

Extracting 3D structure from disparity

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The neural mechanisms of stereoscopic 3D shape perception have only recently been investigated. Here we review the two cortical regions in which these mechanisms have been studied so far in macaques: a small subpart of inferotemporal cortex called TEs, and the caudal intraparietal (CIP) region. Neurons in TEs respond selectively to the orientation and curvature in depth of stereoscopic surfaces and this region provides a detailed 3D shape description of surface boundaries and surface content. This description is evoked only by binocular stimuli in which subjects see depth and it does not vary if depth is specified by different cues. Neurons in CIP are a selective for orientation in depth of surfaces and elongated objects, and their responses are also unaffected by changes in depth cues. Thus, stereoscopic 3D shape is processed in both the dorsal, occipito-parietal and the ventral, occipito-temporal streams.

Introduction

Stereoscopic processing serves many behavioral purposes (Box 1), just as motion does [1,2]. The neural mechanisms underlying the extraction of depth from disparity signals have received a great deal of attention (reviewed in Refs [3–6]) since the early work of Bishop, Pettigrew and colleagues [7,8]. However, extraction of 3D shape from disparity signals has only recently been tackled and is the topic of this review. 3D shape is important both for identification of objects (e.g. distinguishing a disc from a ball) and for grasping or manipulating objects [9].

To distinguish 3D shape processing from simple depth processing, it is useful to remember the different orders of depth (Figure 1, Box 2). Zero-order depth corresponds to position in depth of an object and, for stereoscopic processing (Box 1), the position with respect to the fixation point (i.e. far versus near). This corresponds to absolute disparity. Relative disparity (Box 1) reflects position in depth with respect to another object in space. First-order depth refers to a linear gradient of depth (e.g. along a surface tilted in depth). This corresponds to a linear gradient of disparity. Finally, second-order depth indicates curvature in depth, which for stereoscopic processing corresponds to disparity curvature (the second spatial derivative of disparity). Disparity curvature reflects an intrinsic property of the object and is a robust parameter given its constancy for viewing distance [10]. First-order disparity can be either intrinsic or extrinsic to a 3D object. When intrinsic, it is part of the 3D shape description of an object that is

bounded by tilted planes; when extrinsic, it represents the overall orientation of an object in space.

It was long ago shown that monkeys have the ability to perceive the depth of objects using their two eyes (stereopsis) [11]. There is now also good evidence [12] that, very much as humans do, monkeys perceive 3D shape defined by disparity, because they can discriminate very well between convex and concave surfaces (Figure 1c). In addition, in monkeys this ability vanishes with anti-correlated stereograms (in which the luminance contrast of corresponding pixels are reversed in the two eyes; Box 3, Figure 1c), just as it does in humans [13]. Furthermore, Tsutsui *et al.* [14] have shown that monkeys can match planes tilted in depth defined either by disparity or by texture gradients.

Neuronal selectivity for higher-order disparity has so far been documented mainly in two cortical regions: the caudal part of the lateral bank of the intraparietal sulcus (CIP), which has been explored by Sakata, Taira and colleagues, and a small region in the lower bank of the rostral superior temporal sulcus (STS) known as TEs, which has been explored by our group. Hence this review concentrates on these results, which nonetheless enable us to state that higher-order disparities are processed in both dorsal and ventral streams. Because several reviews have been devoted to CIP [15–17], we will start by reviewing the neuronal properties observed in the TEs region and then compare them with those of CIP.

Higher-order disparity selectivity in TEs, part of the inferotemporal complex

The report by Janssen *et al.* [18] (see Box 3 for stimuli used) that a fraction of inferotemporal (IT) neurons were selective for 3D shape defined by disparity was not only the first study to report selectivity for second-order disparity stimuli, but also the first to report disparity selectivity as such in the ventral stream. Indeed, stereoscopic processing was classically associated with the dorsal stream [19,20], although lesion studies had indicated some involvement of the ventral stream [21,22]. Many subsequent studies have confirmed that stereoscopic information is processed in the ventral stream [23–32]. The higher-order selectivity was demonstrated by showing that the selectivity for curved surfaces of opposite sign (convex versus concave) did not depend on the absolute disparity (far versus near). It is noteworthy that the whole range of modulation of second-order disparity selectivity by absolute disparity was observed, from neurons showing higher-order selectivity only for restricted sets of absolute disparity to neurons showing equal higher-order selectivity for all absolute disparities tested. The position (in depth) invariance

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Box 1. Absolute and relative disparities, distance, and behavioral use of stereoscopic processing

Stereopsis or binocular depth perception exploits the fact that our two eyes view the world from slightly different perspectives. Given these different viewpoints, the images of an object on the two retinæ differ, primarily in position [75]. If azimuth is defined as the angular distance on the retina between the image of a point and the fovea in the horizontal direction and elevation of the distance in the vertical direction, then horizontal and vertical disparities of the images of the point are the differences in azimuth and elevation, respectively, between the two eyes [76]. Because the eyes differ in their horizontal position, the information about the position of the point in depth is provided by the horizontal disparities. These disparities, defined for a single point, carry information about the position of that point relative to the fixation point. They are referred to as absolute disparities, in contrast to relative disparities between two points, which are the difference in the absolute disparities of these points [77,78] and do not depend on vergence (i.e. convergence and/or and divergence eye movements, on which absolute disparities do depend). Not surprisingly, humans and monkeys can make much finer depth judgments using relative than using absolute disparities [77,79]. However, absolute disparities are the signal used to control vergence eye movements. The transformation of absolute disparity into distance from the head requires a combination of disparity with information about the accommodation and convergence of the two eyes. This might be achieved by the posterior parietal cortex for the control of reaching and grasping, in ways similar to the coordinate transformation of direction in visual space from eye-centered to head-and-body-centered [80].

