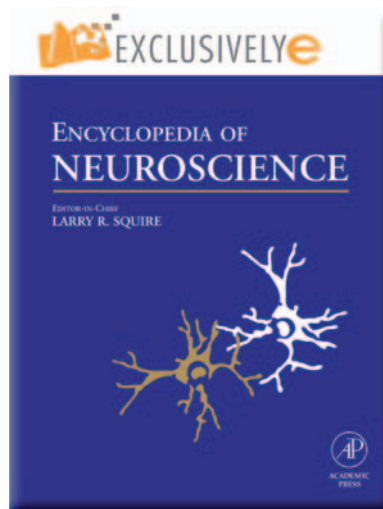


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## Visual System: Functional Architecture of Area V2

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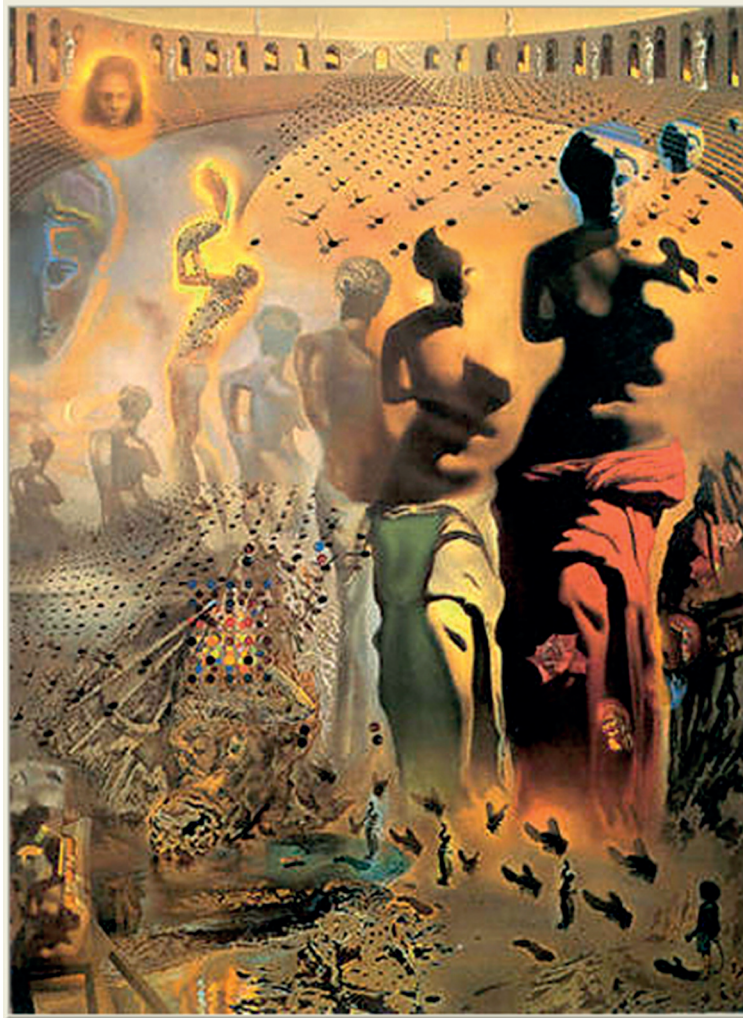
### Competing Local versus Global Views

The visual world appears to us in its entirety, coherent and understandable. Despite our belief that this view is unitary, it is actually comprised of multiple competing views at the local and global scales. This point cannot be better illustrated than by the paintings of Salvador Dali, the quintessential craftsman of depicting competing and conflicting cues within a single scene. In *The Hallucinogenic Toreador* (Figure 1), which is a 13 foot × 10 foot (4 m × 3 m) painting (exhibited at the Salvador Dali museum in St. Petersburg, FL), different scenes become apparent depending on the viewing distance. When standing close to the painting, in the bottom right corner a small boy is seen viewing a lake with a woman in a bikini on a pool chair and a dalmatian dog headed toward the lake. From a little farther back from the painting, just above the lake a bull can be seen stuck with multiple colorful spears. Several Venus statues can be seen across the center of the painting, one with a white dress, partly shadowed in green, and another with a red dress. At an even greater distance, one begins to appreciate the toreador himself, who's shirt and green tie are formed by the fabric and shadow of Venus's white skirt, respectively, his chin by her stomach, his nose by her breast, and his eye by the shadow of her neck. The outline of his cheek is formed by the hips of the Venus draped in red, his beret and cape dotted by the patterns of flies in the stadium and those above the bull. Thus, depending on the scale at which this painting is viewed, different scenes become apparent to the viewer. Moreover, an attempt to take in all views at once may lead to a sense of rivalry between local and global scales: at one scale the green swath is a tie, and at another it is the shadow of Venus's white dress.

A few simple visual illusions may help break this complex image into simpler components. Such illusions can be very useful tools for studying how competing cues are encoded in the brain. One example is shown in Figure 2(a). In this 'watercolor illusion,' blue and yellow dotted lines separate regions of a white background. Regions between the yellow lines appear yellowish and those between the blue lines appear bluish. In actuality (as measured by a spectrophotometer), the white regions are all the same in color. This is a demonstration of how local cues (white) can be

overridden by distant, global cues (the blue and yellow lines), leaving the illusion of differently colored regions. Figure 2(b) is the classic 'cafe wall' illusion, in which parallel horizontal lines appear to be sloping. Superimposition of a horizontal bar demonstrates that these lines are indeed horizontal. Again, the local cues signaling horizontal are overridden by the global percept of sloping lines. In the realm of depth perception, in the random dot stereogram (RDS) illustrated in Figure 2(c), the borders of the square central region in the left figure are offset from that in the right figure. When fused by the two eyes, this induces a percept of a square surface behind (more distant than) four round holes in a nearer surface. This is perceived despite the fact that the pixels within the square are identical and have no disparity. Thus, the local disparity cues are overridden by the global border cues of the square. Similar illusions are used in the studies described in this article to distinguish the roles of primary (V1) versus secondary (V2) visual areas in the perception of contour, stereoscopic depth, and color and brightness (see Table 1). Moreover, the conflicting local versus global cues present in these illusions are used to elicit competition between V1 (which is local) and V2 (which is global).

The inherent conflict illustrated by these examples calls for a revision of the traditional view of hierarchical processing within the visual pathways. In the traditional view, early visual stages first identify elemental features by means of neurons with small, spatially and 'featurally' restricted receptive fields. These elemental inputs are then integrated into higher-order representations at higher cortical areas. Receptive fields of neurons in higher cortical areas are spatially larger and tend to be less sensitive to elemental 'featural' specificity and, via some unknown 'invariance circuitry,' become tuned to more-global features. This integration process is iterated at multiple cortical levels, culminating in a relatively complete spatial and featural representation that enables object recognition. This hierarchical view, in its strictest interpretation, raises the question of how the visual system maintains knowledge of details when higher cortical areas no longer track these details. It is apparent that the details encoded in earlier areas and the global views encoded in higher areas must be simultaneously accessible. Moreover, these different views can (and often do) give conflicting signals. Resolving this local versus global competition is likely to be context dependent and therefore dynamic. Thus, while the hierarchical view still carries validity, it alone is inadequate for creating the illusion of coherence across multiple spatial scales.



**Figure 1** *The Hallucinogenic Toreador* by Salvador Dali (Salvador Dali Museum, St. Petersburg, FL).

This competition forms the basis for three theses presented in this article. Evidence supporting the first two theses is presented, and the third thesis is discussed largely as a future direction of study. The theses are as follows:

1. Each cortical area processes the visual world at a different spatial scale and, in that sense, ‘sees’ a different visual world.
2. Multiple views of the world which are encoded in parallel by multiple cortical areas can compete with each other. The dominance of one view over another may be resolved by a competitive balance between ‘feedforward’ and ‘feedback’ signals between different cortical areas.
3. This competition is dynamic and context dependent.

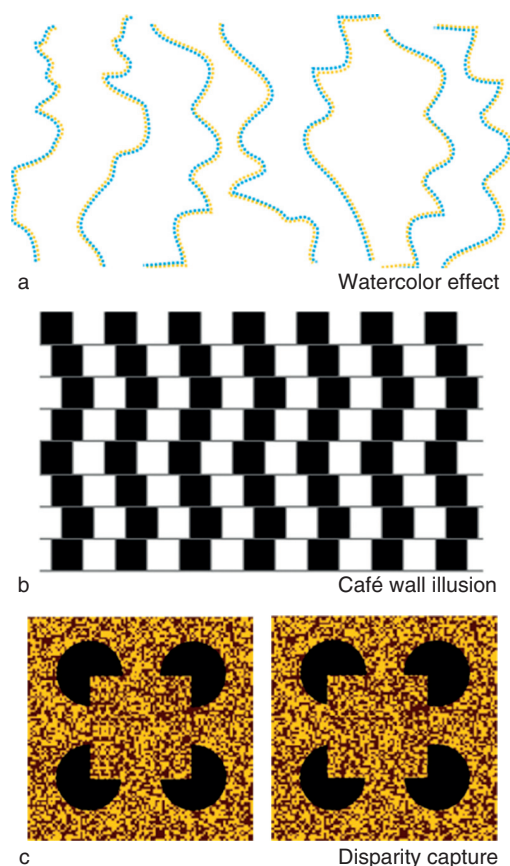
These theses are presented in this article through a set of studies which examine responses of primary (V1) and secondary (V2) visual areas in the macaque monkey. In this framework, V1’s and V2’s views of

three featural spaces are examined: visual contours, visual color and brightness, and visual depth. These studies demonstrate the following:

1. V2 ‘sees’ different things than V1 sees (see [Table 1](#)).
2. There is a balance of power between V1 and V2.
3. There is a dynamic network of V1 and V2 modules that participate in this power struggle.

### Functional Organization in V2 Is Modular

V2 has been described as a distribution center from which modality-specific information feeds into the ventral and dorsal visual processing streams. In addition to its role in distribution, V2 plays a crucial preparatory role in midlevel vision, performing transformations that link local detail to higher-order percepts. A great deal of attention has been focused on the interareal interactions and integration between cortical areas. V2 holds a unique position in the



**Figure 2** Global versus local competing cues in visual illusions. (a) The watercolor effect; see Pinna B, Brelstaff G, and Spillmann L (2001) Surface color from boundaries: A new 'watercolor' illusion. *Vision Research* 41(20): 2669–2676. (b) The cafe wall illusion. (c) Disparity capture illusion.

