey looks at a screen (**a**) with a few binocularly correlated dots and judges whether they are nearer or farther than the binocular fixation target (**b**). The receptive field (large circle in **a** and grey ellipsis in **b**) also receives dots of randomly different disparities. The movement of all dots matches the direction and speed preferences of the neurons. The proportion of dots at near or far disparity controls the task difficulty. **c** | The fixation point (FP) switches on, after which the dots appear as soon as the animal is reliably fixating. At the end of the trial, the fixation point disappears and the animal chooses the upper or lower choice target, indicating a 'far' or 'near' judgement respectively. **d** | The pooled activity of a number of neurons near the electrode (multi-unit activity, MU) is shown as a function of binocular disparity (left, top and bottom). On half the trials only, a weak electrical microstimulation is applied via an electrode tip in cortical area V5/medial temporal area (MT) (right, top and bottom). The effect of electrical microstimulation in the coarse stereo task is to shift the perceptual judgements in favour of the disparities preferred by the neurons at the electrode site. **e,f** | In the same cortical area V5/MT, a fine depth discrimination, whether a central region of binocular dots is in front of or behind a background plane of dots, has also been studied. When the task requires discrimination of fine depth differences between the central region and its surround, electrical microstimulation is ineffective. **g** | Positioning of the microelectrode in cortical area V5/MT. Panels **a–c,e,f** reproduced, with permission, from REF. 40 © (2006) Society for Neuroscience. Panel **d** reproduced, with permission, from *Nature* REF. 84 © (1998) Macmillan Publishers Ltd.

Evidence from other cortical areas is patchy. Using rotating random-dot cylinders, it was found that V1 neurons do not show choice-related firing⁸⁶, although no attempt was made to adjust the cylinder stimuli to match V1 receptive fields in order to favour the detection of their contribution. A more systematic analysis has been undertaken with the coarse stereo task⁸⁴. Even when factors such as receptive field size and tuning preferences were carefully analysed, firing of V2 neurons provided significant prediction of choice, but this was not so for V1 neurons⁸⁰. This highlights again the transformation in the processing of stereo information between V1 and V2. It would be helpful to know whether the neurons in V2 that provide significant choice probabilities in this task are also the neurons that respond to the relative depth between surfaces^{31,32}.

Beyond early cortical areas, in the ventral stream, neurons in the inferotemporal region show choice-related responses during a fine-scale, stereoacuity task⁷². One issue is that this study used stereo figures, for which the shape is clearly visible to one eye alone. Most studies discussed here used random-dot stereo figures, in which hidden contours are revealed only after binocular combination. The following point may therefore become relevant: some neurons in the ventral visual pathway have a different selectivity for stereo depth, depending on whether the neuron is tested with a solid figure, visible to each eye separately, or a random-dot stereo figure^{16,87}.

In the dorsal stream, focal temporary inactivation in the caudal intraparietal area may result in defects in slant judgements, but the effect is not entirely reliable, for unknown reasons⁷⁴.

These results add weight to the hypothesis advanced earlier. The earliest stages of binocular processing in V1 are remote from cortical stages involved in the formation of perceptual decisions about stereoscopic depth. The dorsal stream appears to concentrate on the processing of extended surfaces and the generation of control signals for eye and hand movements. The ventral stream is more concerned with the three-dimensional shape of objects, building this representation out of sensitivity to the relative depth between adjacent visual features. A significant gap in our current knowledge is to find out what stereo cues are used by the parietal regions to support their role in the generation of reaching and grasping movements^{68,88}. Moreover, the possible role of binocular depth in more recently characterized cortical structures — such as dorsomedial areas V6 and V6A^{89–92} — also remains largely unknown.

Amblyopia and awareness

Binocular vision presents a challenge for developmental mechanisms, which may go wrong, resulting in the clinical conditions of squint and amblyopia⁹³. Human amblyopia is normally defined as a significant reduction in visual acuity that cannot be improved by corrective lenses and has no obvious retinal disease-related cause. About 2–2.5% of the adult population worldwide are affected. There is a strong association with disordered binocular function, either because the two eyes are not properly aligned (strabismus) or because one eye has

experienced a loss of pattern vision at some point, perhaps because its image was strongly out of focus with respect to the other eye (anisometropia).

Experimental models of this condition have been developed by inducing squint surgically in experimental animals or by rearing animals with periods of reduced pattern vision in one eye. The general conclusions from these studies have substantially vindicated early views⁹⁴ that disruption of inputs from one eye affects the coordination of binocular connections within V1, with consequent losses of stereoscopic depth sensitivity and more widespread disruption of pattern vision. The animal studies point to a crucial period in neural development⁹⁵, beyond which it becomes almost impossible to intervene correctively.