Disparities between the two eyes serve additional behavioral purposes, using the information contained in the spatial distributions of disparity. Sudden changes in absolute disparity give rise to discontinuities that, like discontinuities in motion or texture, can be used as a cue for segmentation and extraction of 2D shape [51,24]. Smooth changes in absolute disparity provide information about the 3D shape of objects and the 3D layout of the environment. This environment layout information is, unlike that provided by motion, veridical in the sense that it specifies the sign of curvature. 2D and 3D shape information are important for visual control of prehension, visual recognition and categorization, whereas layout of the environment is crucial for controlling motion and navigation through that environment.

criterion used in the disparity studies is reminiscent of the position invariance of direction selectivity used by Lagae *et al.* [33] to demonstrate higher-order motion selectivity of neurons in the medial superior temporal area.

Subsequent studies [34] indicated that neurons selective for 3D shape defined by disparity (also known as 3D shape from disparity, or 3D SFD) were not scattered throughout IT, but were concentrated in a small region in the rostral part of the lower bank of the STS. This region (Figure 2), called TEs, houses many 3D SFD-selective neurons, in contrast to the convexity of TE (anterior part of IT), where there are relatively few. The two parts of IT also differ in the degree of binocular summation, which is stronger in TEs than in lateral TE [34]. Because the anatomical connectivity of this lower STS region is also different from that of the convexity [35,36], we proposed that TEs is a separate cortical region linked to the intraparietal sulcus (IPS) [34].

More recently, TEs neurons have been endowed with another higher-order property that had been frequently postulated but never observed: lack of response to anti-correlated stereograms (Box 3) [12]. TEs neurons, which are selective for 3D shape depicted by correlated random dot stimuli (RDS), do not respond selectively to anti-

Box 2. Depth orders and orders of disparity

A zero-order depth stimulus (Figure 1) refers to a flat surface orthogonal to the line of sight, the main parameter of which is distance from the observer or depth. First-order depth is present in a flat surface making an angle other than 90° with the line of sight; its parameters are distance and 3D orientation. A simple second-order stimulus is a surface curved in a single direction (vertical direction in Figure 1), which has parameters distance, orientation and curvature. Notice that a higher depth order can be approximated by a small number of steps in lower depth order (Figure 1). The different orders of depth map onto orders of disparity: absolute disparity, disparity gradients and disparity curvatures, respectively. These mappings are relatively simple for small surfaces (<10°) close to the visual axis, for which a zero-order surface corresponds to points that have constant absolute disparity [5]. Hence, we will restrict the discussion to this particular case. We have seen that the relationship between absolute disparity and depth is complex (Box 1); the relationship with distance is simpler for higher orders, although for all of them except the second order, the relationship depends on distance. The two disparity gradients in Figure 1(b) are both halved when doubling the viewing distance. However, because the distance (in visual degrees) between them is also halved, the change in disparity gradient (i.e. the second-order disparity) remains roughly constant, at least for surfaces close to the median plane of the head. This independence of second-order disparity from distance [10] suggests an important role in the extraction of 3D shape, although it has been shown that various tasks used to investigate 3D shape processing depend differently on distance [5].

Whereas disparity gradients require two directions of differentiation (e.g. vertical and horizontal) if they are to be described fully, four disparity curvatures can be defined by differentiating twice in two directions. Of these four possibilities, we have studied only two: those arising from differentiation twice in the vertical direction (corresponding to the surface shown in Figure 1) or twice in the horizontal direction. These two curvature disparities defined in orthogonal directions correspond to principal curvatures in a surface patch. Koenderink [44] has shown that the sign and magnitude of these principal curvatures enable one to define a shape index and curvedness respectively, describing the qualitative (pattern of deviation from a flat surface) and quantitative (degree of deviation from a flat surface) aspects of 3D shapes (figure 268 in Ref. [44]).

correlated RDS, in contrast to V1 neurons [37]. In this respect, anti-correlated RDS are similar to decorrelated RDS, which also evoke no differential response from TEs neurons. Thus, at the level of TEs, the stereo correspondence problem [38] (Box 3) is solved. This need not mean that the problem is not also solved at an earlier level. Recent results suggest that selective responses to anti-correlated RDS are significantly lower than responses to correlated RDS in V4 [28] but not in V2 [39].

Thus, neurons in a small region of the lower bank of STS (TEs) are selective for higher-order disparities (Box 4) and their responses match stereoscopic perception when tested using different types of RDS.

