

Processing local signals into global patterns

Yuka Sasaki

Perceptual organization or grouping is one of the central issues in vision research. Recent reports in the neuroimaging literature suggest that perceptual organization is mediated by distributed visual areas that range from the primary visual cortex (V1) to higher visual areas, depending on the availability of grouping cues and on the weight of contribution of each visual area. Evidence suggests that grouping by proximity and collinearity, and also perhaps filling-in, involve V1, whereas grouping by similarity and symmetry seems to depend on activation of higher visual areas. Further studies should include deliberate controls for confounding factors such as attentional artifacts and radial orientation bias, to clarify how spatiotemporal information in visual areas is integrated to give rise to perceptual organization.

Addresses

Athinoula A Martinos Center for Biomedical Imaging, Department of Radiology, Massachusetts General Hospital, Harvard Medical School, 149 13th Street, Charlestown, MA 02129, USA

Corresponding author: Sasaki, Yuka (yuka@nmr.mgh.harvard.edu)

Current Opinion in Neurobiology 2007, 17:132–139

This review comes from a themed issue on
Cognitive neuroscience
Edited by Keiji Tanaka and Takeo Watanabe

Available online 21st March 2007

0959-4388/\$ – see front matter

© 2007 Elsevier Ltd. All rights reserved.

DOI [10.1016/j.conb.2007.03.003](https://doi.org/10.1016/j.conb.2007.03.003)

Introduction

The human brain is able to aggregate local sensory elements to generate global patterns. This process, which is called grouping or perceptual organization, is a central issue in research on early visual processing. Gestalt psychologists (*Gestalt* is a German word that means ‘form’ or ‘shape’) have suggested [1,2] that a whole differs from or is more than a sum of its parts (superadditivity), and that a whole percept will be retained even if local parts are modified (transposition). These concepts are illustrated in Figure 1a–c: in Figure 1a, four black ‘Pac-Man’-like shapes are perceived to be complete circles behind a square that does not exist (demonstrating superadditivity); and in Figure 1b,c, although the shapes of the local elements are different, as a whole the same rectangular shapes are perceived (demonstrating the concept of transposition).

Gestalt psychologists have founded several important laws that drive the rules of grouping, including the laws

of proximity (Figure 1e,f), similarity (Figure 1g,h), good continuation or collinearity (Figure 1i), and symmetry (Figure 1j) (see later in this review for more detail) [3]. Although these Gestalt laws were founded in the early 20th century, the neural correlates that govern them have yet to be entirely clarified. However, recent neuroimaging techniques such as functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG) and electroencephalography (EEG) have revealed brain activity related to Gestalt laws and perceptual organization. The basic approach employed by such human neuroimaging studies is to assess differential brain activity with and without a global percept by manipulating the same local elements, thus dealing mostly with superadditivity. This review aims to summarize neuroimaging reports published within the past few years, and to point out key factors that should be controlled and important issues that should be addressed in future studies. For a review on studies of perceptual organization by methods other than brain imaging, see [4].

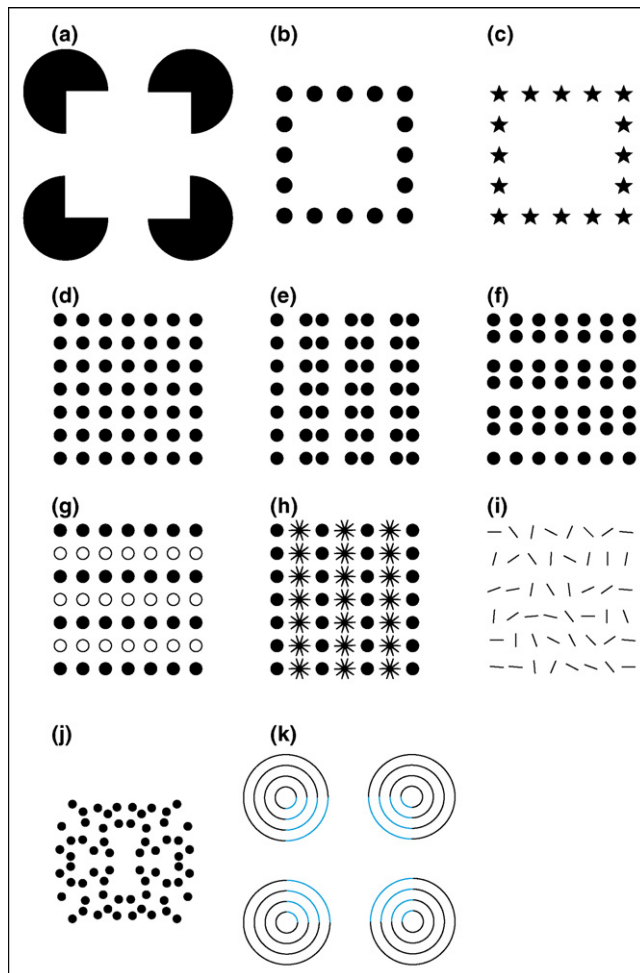
Collinearity, proximity and similarity

Brain imaging studies have shown that different Gestalt laws are not all necessarily processed in the same or a similar manner. Studies suggest that both collinearity (Figure 1i) and proximity (Figure 1e,f) involve an extensive array of visual areas that includes the primary visual cortex (V1) [5–8]; similarity (Figure 1g,h), by contrast, seems not to particularly involve V1 [7–11].