**Table 1** V1 and V2 see different percepts

	V1	V2
Brightness	Luminance	Illusory brightness
Depth	No percept	Percept
Contour	'Real' contours	Illusory contours

sense that it funnels information, both feedforward and feedback, between V1 and the larger cortical network.

To appreciate the role of V1 and V2 in contour, color–brightness, and disparity processing, it is first important to recognize the modularity of these areas. In contrast to V1, which is characterized by ocular dominance structure, a regular array of orientation domains, and a lattice of densely staining cytochrome oxidase blobs, V2 contains a pattern of large (millimeter-size) cytochrome oxidase stripes. Some evidence indicates these thin (cytochrome dark), pale (cytochrome light), and thick (cytochrome dark) stripes are involved in contour, color–brightness, and disparity processing,

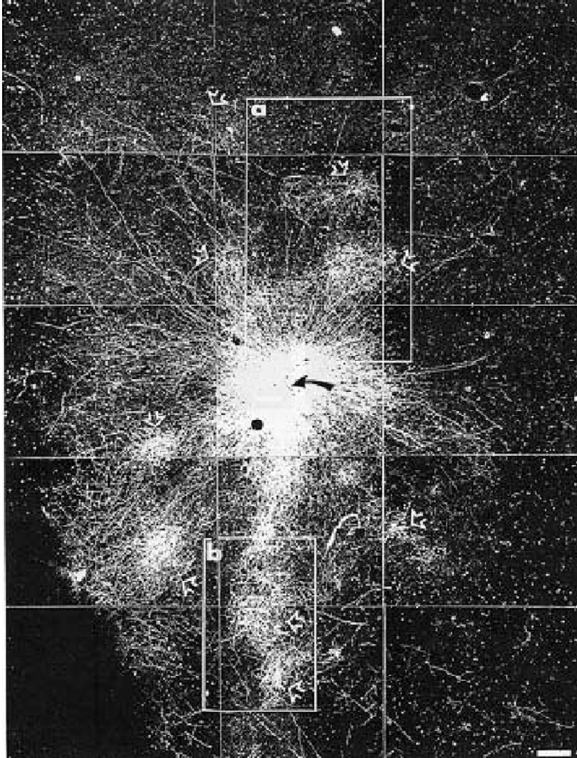
respectively. In macaques, these stripes are oriented roughly perpendicular to the V1–V2 border and are commonly seen in a repeating thin, pale, thick, pale sequence. There are also reports of interanimal variability and/or variability of stripe thickness (e.g., thin is not thin) or stripe sequence (e.g., thin, pale, thin, pale). A few studies have hinted that functional differences may accompany these differences in individual architecture.

Within these larger stripe structures are collections of 100–200  $\mu\text{m}$  domains. The presence of substructure within stripes was perhaps first suggested by nonuniform staining in cytochrome oxidase-stained tissue and by patchy labeling of injected tracers in V1, V2, and V4. Studies with 2-deoxyglucose have revealed further patchy activation within V2 stripes. Optical imaging further confirmed the presence of subdomains (e.g., color-preferring and luminance-preferring domains within thin stripes). Although both anatomical and functional evidence support the presence of modules, the relationship of functional subdomains and anatomical patchiness is unknown. Functional evidence indicates that different modules play distinct functional roles and have specific connectivities. Indeed, this is visually apparent from localized injection of tracer into V2, which reveals arrays of clusters about 100–200  $\mu\text{m}$  within V2 (Figure 3). These anatomical data suggest a degree of intra-V2 connective specificity that parallels that of functional networks observed in V1.

In addition to summarizing more recent findings regarding V2, this article presents a common framework for understanding the different featural modalities in V2 and thereby the common functional transformations that V2 performs on its input, regardless of feature space.

### Are There Functionally Distinct Domains in V2?

Following the discovery of cytochrome oxidase 'blobs' (also referred to as 'puffs' and 'patches') in macaque monkey visual cortex, researchers reported that blobs are characterized by a predominance of color-selective neurons which lacked strong orientation selectivity, whereas interblobs are characterized by a preponderance of orientation-selective cells lacking in color selectivity. Functional distinctions within V2 have also been reported whereby thin stripes are color selective and poor in orientation selectivity and pale and thick stripes are orientation selective and less selective for color. This proposed dichotomy led to a number of studies, some of which supported whereas others contradicted these findings. This controversy has continued without apparent resolution.



**Figure 3** Intrinsic connections in V2 reveal 200  $\mu\text{m}$  modules. (a, b) Boxed areas indicate regions of patchy label (indicated by arrowheads). Arrow: site of tracer injection. Scale bar = 100  $\mu\text{m}$ . From Amir Y, Harel M, and Malach R (1993) Cortical hierarchy reflected in the organization of intrinsic connections in macaque monkey visual cortex. *Journal of Comparative Neurology* 334(1): 19–46.

The debate is fueled by two main issues. The first is whether color and orientation information are segregated in V1 (and V2). Some studies have found a clear association between color selectivity and a lack of orientation tuning. This finding is supported by studies which report that color-selective cells prefer low spatial frequencies and exhibit high contrast sensitivity. Results with 2-deoxyglucose are also consistent with these views, indicating blobs in V1 are preferentially activated by color stimuli and low spatial frequency stimuli.

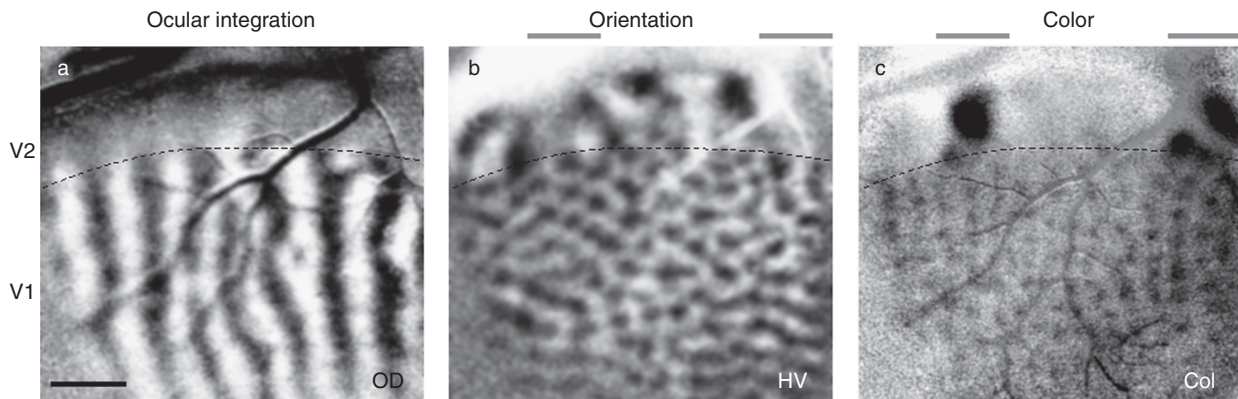
With respect to spatial distribution, electrophysiological studies have also reached different conclusions. Some support the view that cytochrome oxidase blobs are centers of color preference and poor orientation preference. Others have found that centers of blobs exhibit higher contrast gain and lower spatial frequency response, which suggests that blobs do exhibit responses functionally distinct from that of interblobs. However, other studies differ. Some single-unit electrophysiological studies find blob and interblob domains exhibit no significant difference in color and orientation preference and report a range of associations

between color selectivity and orientation selectivity within single cells of V1. Experimental factors may contribute to some of this controversy. Although electrode recording sites were carefully reconstructed in these studies, there is some intrinsic error associated with reconstruction of recording sites. Since cytochrome oxidase blobs are small (100–200  $\mu\text{m}$ ), a small degree of error could be significant. There are also differences in sampling methods and methods of receptive field characterization (e.g., hand plots with color filters, characterization with sinusoidal isoluminant gratings, mapping with reverse correlation of cone-isolating stimuli).

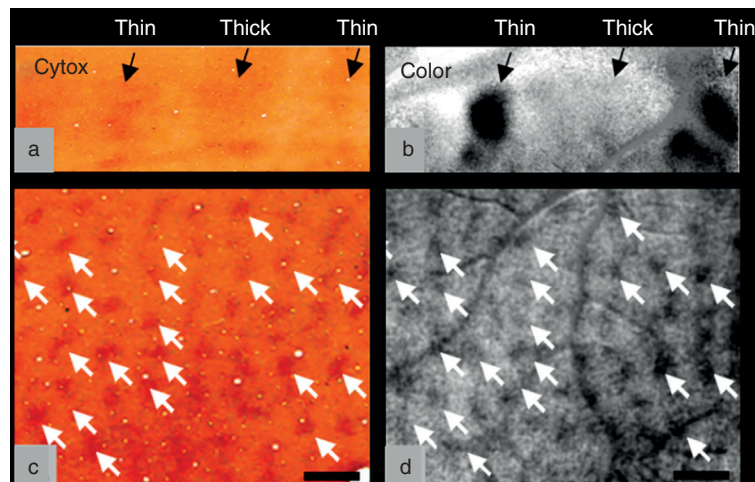
A related but distinct issue regards the association of color and orientation with blobs and interblobs, respectively. Studies which reveal population responses (2-deoxyglucose and optical imaging methods) tend to support the role of blobs in the processing of low spatial frequency and color information. As shown by 2-deoxyglucose methodology, blobs are preferentially activated by color-varying gratings of low and middle spatial frequencies and by spatially diffuse color stimuli. Optical imaging studies have shown good alignment between cytochrome oxidase blobs and centers of monocularity and between cytochrome oxidase blobs and regions of poor orientation selectivity. Less clear correspondence between blobs and color response has also been reported. Although one study reported a general correspondence between color domains and cytochrome oxidase blobs, it was not a simple one-to-one relationship: Some color-activated domains were irregular in shape and were observed to span two or more blobs.

A similar controversy exists on V2. Some researchers found little difference in the number of color-selective cells across the different cytochrome oxidase stripes in V2. Some single-unit studies have emphasized the multidimensional aspects of single cell function in V2. Others have reported some concentration of color-selective responses in thin stripes of V2, in contrast to some earlier studies.