Fine coding of 3D shape from disparity by TEs neurons

In the initial studies of TEs neurons, their selectivity for second-order disparity stimuli was emphasized [18,34]. In fact, TEs houses neurons selective for all three orders of depth signaled by disparity. Figure 3 shows examples of zero-order, first-order and second-order disparity-selective neurons. The defining criterion for a higher-order neuron was a selectivity that did not reverse at any position in depth. This criterion was initially implemented by the requirement that the response to the preferred shape at

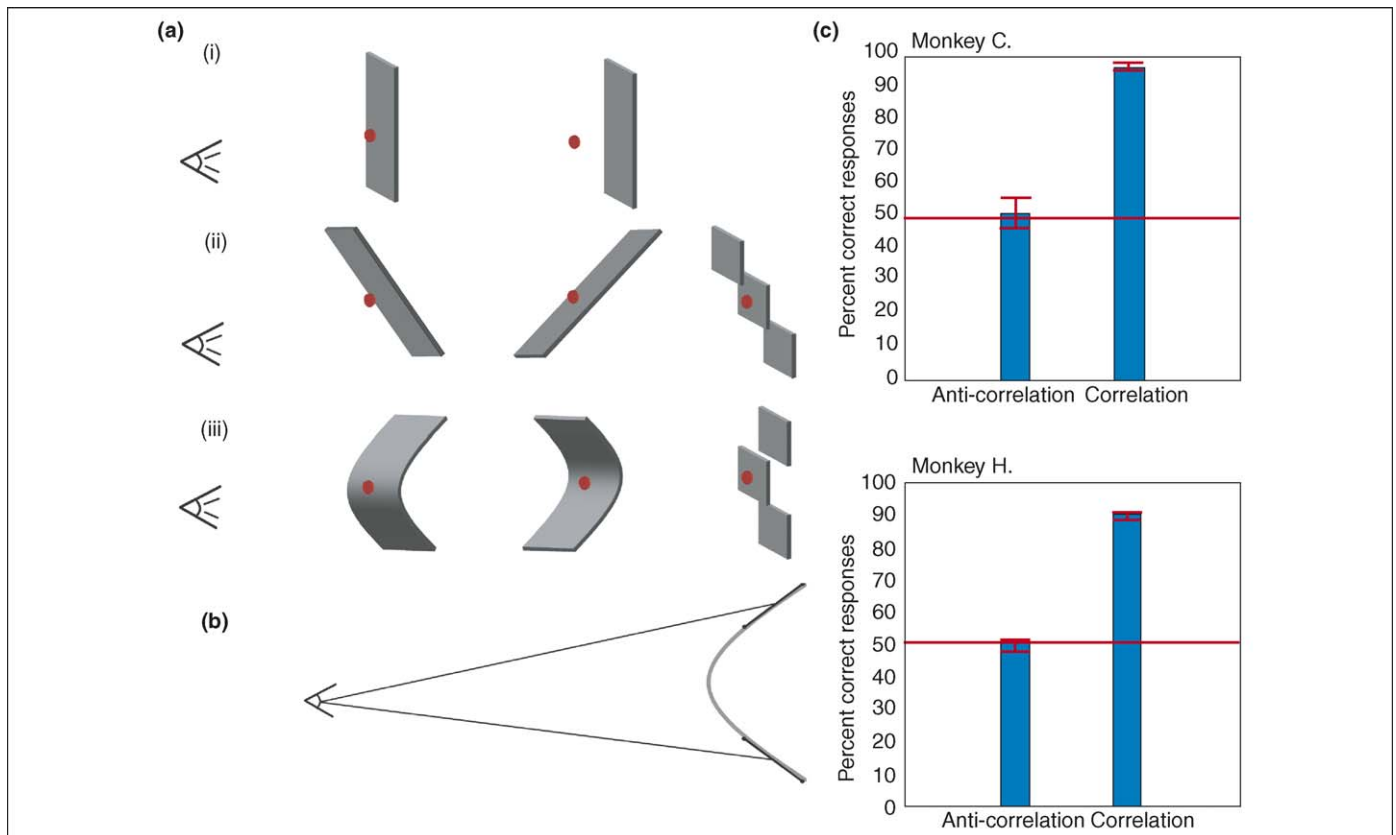


Figure 1. Stimuli and perception. (a) Side views of surfaces at different positions relative to the fixation point (red dot), seen from the left (eye icon) portraying variations in different depth orders: zero order (i), first order (ii) and second order (iii). Approximations of these stimuli using only zero-order depth are indicated in (ii,iii). Notice that in the first-order and second-order disparity stimuli presented on computer screens [40], disparity also changed in discrete steps, but these steps were very small (2 minarc). (b) Viewing of curved surface with an indication of tilted planes (dark lines) giving rise to disparity gradients. (c) Percentage of correct responses by monkeys C and H for distinguishing between convex and concave surfaces in anti-correlated RDS and correlated RDS (Box 3). Reproduced, with permission, from Ref. [12].