Altmann *et al.* [5] found that collinear grouping of Gabor patches (Box 1) generated greater activity in the V1, V2, VP and V4v areas of the visual cortex and in the lateral occipital area (LO) than did randomly scattered Gabor patches, whether with or without attention control. Analogously, Ban *et al.* [6] compared the fMRI activity produced when an arc was presented in a single quadrant of the visual field with the activity produced when such an arc was presented along with complementary arcs in other visual quadrants, giving rise to the perception of a global circle. These investigators found that the retinotopic areas from V1 to V3 showed greater activation when the arc was perceived as part of a circle than when a single arc was presented alone. This finding is consistent with the study by Altmann *et al.* [5], which suggested that a wide range of activity throughout the visual cortex mediates perceptual organization cued by collinearity.

Proximity grouping is also suggested to involve a multitude of visual areas. V1, in particular, seems to be involved to a greater extent in proximity grouping than in similarity grouping. In fMRI studies of perceptual

Figure 1



Representations of Gestalt laws. **(a)** An illusory contour [42]. Four 'Pac-Man'-like shapes seem to be circles that are complete behind an illusory square. **(b,c)** Two rectangles of the same shape and size are perceived, even though (b) and (c) are made up of different shapes at the local level. **(d-f)** Examples of how grouping occurs according to the proximity between dots (e,f), whereas no such grouping occurs when dots are evenly spaced (d), even though the local dots themselves are identical. **(g,h)** Similarity grouping of local elements according to differences in luminance and shape. **(i)** An example of good continuation by collinearity. Local elements that are smoothly continuous are grouped together. **(j)** Dots in a symmetric array. The dots that are placed symmetrically constitute a global percept. There are two axes (horizontal and vertical) of symmetry in this example. **(k)** A neon color spreading illusion, in which an illusory transparent squared surface is perceived.

grouping, Han *et al.* [7] found that V1 was involved in proximity grouping, but not when grouping was defined by the similarity of local elements, even when local elements were identical for proximity and similarity groupings. A complementary event-related potential (ERP) study that utilized EEG supports these fMRI results, suggesting that, although both V1 and higher visual areas are involved in proximity grouping, similarity grouping is mainly governed by the higher visual areas [8].

Another line of research also indicates that V1 is not particularly involved in similarity grouping. Gamma-band oscillation, defined as brain activity synchronized in gamma-range (30–100 Hz) waves, has been associated with various cognitive processes such as visual grouping, attention and memory [12]. Vidal *et al.* [9] reported that color-based similarity grouping generated an increase in gamma power of 70–120 Hz that was dominant in the central occipital region, which is presumably higher in visual processing pathways than V1. Beta-band (13–30 Hz) synchronization of activity between the left and right hemispheres has also been proposed to be involved in similarity grouping [10,11]. Knyazeva *et al.* [11] found that synchronization of higher beta-band waves (22–28 Hz) in the left and right hemispheres increased more when bilaterally presented gratings were oriented in the same direction as each other (iso-orientation) than when the gratings were orthogonally oriented. This beta-band activity was localized near the VP and/or V4 area, where fMRI activity was also found to increase with iso-orientation gratings [11].

Intriguingly, which frequency band dominates depends on either the required task or the electrodes of interest in both gamma-band [9] and beta-band [11] wave oscillations. Different cognitive tasks such as grouping and focused attention generate gamma-band oscillations at different frequencies over different cortical regions [9], and synchronized beta-band activity tends to elicit different peak frequencies depending on the locations of electrodes and the distances between them [11]. It has been suggested that different frequency bands reflect different spatial scales in cortical synchronization [13]; for example, that low frequencies reflect long-range interactions, whereas higher frequencies reflect more local interactions [13,14]. However, this hypothesis must be more thoroughly tested.

Symmetry

The remarkable ability of humans to detect symmetry (Figure 1j) has fascinated psychologists [15–17,18^{*}]. Symmetry perception is thought to facilitate both sexual selection [19,20] and visual processing [21]. Using various controls, Sasaki *et al.* [18^{*}] examined fMRI activity during symmetry perception by presenting parametrically graded symmetry stimuli (ranging from perfectly symmetrical to random noise in five steps) and measuring psychometric function related to the subjects' perception of symmetry. As expected, perception of symmetry decreased as noise in the stimuli increased. Sasaki *et al.* then examined the correlation between symmetry percept and the fMRI response with subject's attention controls; they did this for each visual area and found correlated activity in V3–VP, V3A, V4v, V4d, V7 and LO. There were strong correlations in V4v, V4d and LO ($r = 0.85, 0.81$ and 0.83 , respectively); in V3–VP, V3A and V7, correlations were significant but not as strong

Box 1 Terminology

Gabor patch: a two-dimensional image (Figure 1a) that is expressed as a combination of a sine wave and a Gaussian function.