In hopes of settling this debate, a recent intrinsic signal optical imaging study closely examined the alignment of large field views of color and orientation response in V1 and V2 of the macaque monkey. As shown in [Figure 4\(a\)](#), the V1–V2 border is well delineated by ocular dominance imaging. Optical images revealed the characteristic orientation maps as well as a regular array of color domains in V1 ([Figure 4\(b\)](#)). In V2, orientation domains are larger than those in V1 and are localized to the thick and pale stripes (white bars in [Figure 4\(b\)](#) and [4\(c\)](#)). Regions of strong color activation in V1 ([Figure 4\(c\)](#)) are punctate and bloblike in appearance, are aligned along centers of ocular dominance columns, and tend to overlay regions of



**Figure 4** Feature maps (ocularicity, orientation, and color) within V1 and V2 of macaque monkey. (a) Ocular dominance (OD) map (left eye minus right eye). V1–V2 border (indicated by dotted line in (a)–(c)). (b) Orientation map (horizontal minus vertical; HV). V2 orientation domains are as much as several times larger than those of V1. (c) Color (Col) map (red–green luminance grating minus luminance grating) reveals V2 thin stripes and V1 blobs. Note that locations of color activations in V2 (dark bars) are complementary to locations of oriented domains in V2 (compare (b) and (c)). Scale bar = 1 mm. From Lu HD and Roe AW (2007) Functional organization of color domains in V1 and V2 of macaque monkey revealed by optical imaging. *Cerebral Cortex* (doi: 10.1093/cercor/bhm081).



**Figure 5** Color domains align with cytochrome architecture. Alignment of cytochrome oxidase (cytox) stripes (a) and color domains (b) in V2, and cytochrome oxidase blobs (c) and color blobs (d) in V1. Tissue was aligned using blood vessels, V1–V2 border, tracer injections, and electrolytic lesions. Black ((a) and (b)) and white ((c) and (d)) arrows point to corresponding structures. Scale bar = 1 mm. From Lu HD and Roe AW (2007) Functional organization of color domains in V1 and V2 of macaque monkey revealed by optical imaging. *Cerebral Cortex* (doi: 10.1093/cercor/bhm081).

low orientation selectivity. In V2, color domains are complementary in location to the orientation-selective areas and overlay the thin cytochrome oxidase stripes. An alignment of cytochrome oxidase stained tissue, and functional images (using blood vessels, tracer injections, and electrolytic lesions as guides) have revealed good alignment of color domains with thin stripes in V2 (Figures 5(a) and 5(b)) and color blobs with cytochrome oxidase blobs in V1 (Figures 5(c) and 5(d)). These findings thus support, at the level of population response, significant functional segregation of color and orientation information in V1 and V2 and

further strengthen their association in V1 with blobs and interblobs, respectively.

Although on the face of it, these studies appear at odds, they are, in fact, mutually consistent. Clearly, single cortical locations contain cells with a mixture of responses and cell types. Furthermore, each cell displays an array of responses in multiple feature domains. There is no question that individual neurons are multi-dimensional and that cells in V2 integrate information across multiple feature domains, a point that is made by a number of electrophysiological studies. This multidimensionality is precisely what leads to different views

of the same cortical area. Different electrophysiological samplings and somewhat different characterization methods can provide quite different impressions, indicating that methodology can strongly influence the apparent population response profile. (Indeed, being able to electrophysiologically target imaged color domains increases the yield of color cells tremendously.) Despite variability due to method, that functional imaging and functional anatomical studies consistently reveal blob and stripe structure suggests that there are overall differences in the local population response. The fact that functional responses reveal stripelike structures within V2 and that distinct responses are recorded in different stripes in V2 suggests the presence of at least some degree of segregation. On average, the cells in blobs and thin stripes prefer color stimuli over achromatic stimuli. Functional imaging provides, in a sense, a more unbiased view of the average population response. Perhaps some of the controversy is due to the perception that functional organization implies strict segregation. However, this is not the case, as each functional structure contains a mixture of neurons with varying selectivities. In sum, although single neurons are multidimensional (have some degree of responsiveness to both contour orientation and color), as a population, they are organized to some degree with respect to contour versus color.

### **Parallel Functional Channels in V2: A Useful Framework?**

A framework that had its roots in the 1980s maintains that thin stripes are vehicles for processing surface feature information whereas thick and pale stripes are involved in contour and depth information processing. This framework has been supported by anatomical, electrophysiological, 2-deoxyglucose, optical imaging, and behavioral and lesion study data. This framework is not to be interpreted as a view of strict segregation. There is ample data to demonstrate that functional organization within V2 is not one of strict segregation. As noted above, single neurons in V2 are multidimensional and integrate different featural spaces. Each stripe type within V2 contains a myriad of cell types. Given the extensive connectivity between stripes in V2, cells from each stripe type have opportunity to influence and integrate information from other stripe types. Nevertheless, the proposal that different stripes subserve somewhat different functions is still a useful one. It is a framework which provides an understanding which can be experimentally tested and modified. To ignore this framework would be foolish. In the language of 'drivers and modulators,' there may be primary functions that can be modified by secondary,

perhaps contextual, influences. A working framework provides much greater utility and testability than an approach in which every neuron is omnifunctional. Indeed, the ubiquity of functional organization in the brain – whether it be at the level of global networks, cortical areas, modules and columns, laminae, or synapses – indicates that such organization is a fundamental tenet of brain organization. Whether they be genetically determined, experientially determined, or a necessary prerequisite for specific computations, it is likely that functional organizations bear a strong (and possibly predictive) link to the brain circuits that produce function and behavior. The following paragraphs are thus presented in this framework.

### **Surface Properties**

Surface features, such as color, brightness, texture, glossiness, and transparency, are those that help us identify the material quality of an object. There are ample demonstrations of the ways the perception of these surface features can be strongly influenced by lighting, local color and contour cues, global context, and experience. The human visual system can distinguish on the order of a million different colors. However, the inputs to the visual system are confined to three types of cones, those responsive to red, green, and blue wavelengths. How does the visual system create the illusion of color and transform a triadic cone-based representation into a perceptual continuum of salient hues? Add to this challenge the fact that the human visual system can adjust to 7 orders of magnitude of brightness (10 million to one, bright sunlight to faint starlight). The visual system must also factor in the influence of contextual cues such as color, brightness, and contrast of nearby borders and surfaces. In addition, the ability to see objects through transparent surfaces means we not only must segregate different planes of depth but also ignore features on the transparent plane.

### **Color Representation in V2**

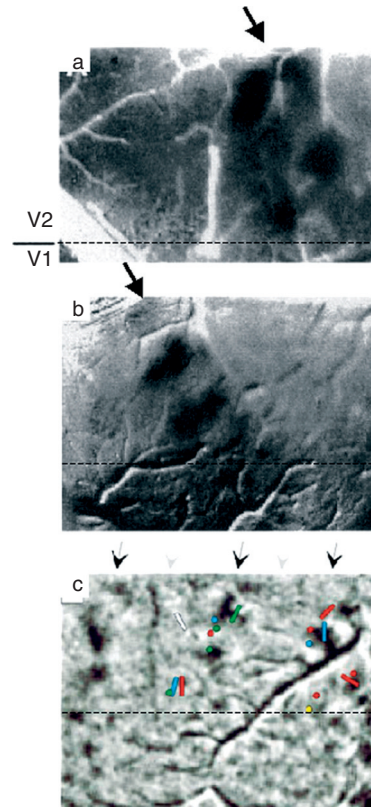
How do V1 and V2 separately and together contribute to these processes? The idea that V1 and V2 participate in encoding color information is well supported. At least one route for color information arises from the parvocellular layers of the lateral geniculate nucleus (LGN) and continues to layer 4Cb of V1, to cytochrome oxidase blobs of V1, and to the thin stripes in V2. Blue cone-driven input from S layers of the LGN project directly to the blobs, with blue-yellow inputs targeting layer 3B–4A and red-green inputs targeting lower layer 4C. There is also evidence to suggest a functional segregation of blue

'ON' and blue 'OFF' inputs within layer 4A of V1. In V2, although there is significant color response in each of the stripe types, a greater concentration of neurons responsive to color stimuli is found in the thin stripes than in either the pale or thick stripes.

**Color versus luminance preference domains** Optical imaging studies have revealed the presence of color-responsive domains within thin stripes. Some studies have used preferential response to isoluminant red–green gratings over achromatic luminance gratings to reveal color preference domains. Although there are both color and luminance contrast differences between these stimuli, experiments directly comparing high- versus low-contrast achromatic responses have revealed no structured maps in V2, indicating that the imaged substructure is not due to luminance contrast differences. Since spatial frequency, drift rate, and mean luminance were identical between these two stimuli, the differential response is attributed to the color content of the stimuli. Such stimuli elicit activations that appear more rounded and interdigitated in some thin stripes (Figures 6(a) and 6(c)) and more elongated across the width of the thin stripe in others (Figure 6(b)). It is not yet known whether there may be functional implications of these different architectures.

**Color: Topography of hue in V2 thin stripes** One of the first studies to establish a systematic representation of hues in V2 used isoluminant color–gray gratings of different hues and mapped responses in macaque V2 using intrinsic signal optical imaging. These images revealed hue-specific domains on the order of 100–200  $\mu\text{m}$ , which were mapped in a systematic fashion in V2. These chromatic color maps were located within single thin stripes and not in thick or pale stripes of V2 (Figure 7(a)). This was the first demonstration of a hue-based map in which topographic location corresponded to hue wavelength. This study underscored three primary points: (1) although V1 contains color-selective cells tuned to red–green and blue–yellow axes, hue representation does not emerge until V2; (2) the topographic basis for this representation is based on 100–200  $\mu\text{m}$  modules, the size of which is fundamental to other featural representations; and (3) the discovery of topographic maps within thin stripes poses perhaps the single strongest piece of evidence in favor of the color–thin stripe association.