its optimal position exceeds the response to the non-preferred shape at any position in depth [18]. Subsequently, this requirement was quantified by an index comparing the best position for the non-preferred shape with the worst position of the preferred shape [40]. The ratio of these responses was not >2 in higher-order neurons and was generally <1.5 . For the cell in Figure 3(a), the ratio was >5 . A simple disparity test with vertical surfaces orthogonal to the line of sight (frontoparallel surfaces) sufficed to confirm that this cell was zero order: the cell was a 'near' neuron [41]. First-order neurons

were invariant in their responses to different positions in depth, and they responded as well to the 3D shapes as to a planar surface tilted in depth (Figure 3b). Liu *et al.* [42] showed these neurons to be tuned to the tilt (3D orientation) in depth. Finally, second-order neurons were invariant for position in depth and responded selectively to 3D shapes but not to first-order stimuli (Figure 3c). In about half of them, the first-order approximation (a wedge) evoked a significantly weaker response than the original curved stimulus (Figure 3c). In the other half, the approximation was as effective as the original stimulus. Note that

Box 3. Stimuli to investigate stereoscopic 3D shape processing

Random dot stereograms (RDS) were introduced by Julesz [81] for study of stereoscopic processing without contamination by depth-edge or figure information because no depth edges are present in the monocular images. Given the well-established selectivity of IT neurons for 2D shape [82], we used a particular type of RDS in which the monocular images contained the outline of a 2D shape [18]. Hence, in our RDS stimuli disparity information is present both on the edges and inside of the 3D shape images. To disentangle the contribution from edges and surface disparities, we used standard RDS without monocular contours and solid figure stereograms (SFS) in which the monocular images were silhouettes (i.e. a 2D shape filled with uniform luminance) [43]. In the experiments of Shikata, E. *et al.*, the SFS could contain texture in the monocular images so that they contained disparity information on both edges and surfaces in the image [54]. These latter stimuli portray real objects, and by manipulating the relative width and thickness of these objects one can distinguish between surfaces (sometimes referred to as plates, in which one dimension is much smaller than the other two) and rods

or elongated objects (in which two dimensions are much smaller than the third).

The correspondence problem refers to that of matching each of the features in one monocular image with those in the other image. For RDS this is a difficult problem, explaining perhaps why it takes time to perceive depth in these stimuli. Experimentally this question has been addressed by comparing responses to correlated and anti-correlated RDS [37], created by inverting the luminance contrast in one of the monocular images, which violates the uniqueness assumption (that the images in the two eyes derive from a single object in a unique position in 3D space) [5].

Because several visual cues provide depth information, the depth orders can be mapped onto orders of cues other than disparity, such as speed or texture gradients for the first order. Cue invariance addresses the issue of whether, for a given order, these cues converge at the single-neuron level. Notice that in single-cell studies invariance does not imply that the response remains constant – it suffices that a basic selectivity such as 2D shape or direction selectivity remains stable [47].