Craik–O’Brien–Cornsweet illusion: a brightness illusion, reported by Craik, O’Brien, and Cornsweet [32–36]. In the top panel of Figure 1b, a darker patch is perceived on the left than on the right. However, the actual luminance profile is as shown in the bottom panel of Figure 1b. Thus, the luminance on the far left of the image is actually the same as that on the far right (place your finger at the center of the illustration to perceive the same grayness on the left and on the right).

Phantom illusion: another illusion related to brightness (see supplementary movie 1 and Figure 1a of [37]). When a low-contrast moving grating is separated by a large black gap, a visual phantom of the real grating is perceived over the black gap.

Amodal completion: an illusory percept of an entire object whose entire figure is not completely shown. For example, in Figure 1a of the main text, four black discs are perceived. However, the black physical shapes are not actually round.

Luminance rules necessary for transparent perception: these rules are summarized as below and as illustrated in Figure 1c.

First, the direction of luminance contrast across an opaque border cannot change in the transparent region. Second, the luminance difference across an opaque border must be reduced in the transparent region. Suppose L_1 in Figure 1c stands for the luminance level of that part, and so on (Figure 1c,i). In Figure 1c,ii, it is perceived as a brighter transparent gray patch overlaid on the darker patch, because the two luminance rules for transparency are both hold, where $(L_1 < L_2 \text{ and } L_3 < L_4)$, and $(L_2 - L_1 > L_4 - L_3)$. By contrast, Figure 1c,iii does not satisfy the first luminance rule ($L_1 < L_2$ and $L_3 > L_4$); thus, no transparency occurs. In Figure 1c,ii, L_1 and L_2 are the same as in Figure 1c,ii but L_3 and L_4 are reversed; L_3 in Figure 1c,iii is the same as L_4 in Figure 1c,iii, and L_4 in Figure 1c,iii is the same as L_3 in Figure 1c,ii. The same luminance rules must be satisfied for perception of a neon color spreading illusion. In Figure 1c,iv, the red color seems to spread until the illusory contour, thus, a reddish disk seems to be overlaid on the black radial bars. This is an example of a neon color spreading illusion. The same luminance rules for transparency hold for this configuration (Figure 1c,v). If the luminance rules do not hold for transparent perception (Figure 1c,vi), the color black does not seem to spread, and thus no neon color spreading occurs.

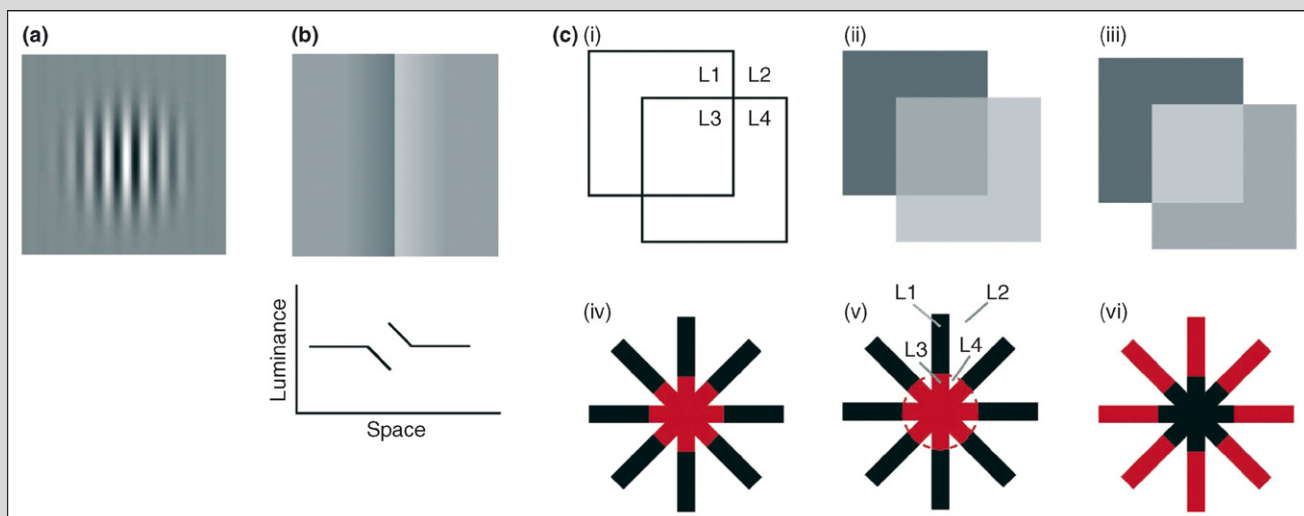


Figure 1

A Gabor patch and displays inducing some of the illusions discussed in this review. (a) A Gabor patch. (b) The Craik–O’Brien–Cornsweet illusion. (c) Luminance rules necessary for transparent perception.

($r = 0.57, 0.67$ and 0.67 , respectively), indicating that V4v, V4d and LO seem to have a particularly strong relationship to symmetry perception. They also found symmetry bias in monkey visual areas that correspond to human visual areas [18], providing evidence that symmetry perception is not specialized to human perception [22] and pointing out the possible evolutionary value of visual processing.

Filling-in

In the natural environment, it is not usual for an entire surface or object to be exposed; often, only its parts are shown. Thus, grouping spatially scattered elements that have the same features as parts of a surface or object is important for correct perception of a surface or object.