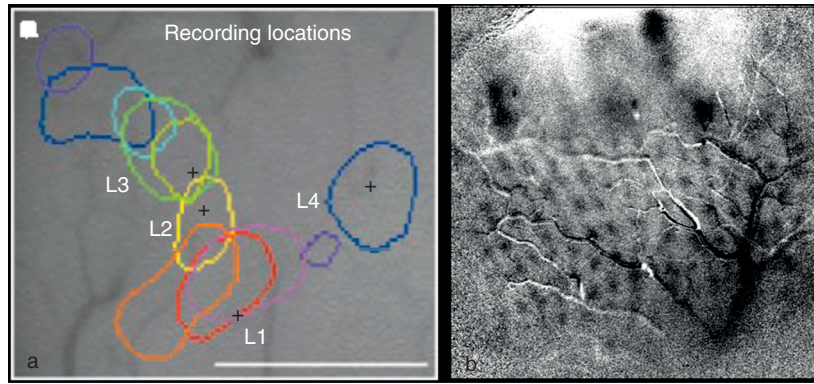
**Where is the blue response?** Attempts at revealing blue response in V1 and V2 with imaging techniques proved unsuccessful. Similarly, comparing responses to isoluminant blue–yellow gratings versus achromatic



**Figure 6** Color domains in thin stripes. (a) A single thin stripe (arrow) contains several rounded color domains. (b) A single thin stripe (arrow) contains color-preferring domains that span the width of the stripe. (c) Three thin stripes in V2, each containing a few color domains. Scale bar = 1 mm. (a) From Roe AW and Ts'o DY (1995) Visual topography in primate V2: Multiple representation across functional stripes. *Journal of Neuroscience* 15: 3689–3715. (b) From Roe AW and Ts'o DY (1999) Specificity of color connectivity between primate V1 and V2. *Journal of Physiology* 82: 2719–2730.

gratings did not reveal any functional organization within either V1 or V2. However, more-recent studies have revealed clear and strong responses to blue stimuli. These studies examined responses to flashing blue versus flashing gray unstructured stimuli each at 30% luminance and drifting blue–gray square-wave gratings versus gray–gray square-wave grating at 30% luminance contrast. In V2, similar to red and green, blue stimuli preferentially activate the thin stripes whereas gray stimuli exhibited preferential thick-stripe activation. Within the thin stripes, color-specific stimuli typically revealed focal activations. Activations to red, green, and blue stimuli have been shown to shift in location within the thin stripes. Examination of responses to gratings of different duty cycles revealed that thin blue lines were a surprisingly effective stimulus. Thin blue lines elicited strong blob-like maps in V1 (Figure 7(b)). These data suggest that blue activations, like red and green hues, are mapped





**Figure 7** Hue maps in V2. (a) Chromatic color maps located within a single thin stripe of V2 (imaged with isoluminant color/gray gratings of different hues). Outline color indicates peak response of that location. (b) Imaged responses Macaque V1 and V2 in response to thin blue oriented stimuli. In V1, blue activation reveals blobs. In V2, blue activation is mainly located in thin stripes. Scale bar = 500  $\mu\text{m}$ . (a) From Xiao Y, Wang Y, and Felleman DJ (2003) A spatially organized representation of colour in macaque cortical area V2. *Nature* 421: 535–539. (b) From Roe AW, Lu HD, and Crewther D (2007) Blue Color Activation in V1 and V2 of Macaque Monkey. Melbourne: International Brain Research Organisation.

within ‘color modules’ in the thin stripes of V2. The surprisingly strong response to thin blue lines may suggest some interaction of color and spatial frequency that may contribute to contour response in V2. Data also suggest, counter to previous notions of dedicated red–green versus blue–yellow blobs in V1, that blue response may reside within every blob in V1.

**A midlevel role in simultaneous contrast and color constancy?** The color of a surface can be dramatically changed by its surround, such as commonly demonstrated with examples of simultaneous color contrast. A first step in achieving simultaneous color contrast response would be demonstrating a chromatically specific effect by the surround. Surround suppression of both achromatic and isoluminant gratings have been examined on the chromatic responses of V1 and V2 neurons. There is little evidence that colored surrounds alter the chromatic tuning of neurons in V1 or V2 (although background color shifts chromatic tuning of V1 neurons to a degree consistent with perceptual color contrast effects). However, V2 neurons, unlike V1 neurons whose surrounds exhibit little chromatic selectivity, have a chromatic signature in the surround similar to that in the receptive field center. Thus, although there is no evidence of the surround shifting chromatic tuning in V2, neurons in V2 are strongly affected by specific chromatic stimuli in the surround.

Another salient aspect of color perception is ‘color constancy.’ This term refers to the fact that the color of a surface remains constant under different lighting conditions (e.g., a red apple will appear red under different spectral lighting conditions, such as bright

sunlight and ambient indoor lighting). This suggests that there must be neurons somewhere in the brain that encode ‘redness’ or ‘greenness’ of a surface regardless of light condition. Do such neurons exist in V2? A few recent studies have tried to dissect the difference between color responses in V2 and those in V1 or V4. Researchers have used isoluminant color patches to characterize the color preference of single cells in V2 thin stripes and Mondrian stimuli to examine the effects of color versus the illuminant. They found that V2 cells responded to the wavelength of the illuminant rather than the color of the stimulus. In contrast, the same stimulus paradigms revealed clear color constancy in a majority of V4 neurons: these neurons exhibited shifts in their color-tuning profiles in the direction of the shifted chromatic component of the illuminant (which was simulated by a shift in the background color presented on the computer monitor). In other words, V2 neurons did not exhibit behavior consistent with color constancy. However, about a third of V2 neurons studied were strongly influenced by the wavelength of the surround.

Thus, these studies suggest that V2 plays a midlevel role in the generation of color percepts such as simultaneous color contrast and color constancy. Although neurons in V1 and even in LGN are reported to be influenced by monochromatic surrounds, shifts of the entire color tuning curve have been reported only for V4 neurons. This is true for units recorded both in anesthetized and awake monkeys. Thus, computations leading to color constancy are likely to begin at stages before V4, but color constancy is not represented in its full extent until V4. V2 is likely an intermediate processing stage in these computations.

### Brightness Representation in V2

With respect to V2's role, if the primary role of thin stripes is to encode surface properties, then in addition to color, thin stripes may be integral to representing surface brightness. The challenges of representing brightness in the visual system include representing light level (lightness and darkness), change in light level (either increase or decrease), and ability to adjust to a large range of light levels. Some of these challenges may be solved by the retina and LGN. However, other challenges are unlikely to be resolved by early precortical levels. Similar to context-dependent effects in color vision, the perceived brightness of a surface can be strongly influenced by surrounding cues. Brightness perception is influenced by multiple factors, including luminance, edge effects, distant color and brightness context (e.g., simultaneous contrast, Mondrians), and experience. Neurons in V1 of both the cat and the monkey exhibit response modulation to large field modulations in luminance and in background luminance modulation. Relatively few studies have examined the representation of brightness information in V1 and V2.

**ON and OFF responses** Many studies have demonstrated that visual cortical neurons exhibit contrast response functions which increase monotonically over a range of contrasts and saturate at higher contrasts. Most neurons in V1 respond to a large patch of luminance increment or decrement in a monotonic fashion. Roughly one-third of neurons are not affected by stimulation in the surround, consistent with the type I cells which lack inhibitory surrounds. The response is often characterized by an initial contrast-independent transient, followed by a sustained response which correlates with the luminance increment or decrement. Another third of neurons are enhanced by luminance in the surround and appear to signal level of illumination. And the remaining third are affected by luminance in the surround (type II) in a manner consistent with simultaneous contrast as first demonstrated in anesthetized cat visual cortex and later also observed in the alert monkey V1.

In addition to light increment (ON) and light decrement (OFF) responses, V1 and V2 contain cells that exhibit bandpass characteristics. That is, they respond to an intermediate range of luminance values (termed 'V-shaped' or 'gray-preferring neurons'). Some of these neurons also exhibit color sensitivity, suggesting a role for luminance response in color encoding.

**ON and OFF domains in V2** Within V2 thin stripes, there are subdomains that exhibit luminance increment (ON) and luminance decrement (OFF) responses.

These domains measure on the order of 0.5 mm and could be the same 'luminance-preferring' domains revealed in isoluminant color versus achromatic imaging experiments. Such domains had been hypothesized based on extended runs of tangentially recorded of ON or OFF single unit responses within V2 thin stripes. Such ON and OFF zones have not been observed in primate V1.

**Contrast response in V2: Thin stripes have greater dynamic range** One test of the hypothesis that thin stripes are brightness-processing structures has taken the form of examining contrast response in V2. The expectation was that if thin stripes were loci of brightness information processing, then they should have contrast response behavior consistent with such a representation. One would expect the contrast response of these stripes to exhibit sensitivity to a large range of contrasts, including sensitivity to low contrasts and nonsaturating response at high contrasts. More specifically, they should have high contrast gain, especially at low spatial frequencies consistent with encoding visual surface features, and they should exhibit large dynamic range for encoding visual brightness.

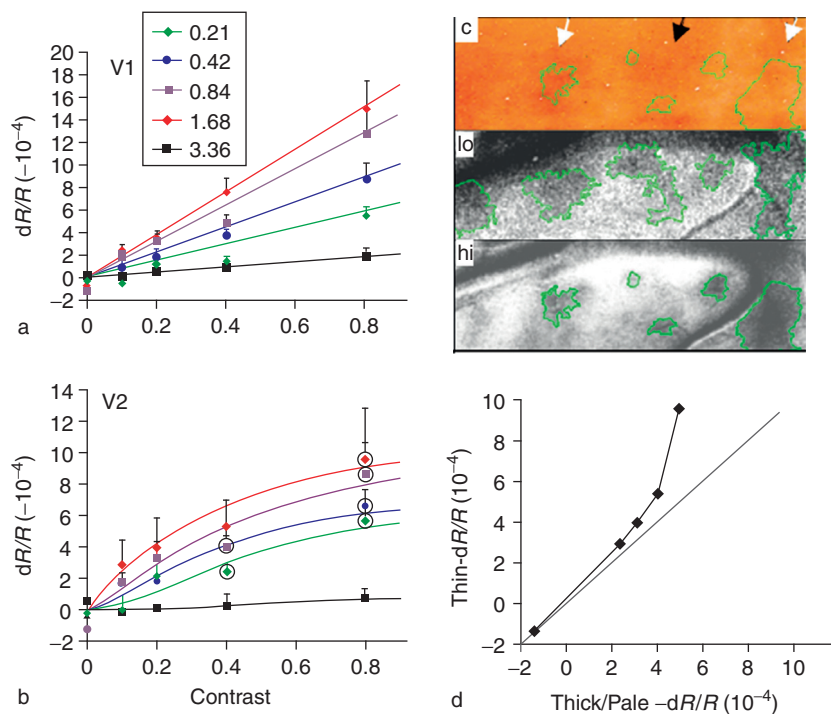
Previous studies had shown that in primates, magnocellular and parvocellular neurons in the LGN are characterized by distinct contrast response signatures. Magnocellular neurons exhibit nonlinear response characterized by greater sensitivity to small changes in contrast (have higher contrast sensitivity), especially at low luminance levels, and tend to saturate at high contrasts. Parvocellular neurons respond in a linear fashion to increasing contrast and are relatively insensitive at low contrasts (in fact, they are not responsive at contrasts lower than around 10%). Koniocellular neurons are a heterogeneous population of neurons and have a broad range of contrast response functions. In V1, interblobs tend to be dominated by parvocellular inputs, while blobs exhibit parvocellular (color selectivity), magnocellular (low spatial frequency, high contrast gain response), and koniocellular (blue response) characteristics. Although thick stripes are dominated by magnocellular inputs and therefore could exhibit higher contrast sensitivity than thin stripes do, in principle both magnocellular and parvocellular inputs reach all the stripe compartments in V2. The thin stripes receive both magnocellular and parvocellular input primarily by way of the blobs, and thick and pale stripes via the interblob columns. Thick stripes have the highest contrast sensitivity values, although semisaturation values have shown no significant difference between thin, pale, and thick stripes. Measures of V2 response have revealed surprisingly