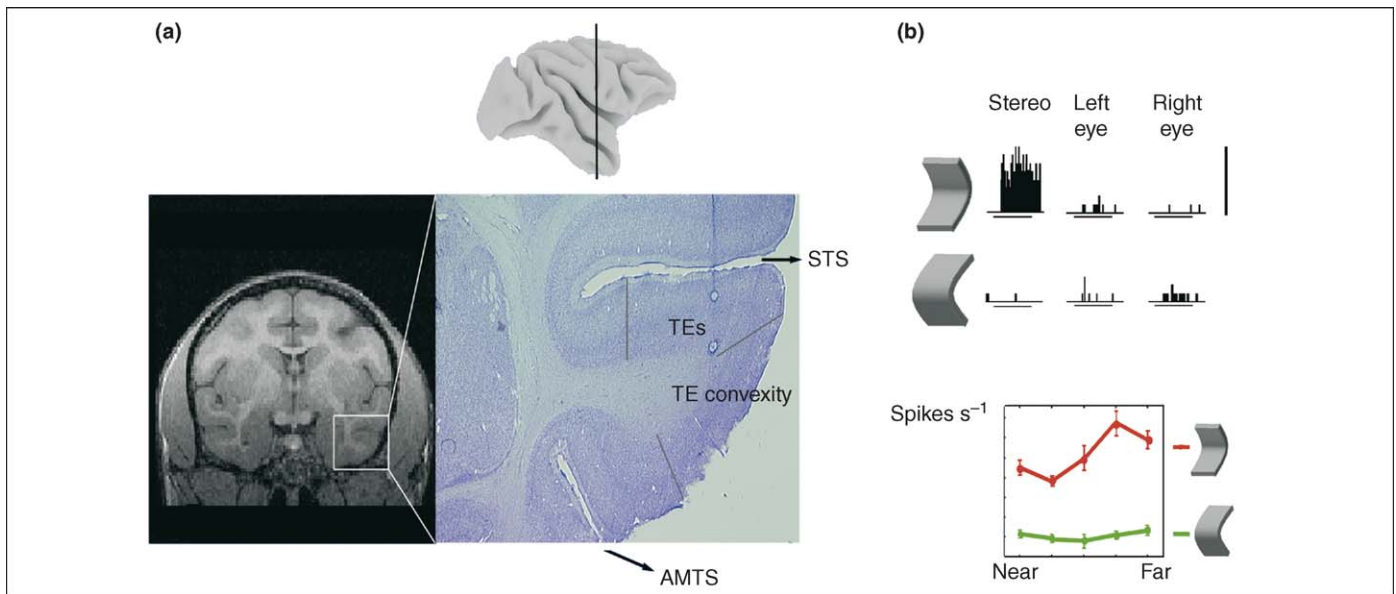


Figure 2. Defining characteristics and localization of higher-order disparity-selective neurons in inferotemporal cortex. **(a)** Localization of recordings on an MRI (coronal section at level indicated) and histological section (monkey H). The approximate locations of TEs and the convexity of TE are indicated, as are the anterior middle temporal sulcus (AMTS) and superior temporal sulcus (STS). **(b)** Peristimulus time histograms (PSTHs) indicating responses to stereo and monocular stimuli, and curves plotting average net responses to curved surfaces as a function of position in depth (1° range). The horizontal lines indicate stimulus duration (300 ms) and the vertical bar indicates 90 spikes per second. Adapted from Ref. [34].

zero-order approximations were effective in only a few higher-order neurons (Figure 3b).

It is worth emphasizing the exquisite sensitivity of TEs neurons for small changes in 3D structure. The difference between curved stimuli and their linear approximation is

only one example. Most neurons remained selective for the sign of curvature down to the smallest amplitude of depth variation (0.03°) tested. In addition, most neurons were sensitive to the amplitude of depth variation in convex or concave stimuli. Their response usually decreased

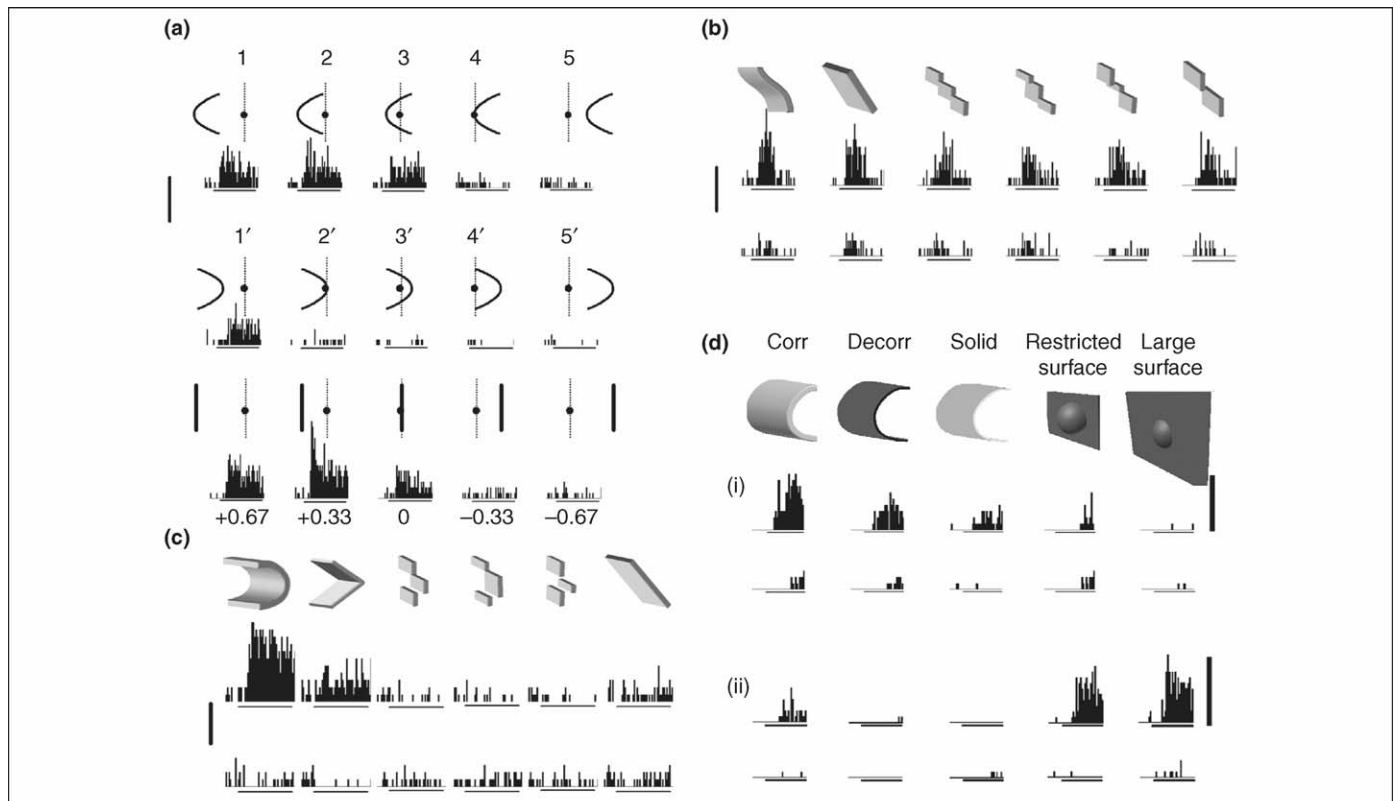


Figure 3. Types of TE neurons. **(a-c)** PSTHs indicating average responses of neurons selective for zero-order **(a)**, first-order **(b)**, and second-order **(c)** stimuli. **(d)** Responses of TE neurons selective for the 3D shape of the edges of surfaces (i) and of texture inside the edges (ii). In **(b-d)** the upper row of PSTHs refers to the preferred curvature and the lower one to the opposite curvature. Abbreviations: Corr, correlated RDS; Decorr, decorrelated RDS. The horizontal lines below the PSTH indicate stimulus duration. In **(a)**, all stimuli are indicated above the corresponding PSTHs; in **(b-d)** only the preferred stimulus polarity is shown. Vertical bars indicate 60 **(a)**, 30 **(b,c)** and 65 **(d)** spikes per second.