Filling-in (Figure 1k) is a perceptual phenomenon in which a visual feature such as color, brightness, texture or motion is perceived in a region of the visual field even though that feature is absent within the region and present only in the surrounding regions [23]; this process is regarded as a manifestation of an important function of perceiving a surface or object. As Komatsu [23] has pointed out, the term filling-in is often used to refer to manifold phenomena, including the blind spot [24–28], neon color spreading [29–31], the Craik–O’Brien–Cornsweet illusion (Box 1) [32–36] or phantom illusions (Box 1) [37,38]. In addition to these illusions, it has been suggested that homogeneous or uniform features such as color and brightness in a surface are mediated by filling-in [39,40]. It is not yet clear whether a unified mechanism

governs all of filling-in and, in fact, recent fMRI and optical imaging data suggest that different mechanisms mediate some types of filling-in phenomena. For instance, the blind spot [24–28], neon color spreading [30], phantom illusion [37^{*}] and brightness-contrast filling-in [41] involve V1 activity, whereas filling-in for the Craik–O’Brien–Cornsweet illusion does not [35,36]. Altogether, there seem to be at least two distinct types of filling-in: one that involves V1 and another that does not. Grossberg and Mingolla [39] suggest that filling-in occurs at both the monocular and binocular levels.

The term filling-in is sometimes also used to describe illusory contours. Such usage of this term can cause confusion, because internal filling-in of surface brightness and color could be functionally different from the illusory contouring that defines a surface. Model studies have suggested that the underlying mechanisms for these two types of filling-in are different [39]. Examining neon color spreading is particularly valuable because psychophysics and neural network modeling have suggested that this phenomenon [31] is an illusion that results from a combination of illusory contour [42] and illusory featural filling-in [39], together with transparent perception. Neon color spreading (Figure 1j; Box 1) requires the same luminance rules necessary for transparent perception [43]. Sasaki and Watanabe [30] used fMRI to compare brain activity when a neon color spreading illusion took place with that when no neon color spreading took place (the control condition) by simply rotating the visual stimuli that were generating the illusion, to break up the luminance rules required for transparency (Box 1). Because the control stimulus was composed of the same visual parts that generate the neon color spreading illusion, total luminance was kept constant throughout the display for both conditions. During neon color spreading, V1 activity was significantly increased relative to control conditions only in the region that corresponds retinotopically to the filled-in region of the neon color spreading illusion. These results demonstrate the importance of V1 in neon color spreading. Moreover, activity was enhanced in the V1, V2, V3–VP, V3A and V4v regions that correspond retinotopically to illusory contours. These results indicate that filling-in of features such as color and brightness is distinctly different from that of illusory contours.

Whether V1 is truly involved in filling-in is still controversial [44,45]. Haynes *et al.* [40] have shown that V1 responses to surface uniformity, and Sasaki and Watanabe [30] have demonstrated that V1 is involved in filling-in caused by neon color spreading. Cornelissen and colleagues [44,45] argue against these findings, suggesting that V1 activity enhancement in a filled-in region is attributed to an artifact related to information at the edge of a surface, rather than internal-feature filling-in, because their model does not postulate filling-in to spread from the edges. However, Komatsu [46] has pointed out that

filling-in could occur from the edges. Furthermore, since the V1 activity reported by Sasaki and Watanabe [30] was obtained by subtracting activity in the neon color spreading illusion condition from that in the control condition, which used a rotated version of the same stimuli, both the illusion and control conditions contained edges. At any rate, resolving this controversy will require further testing to examine whether V1 is involved to the same extent for both the filling-in and edge-only conditions.

Factors that must be controlled

Some brain-imaging experiments of perceptual organization have not taken into consideration possible confounding factors, and have thus led to confusion. Here, I wish to point out two key factors that must be controlled in future studies of perceptual organization: subject attention [47–51] and radial orientation bias [52].

Increased attention to a specific part of the visual field increases fMRI activity in areas of the visual cortex that correspond to the attended region, including V1 [47–51]. To distinguish between activity elicited by perceptual organization and that due to attention, it is crucial to control subjects’ spatial attention in studies of perceptual organization. It has been reported that brain activity can be crucially different with and without attention controls [18^{*},36].

There are at least two approaches for controlling attention: to ask subjects to perform a fixational task or to distribute subjects’ attention over all visual stimuli. As an example of the first, Altmann *et al.* [5] changed the luminance of a fixation point and asked subjects to detect the change in luminance. To illustrate the second approach, Sasaki *et al.* [18^{*}] presented an array of dots at 1 s intervals and modified the hue of one dot in half of all trials; subjects then had to report whether or not a reddish dot appeared.

Which method better controls subjects’ attention, the fixational attention task or the distributed attention task? I have found no significant differences in the results of the fixational attention and distributed attention tasks when studying symmetry perception (Y Sasaki, unpublished data). Although no systematic studies have assessed which attentional control is more effective, effects of interest (the difference between test and control conditions) might become smaller with the fixational attention task than with the distributed attention task [53], because a greater proportion of attentional resources might be taken away from the visual stimuli in a fixational task. Further studies will be needed to address this question.