few quantitative differences between thin, pale, and thick stripes, leading some to argue for homogeneity of stripe function in V2. With 2-deoxyglucose methodology, both thin and thick, but not pale, stripes have exhibited response to low contrast (8%) gratings, suggesting that magnocellular contribution could also be prevalent in the thin stripes.

A study using optical imaging methods has demonstrated that V2 thin stripes have greater contrast gain than thick and pale stripes and relatively nonsaturating response at high contrasts. As shown in Figure 8, contrast response functions of both blobs and interblobs in V1 were linear (Figure 8(a)), consistent with parvocellular-dominated response in superficial layers of V1. However, responses in V2 exhibited a nonlinear response, especially at low contrasts, reminiscent of magnocellular input (Figure 8(b)). At high contrasts, thin stripes exhibited significantly stronger and less-saturating responses than thick or pale stripes (Figures 8(c) and 8(d)). The response of V2 thin stripes is thus reminiscent of magnocellular response at low contrasts and parvocellular response at high contrasts.

At low contrast levels, magnocellular inputs from V1 blobs may converge in V2 thin stripes, thereby conferring high-contrast response at low contrasts. At higher contrast levels, parvocellular-dominated inputs to thin stripes continue to signal changing contrast, while those in thick and pale stripes tend to saturate. Other contributions to nonlinear response in V2 thin stripes (such as koniocellular input and other thalamic inputs) may also be at play. In comparison with thick or pale stripes, these data suggest a larger dynamic range of V2 thin stripes, consistent with a preferential role in brightness perception.

**Real and illusory brightness representation in V2 thin stripes** Perhaps intermediate to local luminance response and lightness and color constancy which require rather large-scale integration are midlevel stages which are encoded in V2 (in cats). A potential example of midlevel integration was demonstrated in a recent study revealing the equivalence of V2 response to different types of brightness stimuli. Response to sinusoidally modulated stimuli counterphasing in



**Figure 8** Contrast response in V2 stripes. (a, b) Contrast response functions in V1 are linear, both in blobs and interblobs, while those in V2 are nonlinear, in thin and thick/pale stripes. Different color lines represent response obtained at different spatial frequencies (same legend in (a) and (b), in cyc/deg). *x*-axis, visual contrast (0.2 = 20%); *y*-axis,  $dR/R$  – reflectance change. (c, d) Thin stripes have greater dynamic range. (c) Top: Cytochrome oxidase stain reveals thin (white arrows) and thick (black arrow) stripe in V2. Middle and bottom: Imaged response to low (lo, 40% contrast) and high (hi, 80% contrast) sinusoidal gratings. At high contrast, thin stripes still exhibit robust response, but thick stripe response is weak. Green outlines indicates activation areas, thresholded and outlined. (d) Thin and thick stripe responses are similar at lower contrasts, but thin stripe response dominates at high contrast. Thin (*y*-axis) and thick/pale (*x*-axis) stripe responses are similar at low contrasts (black, dark gray symbols), but thin stripe response dominates at high contrast light gray, white symbols, ( $dR/R$  – reflectance change). From Lu HD and Roe AW (2007) Optical imaging of contrast response in macaque monkey V1 & V2. *Cerebral Cortex* (doi: 10.1093/cercor/bhl177).

contrast was preferentially localized to the thin stripes of V2 (Figures 9(a) and 9(b)). In fact, similar thin stripe activations were obtained in response to 'illusory' brightness modulations as early as 1970 (Figure 9(c)), when a percept of brightness contrast between the left and right halves was achieved by an intervening 'Cornsweet' border (Cornsweet being one of the researchers involved). This border-induced contrast illusion evokes the percept of brightness differential where none is present. Neurons in V2 were shown to respond not only to sinusoidal modulation of the 'real' brightness stimulus but also to that of the Cornsweet border contrast. Optical imaging of V2 response indicated that such responsiveness was localized to the thin stripes of V2. Consistent with optical imaging evidence, of 89 neurons recorded in V1 blobs and interblobs and V2 thin, pale, and thick stripes, almost all those responsive to the Cornsweet were located in thin

stripes. These results suggest that thin stripes are involved in not only the encoding of luminance response but, more generally, the response related to surface brightness perception.

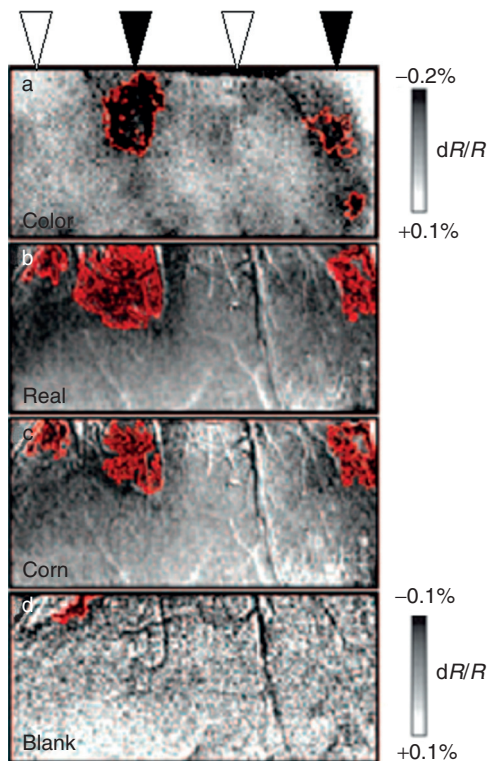
### V1 Sees Local, V2 Sees Global

These data are consistent with the encoding of higher-order brightness processing in V2 and lower-order brightness processing in V1. That is, responses in V1 reflect local luminance values, whereas those in V2 reflect more global, edge-induced percepts. In the Cornsweet stimulus, V1 would report a lack of luminance modulation, whereas V2 would report a salient brightness modulation. To achieve such perceptual saliency, the V2's message must somehow overcome V1's. One obvious means is via feedback projections from V2 to V1 which lead to either relative suppression of V1 response or a modulation of V1 response that concurs with that in V2. This possibility remains to be examined.

### Stereoscopic Depth

Binocular inputs are used by the human visual system to judge object depth in the three-dimensional world. This depth percept is created by the integration of two views of the world received by the two eyes. Stimuli nearer or farther from the fixation point will produce disparities from left and right eye with a negative or positive horizontal shift. In the pathway from retina to thalamus to cortex, ocular input remains segregated in the thalamus (the LGN) and is first combined in V1. In V1, disparity-selective cells have been characterized by their response to offset bars presented to the two eyes ('tuned excitatory,' 'tuned inhibitory,' 'near,' and 'far' cells), response to differential phase of sinusoidal gratings, and response to absolute disparity of RDSs. In V2, disparity-selective neurons have been described as 'obligatory binocular,' selective for disparity-defined contours, and tuned for relative rather than absolute disparity. Despite the number of studies on disparity responses in the visual cortex, there have been no published studies addressing any systematic representation of disparity response in either V1 or V2 of the monkey.

Given the known organizations of the other two featural maps in V2 (color in the thin and contour in the pale and thick stripes of V2), this gap in our knowledge regarding disparity representation in V2 is particularly conspicuous. Disparity-selective responses are believed to be preferentially localized to the cytochrome oxidase thick stripes of V2, but topographic representation within these stripes has not been examined. Thus, at issue are the questions of whether there is

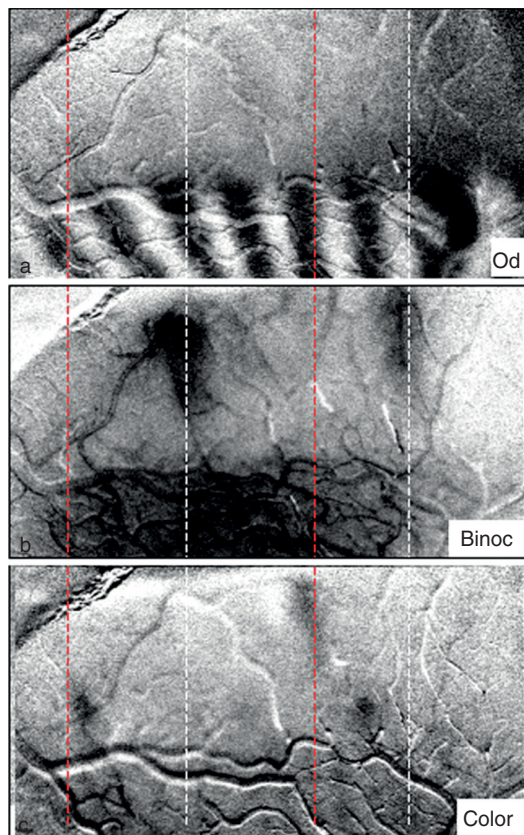


**Figure 9** Optical imaging of brightness response. (a) Single condition color map reveals thin stripes in V2 (black arrowheads above, thick/pale stripes indicated by white arrowheads). Pixels with strongest activation (top 10%) indicated by red outlines. Grayscale in (a) also applies to (b) and (c). (b) Single condition activation map in response to real luminance stimulation. Strongest activation is seen in thin stripes with weaker activation in thick/pale region. (c) Single condition activation map in response to Cornsweet stimulation reveals similar pattern. (d) Blank stimulus map. Scale bar = 1 mm. Each image sum of 50 trials. In all single condition maps, darker pixels indicate larger magnitude reflectance change.  $dR/R$  – reflectance change.

a map for near-to-far depth information and whether disparity and orientation information, which are both represented in the thick stripes, are independently represented or not. The broader issue of parallelism and modularity across featural domains in V2 is also in question. Examination of these issues is further motivated by the presence of maps organized for disparity in the middle temporal area (MT), a primary target of V2 thick stripes.