Box 4. Methodological issues regarding single-unit studies of higher-order disparity

Stimuli containing first-order or second-order disparities will by necessity vary locally in absolute (zero-order) disparities. Mere selectivity for absolute disparity can be examined by determining whether or not the 3D shape preference remains the same at different positions in depth. When varying absolute disparity, it is essential to measure horizontal vergence eye movements (i.e. convergence and/or divergence) because these can, in principle, reduce the effective range of the manipulated position in depth and thus overestimate the degree of invariance of the responses with position in depth. Preferably, horizontal vergence eye movements are measured using the position of both eyes [40] but, because vergence involves both eyes, these eye movements can in principle be detected by examining the position of one eye only [18] if one assumes that vergence is symmetric in both eyes [83] and that measurements are precise enough [4,84].

The coding of higher-order disparities in ventral visual stream areas has so far been examined by using relatively simple 3D shapes. The use of such a restricted set of 3D shapes limits inferences regarding which regions are involved in higher-order disparity coding. Thus, it cannot be excluded that other parts of IT (e.g. the lateral convexity) show selectivity for more complex, disparity-defined 3D shapes. Not only the use of a restricted stimulus set but also the technique of single-unit recording itself biases the examined neuronal population: it is mainly the relatively large pyramidal cells that produce the stable, well-isolated spikes recorded in single-unit studies. This 'electrode bias' should be taken into consideration when linking single-unit data to those obtained using other techniques (e.g. functional imaging) [85].

monotonically with decreasing amplitude, but in some cases was tuned to a particular amplitude.

Selectivity for curvature of 3D surfaces could reflect selectivity for either the edges of the 3D shape or the texture pattern inside the edges (Box 3). In fact, TE neurons can be selective for both components of the surface stimuli [43]. The neuron in Figure 3(d,i) retains its selectivity in decorrelated RDS and solid stereograms in which only the boundary carries depth information, but loses it when the edges are removed in the doubly curved stimuli. This neuron was thus selective for the 3D shape of the edges. The neuron in Figure 3(d,ii) reacted in exactly the opposite way and was selective for the 3D shape of the texture inside the edges. In the same study, it was shown that TE neurons encode the orientation of the 3D curvature, can probably combine selectivity for orthogonally oriented curvatures, and might code a quantity related to the shape index of Koenderink [44] (Box 2).

Thus, TE neurons are selective for all orders of disparity (at least up to second order) and are selective for different aspects of 3D shape, and this selectivity can be carried by both edges and surfaces.

Invariance of 3D shape selectivity in TEs

The 3D shape selectivity was found to be invariant for changes in frontoparallel position and in size [40], as has been observed for 2D shape selectivity [4550]. The