Another factor that must be controlled is radial orientation bias [52]. Radial orientation is defined as orientation passing through the center of the visual field, much like the spokes of a wheel. Given that orientation columns in

the visual cortex were found by Hubel and Wiesel [54] to have an orderly 180° arrangement within 1 mm, the conventional fMRI voxel size of ~3 mm³ is generally considered inappropriate for detection of orientation bias using fMRI. To overcome this limitation, some investigators have sought to develop clever methods to amplify the slightest differences in fMRI voxel signals [55•,56•,57]. However, Sasaki *et al.* successfully used conventional fMRI techniques to detect radial orientation bias, which is directly linked with retinotopy [52]. In fact, although there have been some reports of variation in orientation sensitivity in visual areas [58–61], these reports have perhaps not been paid close enough attention. A full display of vertical gratings activates the vertical representation of the visual cortex more effectively than does a display of horizontal gratings; horizontal gratings better activate the part of the visual cortex that corresponds to representation of the horizontal meridian [52]. The same is true with oblique gratings if positioned radially. Such radial orientation bias was found consistently throughout the retinotopic visual areas, not only in humans but also in monkeys. As such, radial orientation bias might be one of the fundamental properties of the visual cortex.

Radial orientation bias was found in fMRI activity even when gratings did not reach the fixation point at the center of the display [52]. In addition, the contrast detection threshold was dramatically better with radial orientation than with tangential orientation when a small patch of gratings was presented peripherally [52,61]. Given that a curve-tracing task has been shown to propagate object-based attention and to activate V1 [62], this evidence is important because it demonstrates that radial orientation bias is not caused by an object-based attention that is mediated by the grating, a part of which is connected to the fixation point to which subjects paid attention.

The threshold of detection contrast for stimuli of identical orientation is completely different depending on where the stimulus is presented and whether or not it is radial relative to the center of the visual field. Therefore, because visual cortex activity can change significantly whether or not orientation is radial, careful consideration is necessary when deciding on the orientation of stimulus presentation in studies of perceptual organization. At the same time, the radial orientation bias itself might be a neural factor for some aspects of perceptual organization. For example, radially aligned dots might be more easily detected as a group and elicit more substantial brain responses than dots aligned tangentially. Further research in this direction is necessary.

Involvement of visual areas that are higher than V1

Although some types of perceptual organization, including those cued by proximity [7,8], collinearity

[5,6,11,63,64] and filling-in [23•,28,30,37•,46], do involve V1, other types, such as those cued by similarity [7,9], symmetry [17,18•] and amodal illusory shape completion (Box 1) [65], seem not to involve V1.

Higher visual areas such as V4 and LO seem to have a role in many types of perceptual organization. For instance, although LO is best known as an object processing area [66,67], this area might not merely process objects or shapes. In fact, LO has been found to respond more to background than to shapes cued by collinearity [63], perhaps because it might be involved with figure–ground segregation, which is important for global perception [4•,66]. LO might also process some types of perceptual organization. Sasaki *et al.* [18•] found that responses in this area of the cortex that were selective to symmetric patterns were not caused by pattern, shape or contour percepts. Rather, given that symmetry is an important cue for object recognition [68] and that most objects have symmetric structure, it is possible that in some cases LO actually responds to symmetry rather than to an object itself. Further research is needed to clarify this issue.

Moreover, interpretation of activation in higher areas such as V4 and LO might require caution when they are accompanied by activation of lower visual areas including V1. Activation in a higher area might be a passive reflection of activation in lower visual areas or might reflect processing related to perceptual organization, although it is challenging to separate those possibilities empirically.

It is worth noting that, although researchers generally agree about the definitions of the V1, V2 and V3–VP areas, the definitions of the higher visual areas remain somewhat controversial [15,69•]. Areas such as V3A [70], V3B [71], V4d [72], V4v [70], the kinetic occipital region (KO) [73], V8 [74], the ventral surface of the medial occipital area (VO)-1 [75], VO-2 [75], V7 [48], LO [67,68], LO1 [76] and the fusiform face area (FFA) [77] are not entirely separated; in fact, some overlap is present. Although this review refers to LO as a single unit, this area might itself be further subdivided into two regions [5,64]. Adding to the confusion, different researchers sometimes use these similar terms to refer to slightly different regions. Finally, correspondence between human and monkey visual areas is not yet fully understood [78•]. Topographic and functional definitions of higher visual areas need to be clarified in the future.

Conclusion

This review has surveyed recent studies that have used brain imaging techniques to investigate the neural correlates that govern the integration of local elements into global grouping or perceptual organization. Although a multitude of visual areas, from V1 to LO, seem to be involved with this organization process, the areas that are most responsive depend on the cues associated with

global grouping. Interactions between visual areas — for instance, feedforward and feedback processing between V1 and higher visual areas and, perhaps, lateral interaction — might or might not occur depending on the availability of grouping cues. It is important to reveal the information processing that occurs between visual areas to render perceptual organization. For example, V1 involvement in some perceptual organization might be a manifestation of lateral interaction within V1, or might represent feedback from higher visual areas. Further studies must be conducted to incorporate spatial location and timing information, including ERP and synchronization measurements provided by EEG and MEG, to increase our understanding of the mechanisms behind perceptual organization.