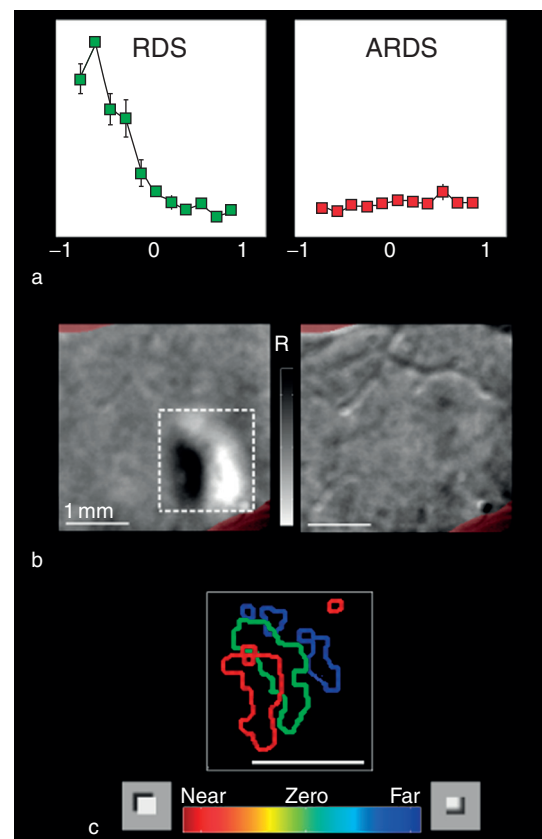
### Topography for Near-Far Disparity

Since it is known that many disparity-selective neurons in V2 include obligatory binocular cells, previous optical imaging studies had indicated localized thick stripes by locating domains preferring activation of two eyes over a single eye. These binocular-preferring domains were located primarily, although not exclusively, within thick stripes (Figure 10). Two recent studies have indicated the presence of topographic organization in V1 and V2. In one, two photon calcium imaging was used to study organization of



**Figure 10** Imaging V2 thick stripes. (a) Ocular dominance (od) map. (b) Color map reveals thin stripes (30% contrast blue/gray minus 30% contrast gray/gray grating). (c) Binocular (binoc) versus monocular preference map reveals thick stripes. Thick stripes (white dotted lines) and thin stripes (red dotted lines) are in complementary locations in V2.

cortical responses to phase offset gratings in the cat. This study revealed beautiful pinwheels of disparity response in cat V1. In another study, RDSs were used to probe disparity organization in primate V1 and V2. These stimuli were designed to produce the percept of surfaces at different depths relative to the background, ranging from  $-0.5^\circ$  near to  $+0.5^\circ$  far. Characterization of single units in V2 revealed that cells in V2 exhibited tuning for specific horizontal disparities (Figure 11(a), RDS). It is important that



**Figure 11** Topography for disparity in V2 thick stripes. (a) Disparity tuning curves of a recorded unit from imaged disparity domain in V2 thick stripe. Random dot stereograms (RDSs) were shifted in disparity from  $-0.42^\circ$  to  $+0.42^\circ$ . This cell is tuned to near  $0.4^\circ$ . Its response to antirandom dot stereograms (ARDSs) shows a flat curve, indicating that the cell's response correlates with the global depth percept and not simply with local disparity cues. (b) Optical images to RDS and ARDS stimuli. Left: RDS, differential image of all near (dark pixels) minus all far (light pixels) stimuli. Dotted box, region of activation in V2 thick stripe. Right: ARDS, differential image of all near minus all far stimuli. (c) Outlines of three disparity domains ( $0.34^\circ$  near,  $0.34^\circ$  far, and zero). Location of activation shifts as disparity changes from near disparity (red) to zero disparity (green) to far disparity (blue). Scale bar = 1 mm (b, c). *R*, reflectance value. From Chen G, Lu HD, and Roe AW (2006) Functional architecture of macaque cortical area V2 for depth surfaces revealed by optical imaging. *Society for Neuroscience* 32: 114–116.

these cells showed little responsiveness to stereograms that do not induce depth percepts; these include anti-random dot stereograms (ARDSs, stereograms in which the contrast of corresponding pixels in the left and right eyes was reversed and uncorrelated stereograms) and stereograms in which the left and right eye dots have a random relationship to each other (Figure 11(a), ARDS). Similarly, optical imaging of such responses revealed strong responses to depth percept-inducing RDSs and little response to ARDSs (Figure 11(b)). Key to the success of these studies was a rapid spot imaging method that permitted quick confirmation of individual eye position and mapping of the imaged field of view. Consistent with previous studies demonstrating preferential disparity response within V2 thick stripes, these activations were located within thick stripes. Furthermore, analogous to a topographic hue representation within thin stripes, a near-to-far topography within the thick stripes was observed (Figure 11(c)). Imaged disparity responses correlated well with disparity preferences of electrophysiologically characterized single unit responses. Furthermore, disparity preferences of units recorded within single vertical penetrations were similar in disparity selectivities, suggesting the presence of a columnar organization for disparity within V2 thick stripes. No such topographies were observed in V1.

### Orthogonality of Disparity and Orientation

It is well established that thick stripes in V2 contain maps for orientation. How, then, do disparity maps relate to orientation in V2? Indeed, how multiple maps coexist within the same two-dimensional cortical space is a fundamental issue that has been addressed by a number of studies. In V1, modeling studies suggest that competing intracortical influences result in observed functional organizations for ocular dominance and orientation. In V2, there is an interdigitation of color, contour, and disparity maps in single thin, pale, thick, pale stripe cycles. However, within single thick stripes, the relative organization of orientation and disparity in V2 has been elusive. Is there a full range of orientations represented at each disparity, and is there a full range of disparities represented at each orientation? Both psychophysical and electrophysiological evidence suggest that representation of horizontal disparity might be biased for vertical orientations. Some researchers have found that disparity-activated regions contained roughly equal representation for different orientations and that on average, each orientation domain overlay a range of disparity domains. This suggests strongly an orthogonality between orientation and disparity within V2 thick stripes.

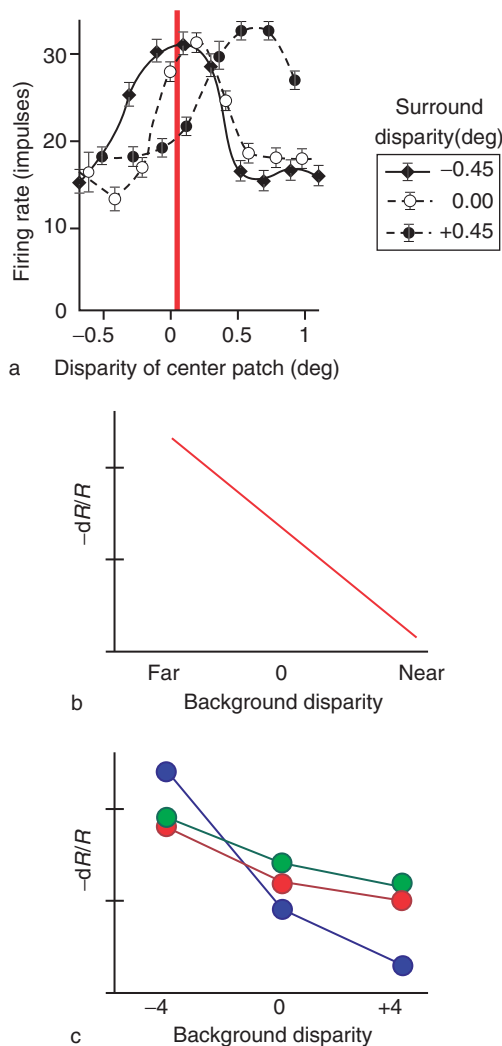
### Absolute versus Relative Disparity

Early studies described the tunings of V1 neurons in terms of absolute disparity. However, depth perception is clearly dominated by relative disparity. That is, if the background disparity moves forward, a relative disparity-tuned cell will shift its tuning forward; if the background moves backward, a relative disparity-tuned cell will shift its tuning backward. The response of an absolute disparity cell would remain unchanged with changing background disparities. Using RDSs and a disparity clamp that permitted stepping absolute disparities without changing any relative disparities within the stimulus, researchers have demonstrated that V1 neurons are tuned for absolute disparity. Of 253 neurons studied, roughly 20% were disparity-tuned. Of these, about 80% exhibited absolute disparity tuning; only two exhibited some (weak) shift consistent with relative disparity tuning. In contrast, others have demonstrated that in V2, many more neurons have responses shifted in the direction of the background shift. Clearly, the influence of surround disparity on center disparity response is greater in V2 than in V1. However, only a few V2 cells exhibit shifts indicative of true relative disparity (i.e., shifts equal to background shift). The distribution of these absolute and relative disparity responses in V2 is unknown. However, given the small number of true relative disparity responses in V2, such organization may not become evident until later processing stages (e.g., V4, MT). Although true relative disparity maps are not expected in V2, V2 activations are expected to be influenced by shifts in background.

As shown in Figure 12(a), a V2 disparity tuning curve shifts toward far if background shifts far (solid line) and shifts near if background shifts near (dotted line). Thus, at a fixed center patch disparity (vertical red line), the neuronal response should decrease for near shifts and increase for far shifts of the background (Figure 12(b)). Findings from one preliminary study have suggested this prediction is met (Figure 12(c)). Optical imaging of a thick stripe in V2 with a fixed center patch disparity (near +4) and different background disparities resulted in predicted decreasing activation values from far to near (imaged signal in three different disparity domains indicated by red, green, blue lines in Figure 12(c)). Thus, responses in V2 thick stripes exhibit some influence by shifts in background in a manner consistent with a degree of relative disparity tuning.