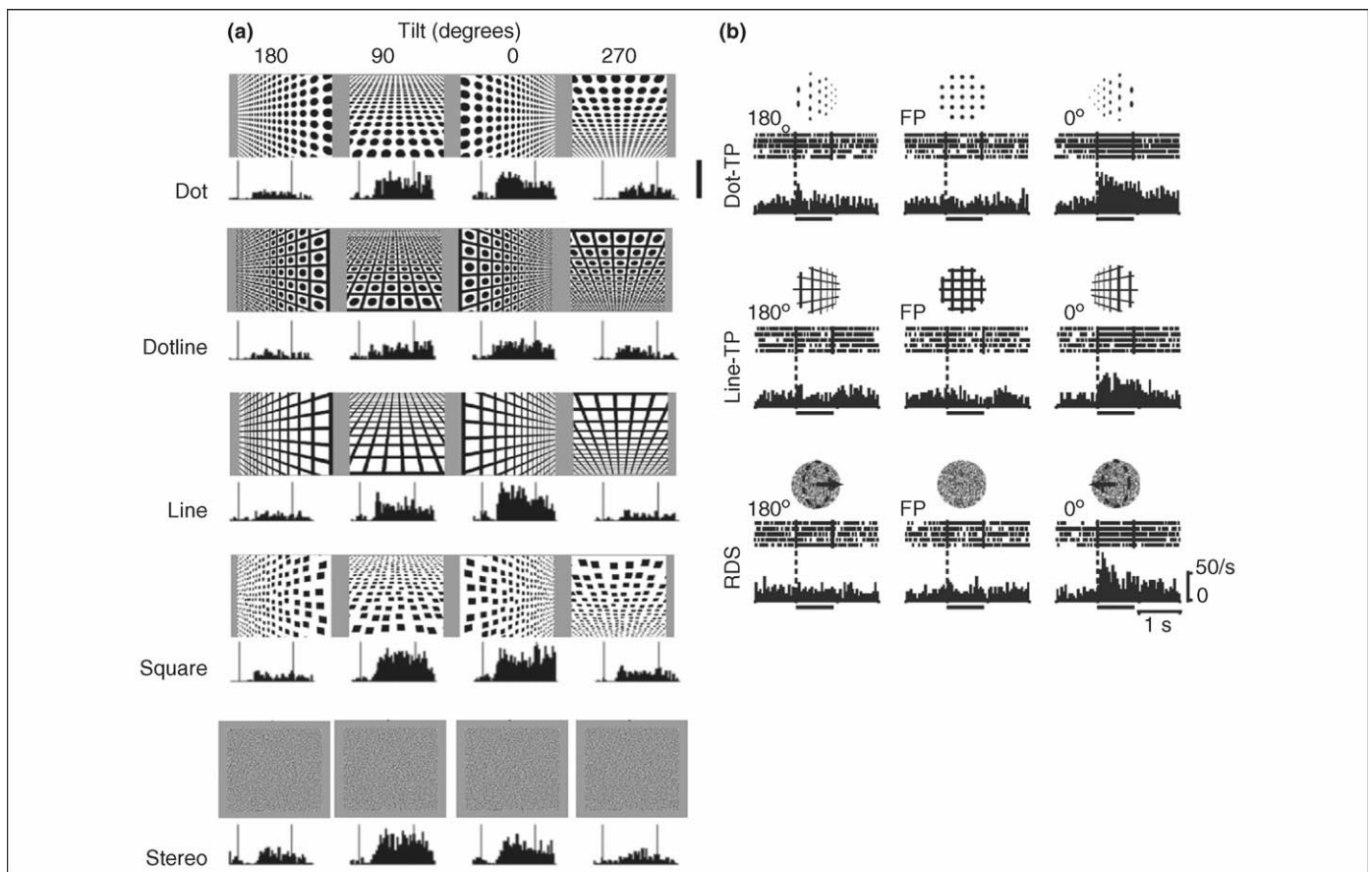


Figure 4. Average responses of TE (a) and CIP (b) neurons to planar surfaces tilted in depth defined by disparity or different types of texture. Data are reproduced from Refs [14,42]. Stimulus duration is indicated by vertical gray lines (a) and by horizontal lines in (b); the vertical bar in (a) indicates 87 spikes per second. Textures in (a) are not drawn to scale (they were $\sim 7^\circ$ in diameter and enclosed in a 2D shape, to match well known shape selectivity of IT neurons). Abbreviations: FP, frontoparallel; TP, texture pattern.

invariance for frontoparallel position complements the invariance for position in depth already reported in the first study of TEs neurons [18], defining a region in 3D space in which these neurons maintain their 3D shape selectivity.

The 2D shape selectivity of IT neurons is cue invariant [51,24]. In the same vein, the 3D shape selectivity of TEs neurons is depth-cue invariant. To investigate this further, selectivity for disparity and texture cues were compared. TEs neurons are selective for tilt specified by disparity and also by texture gradients [42], and the preferred tilt is similar for the two cues (Figure 4b). In addition, the selectivity for tilt specified by texture was invariant for texture type, for slant and for binocular versus monocular presentations. This invariance has also been tested for second-order stimuli, revealing a weak but significant correlation of the selectivity for disparity-defined and texture-defined curvature [52]. Such a result is not surprising because texture is a weak cue in single-curved surfaces [53].

Thus TEs neurons display a high degree of invariance, which is typical for neurons in high-level visual areas.

Selectivity of CIP neurons for first-order disparity

Shikata *et al.* [54] reported that neurons in the caudal part of the lateral bank of the IPS were selective for the tilt of stereoscopic surfaces. This caudal region has been referred to as cIPS [55], CIP [56] or the posterior lateral intraparietal area (LIP) [57], and probably corresponds to the posterior IPS as defined by Denys *et al.* [58] and to the lateral occipitoparietal zone named LOP by Lewis and Van Essen [59]. Although Shikata *et al.* established the disparity selectivity of CIP neurons in 1996, it was only in 2000 that the higher order nature of the selectivity was established, when Taira *et al.* showed that it is invariant for changes in fixation distance [56]. It has been reported in abstract form that CIP neurons also have solved the correspondence problem [60,61]. Importantly, Tsutsui *et al.* have demonstrated that inactivation of CIP interferes with judgments about surface tilt, which is in agreement with combined behavioral and single-cell results from the same study [62].

So far, only first-order selectivity has been demonstrated in CIP, although second-order selectivity has also been suggested [63]. Cue convergence has been documented for CIP neurons, for the combination of texture and disparity [14], and for perspective and disparity [62]. However, the perspective and disparity cues were not applied to the same part of the stimulus.

Finally, some CIP neurons, rather than being selective for the orientation in depth of surfaces (surface-orientation selective), can be selective for the orientation in depth of elongated stimuli (axis-orientation selective) [15].

Thus, although it has been repeatedly claimed that CIP neurons are important in 3D shape processing, their higher-order selectivity is less well documented than that of TEs neurons.

A network of 3D shape selectivity?