Acknowledgements

I would like to thank Nichole Eusemann for editing the manuscript. This work is partially supported by Exploratory Research for Advanced Technology, Shimojo Implicit Brain Function Project, and Massachusetts General Hospital. My imaging work was supported by National Center for Research Resources P41RR14075, the Mental Illness and Neuroscience Discovery (MIND) Institute, and the Athinoula A. Martinos Center for Biomedical Imaging.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. von Ehrenfels C: **Über Gestaltqualitäten**. *Vjschr Wiss Philos* 1890, **14**:249-292.
2. Spillmann L, Ehrenstein WH: **Gestalt factors in the visual neurosciences**. In *The Visual Neuroscience*. Edited by Chalupa LM, Werner JS: MIT Press; 2004:1573-1589.
3. Wertheimer M: **Untersuchungen zur Lehre von der Gestalt II**. *Psychol Forsch* 1923, **4**:301-350.
4. Roelfsema PR: **Cortical algorithms for perceptual grouping**. • *Annu Rev Neurosci* 2006, **29**:203-227.
This study provides a conceptual framework of how perceptual grouping might be implemented in the visual cortex, on the basis of findings from single-unit recordings.
5. Altmann CF, Bulthoff HH, Kourtzi Z: **Perceptual organization of local elements into global shapes in the human visual cortex**. *Curr Biol* 2003, **13**:342-349.
6. Ban H, Yamamoto H, Fukunaga M, Nakagoshi A, Umeda M, Tanaka C, Ejima Y: **Toward a common circle: interhemispheric contextual modulation in human early visual areas**. *J Neurosci* 2006, **26**:8804-8809.
7. Han S, Jiang Y, Mao L, Humphreys GW, Gu H: **Attentional modulation of perceptual grouping in human visual cortex: functional MRI studies**. *Hum Brain Mapp* 2005, **25**:424-432.
8. Han S, Jiang Y, Mao L, Humphreys GW, Qin J: **Attentional modulation of perceptual grouping in human visual cortex: ERP studies**. *Hum Brain Mapp* 2005, **26**:199-209.
9. Vidal JR, Chaumon M, O'Regan JK, Tallon-Baudry C: **Visual grouping and the focusing of attention induce gamma-band oscillations at different frequencies in human magnetoencephalogram signals**. *J Cogn Neurosci* 2006, **18**:1850-1862.
10. Knyazeva MG, Fornari E, Meuli R, Maeder P: **Interhemispheric integration at different spatial scales: the evidence from EEG coherence and fMRI**. *J Neurophysiol* 2006, **96**:259-275.
11. Knyazeva MG, Fornari E, Meuli R, Innocenti G, Maeder P: **Imaging of a synchronous neuronal assembly in the human visual brain**. *Neuroimage* 2006, **29**:593-604.
12. Herrmann CS, Munk MH, Engel AK: **Cognitive functions of gamma-band activity: memory match and utilization**. *Trends Cogn Sci* 2004, **8**:347-355.
13. Engel AK, Fries P, Singer W: **Dynamic predictions: oscillations and synchrony in top-down processing**. *Nat Rev Neurosci* 2001, **2**:704-716.
14. von Stein A, Chiang C, Konig P: **Top-down processing mediated by interareal synchronization**. *Proc Natl Acad Sci USA* 2000, **97**:14748-14753.
15. Beck DM, Pinsk MA, Kastner S: **Symmetry perception in humans and macaques**. *Trends Cogn Sci* 2005, **9**:405-406.
16. Tyler CW (Ed): *Human Symmetry Perception and its Computational Analysis*. VSP International Science Publishers; 1996.
17. Tyler CW, Baseler HA, Kontsevich LL, Likova LT, Wade AR, Wandell BA: **Predominantly extra-retinotopic cortical response to pattern symmetry**. *Neuroimage* 2005, **24**:306-314.
18. Sasaki Y, Vanduffel W, Knutsen T, Tyler C, Tootell R: • **Symmetry activates extrastriate visual cortex in human and nonhuman primates**. *Proc Natl Acad Sci USA* 2005, **102**:3159-3163.
This research used fMRI to examine the neural correlates for symmetry perception in humans and monkeys. Using alert fixating macaques and state-of-the-art MRI technology such as 7T MRI, the authors found symmetry bias in the macaque visual areas that correspond to human visual areas that also show a symmetry bias.
19. Little AC, Burt DM, Penton-Voak IS, Perrett DI: **Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces**. *Proc Biol Sci* 2001, **268**:39-44.
20. Little AC, Jones BC: **Evidence against perceptual bias views for symmetry preferences in human faces**. *Proc Biol Sci* 2003, **270**:1759-1763.
21. Wilson HR, Wilkinson F, Lin LM, Castillo M: **Perception of head orientation**. *Vision Res* 2000, **40**:459-472.
22. Waitt C, Gerald MS, Little AC, Kraiselburd E: **Selective attention toward female secondary sexual color in male rhesus macaques**. *Am J Primatol* 2006, **68**:738-744.
23. Komatsu H: **The neural mechanisms of perceptual filling-in**. •• *Nat Rev Neurosci* 2006, **7**:220-231.
The paper reviews neural correlates for various filling-in phenomena, and suggests that neurons in deep layers of V1 respond to filling-in.
24. Matsumoto M, Komatsu H: **Neural responses in the macaque V1 to bar stimuli with various lengths presented on the blind spot**. *J Neurophysiol* 2005, **93**:2374-2387.
25. Komatsu H, Kinoshita M, Murakami I: **Neural responses in the primary visual cortex of the monkey during perceptual filling-in at the blind spot**. *Neurosci Res* 2002, **44**:231-236.
26. Komatsu H, Kinoshita M, Murakami I: **Neural responses in the retinotopic representation of the blind spot in the macaque V1 to stimuli for perceptual filling-in**. *J Neurosci* 2000, **20**:9310-9319.
27. Tani T, Yokoi I, Ito M, Tanaka S, Komatsu H: **Functional organization of the cat visual cortex in relation to the representation of a uniform surface**. *J Neurophysiol* 2003, **89**:1112-1125.
28. Tong F, Engel SA: **Interocular rivalry revealed in the human cortical blind-spot representation**. *Nature* 2001, **411**:195-199.
29. Shimojo S, Kamitani Y, Nishida S: **Afterimage of perceptually filled-in surface**. *Science* 2001, **293**:1677-1680.
30. Sasaki Y, Watanabe T: **The primary visual cortex fills in color**. *Proc Natl Acad Sci USA* 2004, **101**:18251-18256.
31. van Tuijl HF: **A new visual illusion: neonlike color spreading and complementary color induction between subjective contours**. *Acta Psychol (Amst)* 1975, **39**:441-445.