### Summary

Together, these data suggest that topographic organization for near and far disparities may be established relatively early in the visual pathway, in V1 in the cat



**Figure 12** Relative disparity in V2. (a) Disparity tuning curves of a relative disparity cell in V2. Tuning curves shift in direction of background shift. (b) For a fixed surface depth, shifting background from far to near should result in decrease of neuronal firing. (c) Reflectance amplitudes from three disparity domains (red, green, and blue) across shifts in background disparities from  $-0.34^\circ$  to  $+0.34^\circ$  far are consistent with predicted relative disparity response. Deg, degree;  $-dR/R$ , change in reflectance. (a) From Thomas OM, Cumming BG, and Parker AJ (2002) A specialization for relative disparity in V2. *Nature Neuroscience* 5(5): 472–478.

and in V2 in the macaque monkey. These data also suggest that the parameters of disparity and orientation in the thick stripes may be orthogonally represented. That is, within each orientation domain is a range of disparities, and within each disparity domain is a range of orientation representation. Further computational modeling may suggest how orientation and disparity maps are mutually arranged within V2. The overlap of orientation and disparity also suggests that orientation-selective domains within thick stripes are distinct from those in pale stripes. It is important that these data also raise the possibility that

at least some aspects of the disparity organizations observed in MT derive from V2 and are not established *de novo* in MT.

### V1 Sees Local, V2 Sees Global

The finding that V2 neurons are more strongly influenced by shifts in background disparity suggests that V2 encodes not simply the absolute disparity of a surface but, at least to some extent, the relative disparity. Thus, similar to the proposed view of V2 in color and brightness representation, these data are consistent with the encoding of what can be considered higher-order disparity processing in V2 and lower-order disparity processing in V1. Relative disparity signals may be important for figure-ground segregation, which suggests that V2 may be involved in coarse stereo vision.

Another example of V2's role in global perception is the presence of neurons in V2 which achieve disparity capture. The elements within the subjective figure are perceptually 'captured' and 'pulled' on the same depth plane as the figure. The phenomenon has been interpreted as the result of spreading of disparity signals from the subjective figure. In this sense, we consider disparity capture an illusory percept, one which is induced not by true disparity of elements on the surface but by disparity of distant features. In fact, some neurons in V2 have been reported to shift their disparity tuning curves in a manner consistent with disparity capture. If V2 encodes surface depth, then it is conceivable that such disparity capture responses may map to locations similar to those of the surface disparity responses. Again, to achieve such perceptual saliency, the V2's message (the entire surface is at the depth of the border) must somehow overcome V1's (the actual disparity of elements on the surface). This could occur via feedback projections from V2 to V1, resulting in relative suppression of V1. This possibility also remains to be examined.

### Visual Contours

There are a myriad of contours in our visual world, some of which are defined by luminance contrast and many more which are defined by cues without luminance contrast. In addition to 'real' luminance-defined contours (sinusoidal grating or line grating), different texture patterns or abutting line stimuli can create strong percepts of borders or contours. These percepts can be perceived regardless of the orientation of the real line inducers (either with acute or obtuse inducers). Borders between motion fields can also produce very salient percepts of contours (motion contrast contours).

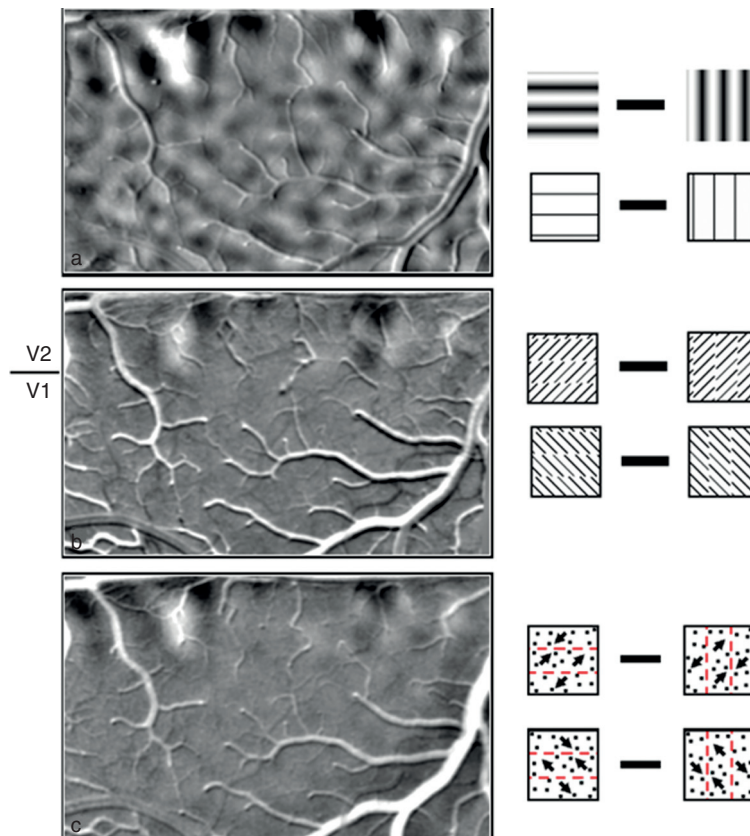
### Cue Invariance

V2 neurons exhibit responses to so-called cognitive contours (also termed ‘illusory contours’). Electrophysiological recordings of single units in V2 have demonstrated a population of cells that share tuning for orientations of both real and illusory contours (both abutting line and occluded contours). Optical imaging studies have demonstrated that orientation domains imaged in response to real contours (real lines or gratings) coalign with those imaged in response to illusory contours, suggesting the presence of higher-order orientation domains. Recent optical imaging studies in alert monkeys have also extended the invariance of response in V2 to include not only real (Figure 13(a)) and illusory contours (Figure 13(b)), but also motion contrast contours (Figure 13(c)). In V1, these studies reveal either a very weak (awake monkey) or an orientation-reversed (anesthetized monkey) response to illusory contours. This may be attributed to the difference in relative activation magnitudes in the alert versus the anesthetized states: V2 activation in the anesthetized monkey

is typically weaker than that in V1 whereas it is at least as strong in the alert monkey.

### V1 Sees Local, V2 Sees Global

The key observation is that real contours strongly activate both V1 and V2, whereas illusory contours (of several different types) elicit activation in V2 but not in V1. Thus while the ‘essence’ of the orientation signal is similar between real and illusory contours, the views in V1 and V2 of these two contour signals are quite different. The key point is that whereas V2 can readily distinguish the orientations of different types of contour stimuli, it is clear that V1 cannot distinguish the orientations of illusory contours. A corollary is that the encoding of contour type (real or illusory) cannot be accomplished by either V1 alone (signals either lack orientation contour or orthogonal orientation) or V2 alone (V2 cannot distinguish between real and illusory). Only with a paired V1 and V2 signal can the real versus illusory nature of a contour be decoded. Thus, both higher



**Figure 13** Local and global V1–V2 networks inferred from cross-correlation studies. (a) Local networks are those that require spatially overlapping receptive fields. Such interactions are typically seen between orientation-matched cell pairs and between spatially overlapped nonoriented V1 and oriented V2 cells. (b) Global networks are those that do not require receptive field overlap. Strong interactions are typically seen between nonoriented V1 and nonoriented V2 cell pairs (surface–surface), oriented V1 and nonoriented V2 cell pairs (border–surface), and nonorientation-matched V1–V2 cell pairs.



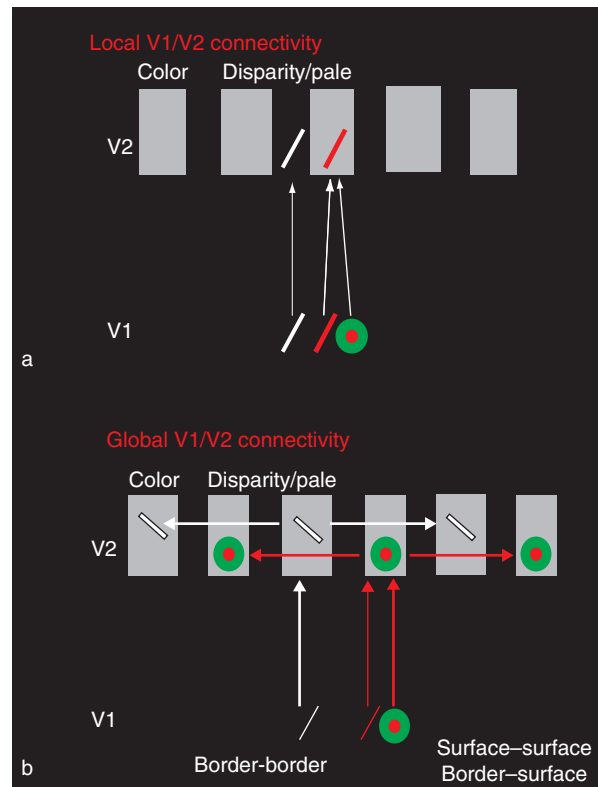
and lower-order signals are necessary for proper contour identification.

## Local versus Global Networks

### How Is a Contour-Specific Paired V1–V2 Signal Achieved?

There is a broader view of V2 function which applies to the multiple feature spaces represented within V2. The view described earlier is a three-stage view of the relationship between V1 and V2. It is a framework based on both anatomical and functional connectivities between different types of V1 and V2 neurons. In brief, the first stage (V1) identifies elemental features such as local color, orientation, absolute disparity, and motion. The second stage (V1–V2 or intra-V2) involves surface-border capture, in which appropriate assignments of surfaces to borders and borders to surfaces are achieved. The third stage involves a competitive balance of feedforward and feedback interactions between V1 and V2. This is the stage via which global percepts might achieve dominance over local cues, perhaps via feedback from V2 to V1.