Most current explanations of the normal and abnormal development of binocular vision refer to changes within V1 (REF. 94). However, now that we understand that there are important processing stages for stereoscopic depth perception in both the striate and the extrastriate visual cortex, it is clear that there must be multiple levels at which the system needs to adapt during development. This opens up the possibility that some aspects of human amblyopia may reflect disruptions of neural connections deeper in the visual pathways beyond V1 (REFS 96,97), a view that agrees with other evidence. For example, some forms of amblyopia arise much later than the critical period for human binocular development⁹⁸. In addition, adults with amblyopia demonstrate performance losses that can only be explained on the basis that their higher-level vision beyond V1 is also disrupted^{96,99}. Furthermore, the behavioural consequences of disrupted vision in the animal studies are more profound than the losses in performance assessed at the physiological level in V1 (REF. 97).

Some recent results go further and suggest that dysfunctional cortical connections may emerge even when the afferents projecting into V1 show signs of normal functioning¹⁰⁰. In an experimental model of strabismus, brief periods of surgically induced esotropia were capable of inducing defects of stereopsis with no evident defect of convergent eye movements¹⁰¹. On the hypothesis advanced in this article, the representation of absolute disparity in V1 may be sufficiently unscathed by this experience to provide the basic signal required to drive vergence movements, whereas the connections between V1 and cortical sites where relative disparity is computed may have been disrupted because these depend on a later stage of visual development.

The capacity for rearrangement and perceptual learning in adulthood has been studied in various ways⁹⁶. Intensive training in adulthood can, in some cases, alleviate the dysfunction of amblyopia^{102–104}. The consequences of disrupted binocular function may not be limited to the generation of the clinically defined syndrome of amblyopia. In developmental dyslexia too, there are at least some individuals who have disruption of binocular function^{105–107}. Interventions that alter binocular function, such as covering one eye, improve reading performance¹⁰⁶, as can interventions that apparently have no relationship with binocular function, such as wearing coloured spectacle

Squint

A human clinical condition, manifest when a person tries to look at a target with both eyes, but the line of sight of one eye consistently deviates from the target while the other eye is successfully aligned.

Amblyopia

Poor vision through an eye that is otherwise physically healthy, but has faulty connections with the rest of the brain; there is disrupted transmission of the visual image, most often due to adverse events during a developmental critical period. It affects 2–5% of the global population.

Esotropia

Form of squint in which the deviating eye turns inwards, towards the nose (in exotropia the eye turns outwards, away from the nose).

lenses. One interpretation of this result is that these children have dorsal visual pathways that are binocularly defective but are nonetheless engaged when they try to read¹⁰⁸. Use of coloured lenses may provide a bias against the engagement of these defective dorsal cortical areas, in favour of processing through another cortical route, thereby improving reading performance.

The conditions discussed here are problems of conscious vision. It has been argued that the human ventral visual pathways are uniquely associated with conscious visual perception. This view assigns a role for action to the dorsal visual pathways and perception to the ventral visual pathways⁶⁴. Although it is clear that many elements of the argument advanced in this review are consistent with the idea that the ventral visual pathways are responsible for object recognition, there is little reason to extend this to all aspects of conscious vision. Transcranial magnetic stimulation of cortical area V5 in the human cortex leads to consciously perceived events¹⁰⁹, despite the fact that this area is in the dorsal stream. Damage to parietal areas as well as brain imaging studies indicate an important role for these regions of the cortex in some aspects of conscious awareness^{110–112}.

Concluding remarks

Recent progress has transformed our knowledge of the pathways for binocular vision in the cerebral cortex. The generation of a full, stereoscopic depth percept is a multi-stage process that involves both dorsal and ventral cortical pathways. Dorsal and ventral pathways are adapted to perform different visual tasks and it is proposed here that they consequently perform different types of stereo computation. According to this hypothesis, dorsal pathways perform something close to a region-based cross-correlation¹¹³ between the cortical representations of the two eyes' images, whereas the ventral pathways appear to solve the multiple matching problem⁴⁷. Both pathways may contribute to perceptual judgements about stereo depth, depending on the task presented to the visual system. Most of our knowledge about the development of stereoscopic vision at the neuronal level has been based on events within the primary visual cortex. An important future task is to understand how developmental events in the extrastriate cortex contribute to the maturation of a fully functional system for the perception of stereoscopic depth.

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Competing interests statement

The author declares no competing financial interests.

FURTHER INFORMATION

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