32. Cornsweet TN: *Visual Perception*. Academic Press; 1970.
33. Craik K: *The Nature of Psychology*. Cambridge University Press; 1966.
34. O'Brien V: **Contour perception, illusion and reality**. *J Opt Soc Am* 1958, **48**:112-119.
35. Perna A, Tosetti M, Montanaro D, Morrone MC: **Neuronal mechanisms for illusory brightness perception in humans**. *Neuron* 2005, **47**:645-651.
36. Roe AW, Lu HD, Hung CP: **Cortical processing of a brightness illusion**. *Proc Natl Acad Sci USA* 2005, **102**:3869-3874.
37. Meng M, Remus DA, Tong F: **Filling-in of visual phantoms in the human brain**. *Nat Neurosci* 2005, **8**:1248-1254.
This study examined the visual cortex when filling-in of visual phantoms was perceived, and demonstrated that V1, V2 and V3 were strongly involved in the filling-in of visual phantoms. In particular, the visual rivalry technique was used to show that activity in these visual areas is directly correlated with perception.
38. Tynan P, Sekular R: **Moving visual phantoms: a new contour completion effect**. *Science* 1975, **188**:951-952.
39. Grossberg S, Mingolla E: **Neural dynamics of form perception: boundary completion, illusory figures, and neon color spreading**. *Psychol Rev* 1985, **92**:173-211.
40. Haynes JD, Lotto RB, Rees G: **Responses of human visual cortex to uniform surfaces**. *Proc Natl Acad Sci USA* 2004, **101**:4286-4291.
41. Rossi AF, Rittenhouse CD, Paradiso MA: **The representation of brightness in primary visual cortex**. *Science* 1996, **273**:1104-1107.
42. Kanizsa G: **Margini quasi-percettivi in campi con stimolazione omogenea**. *Riv Psicol* 1955, **49**:7-30.
43. Watanabe T, Cavanagh P: **Transparent surfaces defined by implicit X junctions**. *Vision Res* 1993, **33**:2339-2346.
44. Cornelissen FW, Wade AR, Vladusich T, Dougherty RF, Wandell BA: **No functional magnetic resonance imaging evidence for brightness and color filling-in in early human visual cortex**. *J Neurosci* 2006, **26**:3634-3641.
45. Cornelissen FW, Vladusich T: **What gets filled-in during filling-in?** *Nat Rev Neurosci* 2006 DOI: 10.1038/nrn1869-c1031 <http://www.nature.com/nrn/index.html>.
46. Komatsu H: **Activation of primary visual cortex (V1) related to surface brightness**. *Nat Rev Neurosci* 2006 DOI: 10.1038/nrn1869-c1032 <http://www.nature.com/nrn/index.html>.
47. Watanabe T, Sasaki Y, Miyauchi S, Putz B, Fujimaki N, Nielsen M, Takino R, Miyakawa S: **Attention-regulated activity in human primary visual cortex**. *J Neurophysiol* 1998, **79**:2218-2221.
48. Tootell RB, Hadjikhani N, Hall EK, Marrett S, Vanduffel W, Vaughan JT, Dale AM: **The retinotopy of visual spatial attention**. *Neuron* 1998, **21**:1409-1422.
49. Gandhi SP, Heeger DJ, Boynton GM: **Spatial attention affects brain activity in human primary visual cortex**. *Proc Natl Acad Sci USA* 1999, **96**:3314-3319.
50. Somers DC, Dale AM, Seiffert AE, Tootell RB: **Functional MRI reveals spatially specific attentional modulation in human primary visual cortex**. *Proc Natl Acad Sci USA* 1999, **96**:1663-1668.
51. Brefczynski JA, DeYoe EA: **A physiological correlate of the 'spotlight' of visual attention**. *Nat Neurosci* 1999, **2**:370-374.
52. Sasaki Y, Rajimehr R, Kim BW, Ekstrom LB, Vanduffel W, Tootell RB: **The radial bias: a different slant on visual orientation sensitivity in human and nonhuman primates**. *Neuron* 2006, **51**:661-670.
53. Murray SO, Wojculik E: **Attention increases neural selectivity in the human lateral occipital complex**. *Nat Neurosci* 2004, **7**:70-74.
54. Hubel DH, Wiesel TN: **Sequence regularity and geometry of orientation columns in the monkey striate cortex**. *J Comp Neurol* 1974, **158**:267-293.
55. Haynes JD, Rees G: **Predicting the orientation of invisible stimuli from activity in human primary visual cortex**. *Nat Neurosci* 2005, **8**:686-691.
See annotation for [56**].