Based on cross-correlation studies of V1–V2 interactions, two types of V1–V2 networks may be described, one which subserves processing of local cues and another which is more global in extent. Based on approximately 250 recorded interactions between different cell types in V1 and V2 (e.g., oriented broadband, oriented color-selective, nonoriented broadband, nonoriented color-selective), two types of V1–V2 interactions have emerged. The local type of interaction requires spatial overlap of receptive fields. We have found that V1–V2 orientation-matched interactions, as well as some interactions between nonoriented color cells in V1 and oriented color cells in V2, are highly dependent on spatial overlap (Figure 14(a)). In contrast, interactions between nonoriented color cells and oriented cell pairs with nonmatching orientation selectivity do not require spatial overlap (Figure 14(b)). The interactions without spatial overlap may be mediated via extensive intra-V2 connections (stripe-to-stripe arrows in Figure 14(b)). Based on these recordings, it is hypothesized that the local interactions subserves local cue identification (e.g., local contour identification could arise via either Hubel–Wiesel-like integration of nonoriented input from V1 or feedforward of oriented signals already generated within V1). Global interactions subserves surface integration (integration and dissemination of surface feature information) as well as appropriate integration of surfaces and borders. This integration may involve surface capture (feedforward of surface-to-border signals via oriented V1 to nonoriented V2 interactions) or border capture. It is proposed that

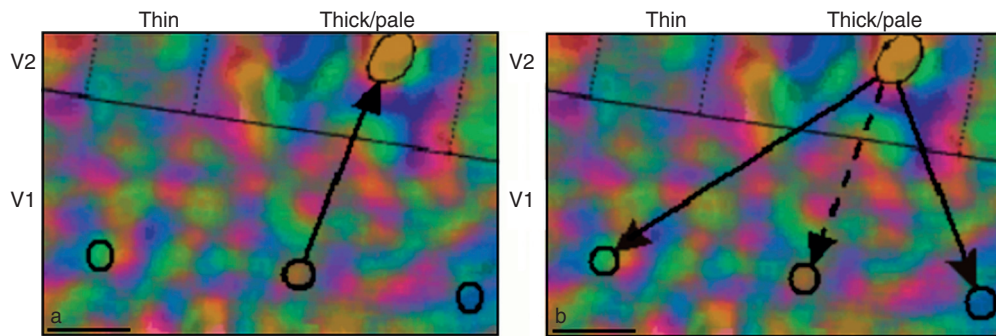


**Figure 14** Cue-invariant orientation domains in V2. (a) Different types of contour stimuli: sine wave gratings, line gratings, illusory contours with acute inducers, illusory contours with obtuse inducers, motion contrast illusory contours. (b) Orientation maps derived from real lines (left) and from illusory contours (right). (a) From Lu HD and Roe AW (2007) *Response to Motion and Motion Boundary in Monkey V2*. Sarasota, FL: Vision Sciences Society. (b) From Ramsden BM, Hung CP, and Roe AW (2001) Real and illusory contour processing in Area V1 of the primate: A cortical balancing act. *Cerebral Cortex* 11: 648–665.

the larger global network within V2 is able to exert influence on the local network, resulting in context-dependent override. Although the mechanisms by which such override occurs are unknown, one possibility is that the strength and/or extensiveness of the global network in V2 results in activation of a suppressive feedback influence on V1.

### A Competitive Balance

Based on these studies, a model of contour processing in early visual cortex has been proposed which comprises a competitive balance between feedforward V1–V2 and feedback V2–V1 influences (Figure 15). In this model, during real contour processing, the feedforward signals dominate and activate matching orientation domains in V1 and V2 (Figure 15(a), solid arrow). During illusory contour processing, feedback signals gain prominence and suppress domains which encode matching ‘real’ contour orientations



**Figure 15** Depiction of feedforward versus feedback forces between V1 and V2. Color-coded orientation map in V1 and V2 (V1–V2 border and stripe borders are indicated). (a) Arrow depicts orientation-specific feedforward influence (local spatial network). (b) Dotted arrow depicts orientation-specific (local spatially localized network) feedback influence from V2 to V1. Solid arrows depict orientation-diverse and spatially extensive (global, spatially less restricted network) influence. Feedback activation is thought to differ between real and illusory contour stimulation. Real contour stimulus preferentially activates orientation-specific feedback (dotted arrow). Illusory contour stimulation preferentially activates orientation-diverse feedback (solid arrows). Scale bars = 1 mm (a, b).

(thereby leading to orientation reversal; [Figure 15\(b\)](#), dotted arrow). In this sense, there is a competitive process between real (feedforward, [Figure 15\(a\)](#)) and illusory (feedback, [Figure 15\(b\)](#)) signals. The perception of any contour would result from a competitive balance between these two orientation-selective forces.

This hypothesis has been tested using psychophysical methods. The reasoning is that if illusory contours activate suppressive feedback pathways, then adding a small amount of real input might push the balance in the feedforward direction. In other words, adding a real line on top of an illusory contour should change the balance. Increasing the contrast of this real line (from subthreshold to suprathreshold contrasts) should push the balance further in the feedforward direction and interfere with feedback-dependent illusory contour perception. Furthermore, since the original observation was one of orientation reversal in V1, the feedback interaction should act in an orientation-selective manner. In other words, it should matter whether the real line added is parallel or orthogonal to the illusory contour. Results support the predictions. Parallel lines had little effect at subthreshold contrasts but tended to interfere with discrimination at suprathreshold contrasts. This interference was orientation dependent, as orthogonal lines had no effect on discrimination at suprathreshold contrasts but interfered only at subthreshold contrasts. These psychophysical data thus support an orientation-specific and contrast-specific influence of real contours on illusory contour perception.

## Summary

These studies provide further weight to the idea that V1 responds to local elements within the scene, while V2 encodes more global aspects. Relative to V1, V2

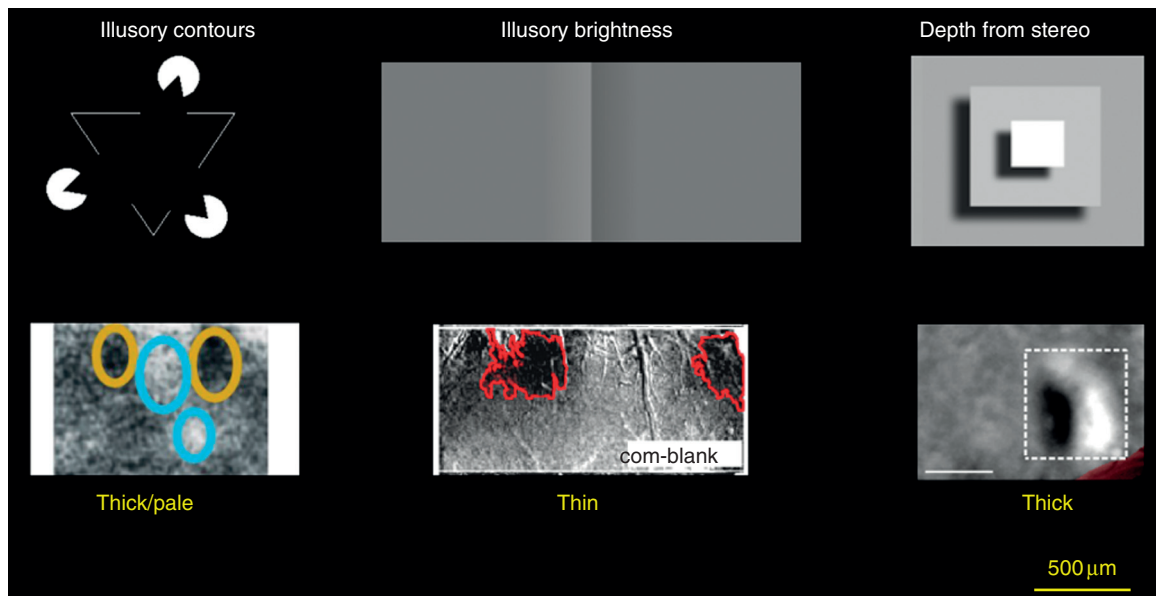
behaves in a more cue-invariant fashion. As summarized in [Table 1](#), whereas V1 responds only to local luminance cues, thin stripes encode generalized brightness percepts. Whereas V1 encodes the orientation of only real contours, V2 exhibits cue-invariant encoding of contour orientation. Whereas V1 contains cells responsive to the disparity between pixels presented to the left and right eyes, whether they are the same or opposite in contrast, V2 contains a map of global coherent disparity response that a global coherent disparity that correlates with the perception near and far percepts.

This article (see [Table 2](#)) has summarized a body of evidence supporting the idea that each cortical area processes the visual world at a different spatial scale and, in that sense, ‘sees’ a different visual world. We suggest that these multiple views of the world compete with each other for dominance, perhaps via a competitive balance between feedforward and feedback signals between different cortical areas. This competition is necessarily context dependent and therefore dynamic. Additional studies in the awake, behaving preparation are likely to provide additional insight into the dynamic aspects of this proposed competition.

These studies have shown that the basis for some global percepts resides within 100–500  $\mu\text{m}$  modules

**Table 2** Local versus global competition

Why so many cortical areas?
Each area ‘sees’ different view (V2 sees different things than V1 sees)
Which view dominates?
Balance of power between areas (Competition between V1 and V2 dominance)
Dynamic network of V1–V2 modules
Correlation with behavior



**Figure 16** Modular basis of behavior. Higher-order percepts such as illusory contours, illusory brightness and color percepts, and stereo depth are encoded in 100–500  $\mu\text{m}$  modules within specific V2 stripes. These modules include orientation domains (left, orange: horizontal; blue, vertical) in thick/pale stripes, ‘brightless’ modules (middle, red: modules responsive to real and illusory brightness modulation) in thin stripes, and stereo depth modules (right, dotted box: all near (dark pixels) minus all far (light pixels)).

in V2 (Figure 16). Cortical modules clearly underlie not only encoding of elemental features such as contour orientation and color preference in V1, but also higher-order percepts such as illusory contour orientation, illusory brightness and color percepts, and stereo depth percepts. In relation to feedforward versus feedback competition, it is likely that in the awake, behaving brain, the relative dominance of V1 and V2 will be evident through the balance of V1 versus V2 modular networks.

*See also:* Contextual Interactions in Visual Perception; Contextual Interactions in Visual Processing; Visual Cortex: Mapping of Functional Architecture Using Optical Imaging; Visual System: Multiple Visual Areas in Monkeys; Visual Cortex in Humans; Visual Cortical Models of Orientation Tuning.

## Further Reading

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