V1 neurons display no higher-order disparity selectivity [64] and are selective for both anti-correlated RDS and

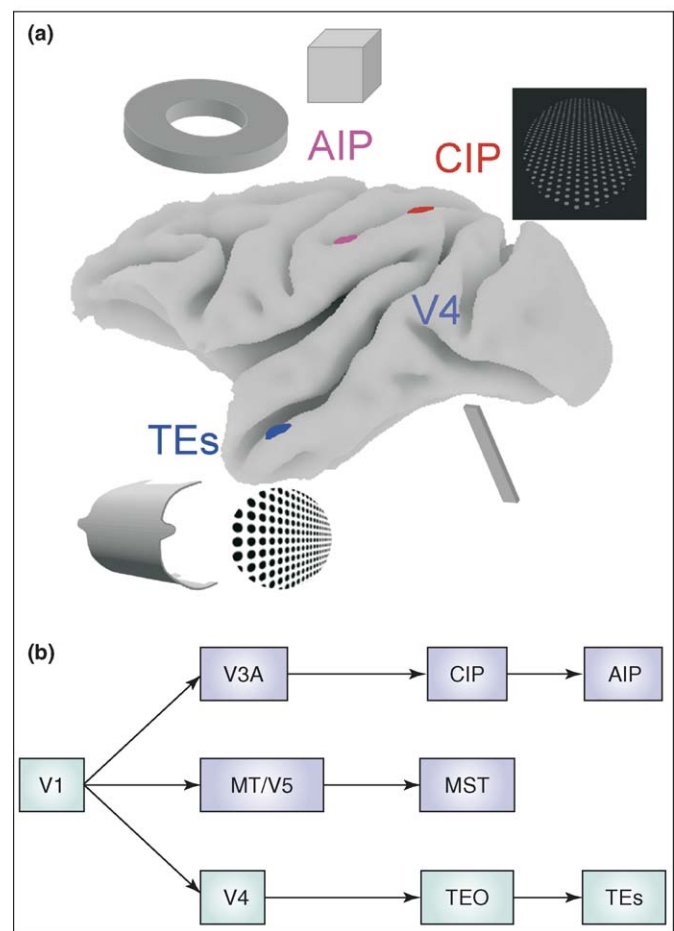


Figure 5. Overview of 3D shape network. (a) Left hemisphere of macaque brain, showing main regions processing higher-order disparity with the prototypical stimuli used to test this selectivity. Note that in anterior intraparietal area (AIP), only real 3D objects have been tested [66]. (b) Connections between the regions illustrated in (a). Blue boxes represent dorsal-stream areas. There are direct connections between areas V1 and MT/V5, but the main route between areas V1 and V4 passes through V2 (not shown). Additional abbreviation: MST, medial superior temporal area.

correlated RDS [37]. Thus, most properties of TEs and CIP neurons reflect processing beyond V1. V4 provides input to the IT, and V4 neurons are selective for the orientation in depth of elongated stimuli [26] but not for surfaces curved in depth [31]. Therefore, either TEs neurons acquire their higher-order selectivity by local connections in TEs or area TEO (posterior part of IT), or TEs receives its selective input from IPS. Indeed, it has been suggested that selectivity for 3D orientation is a property of neurons along the lateral bank of the IPS [56], in agreement with recent fMRI results [65].

Selectivity of AIP neurons, which are at the anterior end of the IPS, has been demonstrated only with real 3D objects. Thus, it is unknown which cue supports this selectivity for 3D shape, which supposedly underlies the role of AIP neurons in control of grasping [66]. Some 3D orientation selectivity has been reported for neurons in area MT/V5, which also have intermediate properties with respect to responses to anti-correlated RDS [67,68]. Thus, although we can state that both dorsal and ventral visual pathways process higher-order disparities (Figure 5), the origin of higher-order disparity selectivity and the extent of this selectivity throughout the visual system are still

unclear. The advent of fMRI in monkeys [69], particularly in awake monkeys [70], opens the possibility at least to map the different cortical regions sensitive to second-order disparities [65]. Once the regions involved have been identified, they can be further investigated by single-cell and inactivation studies.

Moreover, the role of 3D shape selectivity is still under debate. IPS neurons are presumed to process visual input to control grasping and manipulation of objects [15,16,66], yet inactivation of CIP also interferes with judgments about 3D orientation. By contrast, TEs neurons are part of the IT and, therefore, likely to be involved in coding the properties of 3D objects for the sake of recognition and categorization. That 3D SFD selectivity seems restricted to a small region, TEs (Box 4), might indicate that most identification of objects is performed using just 2D representations [71]. Indeed, other 3D shape cues have so far been shown to have little effect in TE [72]. Only in the case of ambiguous or degraded 2D information might 3D shape information be required for identification, and regions such as TEs be called into action. In that sense, 3D shape might have a role in object identification similar to that of color or texture (as a surface property). In turn, knowledge about the object might influence how it is grasped [73]. Thus, there might be much more cross talk between the dorsal pathway (IPS) and the ventral pathway (IT) than initially anticipated [19]. Further studies of 3D shape from disparity and other cues are needed to tackle these questions. These will provide the background crucial for understanding human studies [74], which still have to rely on techniques that have limited resolution.

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