56. Kamitani Y, Tong F: **Decoding the visual and subjective contents of the human brain**. *Nat Neurosci* 2005, **8**:679-685.
This study, along with [55**], introduced methods to amplify very small differences embedded in voxels from the conventional fMRI technique.
57. Kamitani Y, Tong F: **Decoding seen and attended motion directions from activity in the human visual cortex**. *Curr Biol* 2006, **16**:1096-1102.
58. Mansfield RJ: **Neural basis of orientation perception in primate vision**. *Science* 1974, **186**:1133-1135.
59. Leventhal AG: **Relationship between preferred orientation and receptive field position of neurons in cat striate cortex**. *J Comp Neurol* 1983, **220**:476-483.
60. Rovamo J, Virsu V, Laurinen P, Hyvarinen L: **Resolution of gratings oriented along and across meridians in peripheral vision**. *Invest Ophthalmol Vis Sci* 1982, **23**:666-670.
61. Westheimer G: **Anisotropies in peripheral vernier acuity**. *Spat Vis* 2005, **18**:159-167.
62. Roelfsema PR, Lamme VA, Spekreijse H: **Object-based attention in the primary visual cortex of the macaque monkey**. *Nature* 1998, **395**:376-381.
63. Altmann CF, Deubelius A, Kourtzi Z: **Shape saliency modulates contextual processing in the human lateral occipital complex**. *J Cogn Neurosci* 2004, **16**:794-804.
64. Kourtzi Z, Tolias AS, Altmann CF, Augath M, Logothetis NK: **Integration of local features into global shapes: monkey and human FMRI studies**. *Neuron* 2003, **37**:333-346.
65. Murray MM, Foxe DM, Javitt DC, Foxe JJ: **Setting boundaries: brain dynamics of modal and amodal illusory shape completion in humans**. *J Neurosci* 2004, **24**:6898-6903.
66. Grill-Spector K: **The neural basis of object perception**. *Curr Opin Neurobiol* 2003, **13**:159-166.
67. Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB: **Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex**. *Proc Natl Acad Sci USA* 1995, **92**:8135-8139.
68. Biederman I: **Recognition-by-components: a theory of human image understanding**. *Psychol Rev* 1987, **94**:115-147.
69. Wandell BA, Brewer AA, Dougherty RF: **Visual field map clusters in human cortex**. *Philos Trans R Soc Lond B Biol Sci* 2005, **360**:693-707.
This study provides a helpful overview of nine human visual areas that have been defined by various researchers.
70. Tootell RB, Mendola JD, Hadjikhani NK, Ledden PJ, Liu AK, Reppas JB, Sereno MI, Dale AM: **Functional analysis of V3A and related areas in human visual cortex**. *J Neurosci* 1997, **17**:7060-7078.
71. Smith AT, Greenlee MW, Singh KD, Kraemer FM, Hennig J: **The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI)**. *J Neurosci* 1998, **18**:3816-3830.
72. Tootell RB, Hadjikhani N: **Where is 'dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence**. *Cereb Cortex* 2001, **11**:298-311.
73. Dupont P, De Bruyn B, Vandenberghe R, Rosier AM, Michiels J, Marchal G, Mortelmans L, Orban GA: **The kinetic occipital region in human visual cortex**. *Cereb Cortex* 1997, **7**:283-292.

74. Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RB: **Retinotopy and color sensitivity in human visual cortical area V8.** *Nat Neurosci* 1998, **1**:235-241.
 75. Brewer AA, Liu J, Wade AR, Wandell BA: **Visual field maps and stimulus selectivity in human ventral occipital cortex.** *Nat Neurosci* 2005, **8**:1102-1109.
 76. Larsson J, Landy MS, Heeger DJ: **Orientation-selective adaptation to first- and second-order patterns in human visual cortex.** *J Neurophysiol* 2006, **95**:862-881.
 77. Kanwisher N, McDermott J, Chun MM: **The fusiform face area: a module in human extrastriate cortex specialized for face perception.** *J Neurosci* 1997, **17**:4302-4311.
 78. Sereno MI, Tootell RB: **From monkeys to humans: what do we now know about brain homologies?** *Curr Opin Neurobiol* 2005, **15**:135-144.
- This study offers a concise view of homologies between human and monkey brain visual areas.