

The neural mechanisms of perceptual filling-in

Hidehiko Komatsu

Abstract | Filling-in is a perceptual phenomenon in which a visual attribute such as colour, brightness, texture or motion is perceived in a region of the visual field even though such an attribute exists only in the surround. Filling-in dramatically reveals the dissociation between the retinal input and the percept, and raises fundamental questions about how these two relate to each other. Filling-in is observed in various situations, and is an essential part of our normal surface perception. Here, I review recent experiments examining brain activities associated with filling-in, and discuss possible neural mechanisms underlying this remarkable perceptual phenomenon. The evidence shows that neuronal activities in early visual cortical areas are involved in filling-in, providing new insights into visual cortical functions.

Surface interpolation

The ability of our visual system to reconstruct a continuous surface from incomplete visual inputs using surrounding information.

Contrast border

A boundary of a surface generated by spatially discontinuous change (contrast) in brightness or colour. Many neurons in the retina and early visual pathway are sensitive to contrast border.

Filling-in is a remarkable perceptual event. It is a perceptual phenomenon in which visual features, such as colour, brightness, texture and motion, of the surrounding area are perceived in a certain part of the visual field even though these features are not physically present^{1–4}. The phenomenon of filling-in has attracted the interest of both scientists and philosophers. Filling-in can be regarded as the manifestation of a visual function of surface interpolation, which is an important process for life in a crowded environment. The neural processing of contrast border has long been the main topic of physiological studies of cortical visual processing. Although the function of surface interpolation is no less important, investigation of this function has been left behind. However, recently this state of affairs has begun to change. Numerous psychophysical and physiological studies have been conducted in the past decade to identify the neural mechanisms of filling-in. Our knowledge is still far from complete, but at least we have sufficient data to draw preliminary conclusions and to think about the next step.

Throughout this article, I use the term filling-in to indicate a perceptual event without any assumption about the underlying neural mechanisms. The most fundamental question about filling-in that needs to be addressed is whether some neural computation is necessary for filling-in to occur or whether the brain simply ignores the lack of visual information. If filling-in involves neural computation, where and how does this take place in the brain? Does it occur as neural interactions in early visual areas, or as some form of cognitive inference in the higher association areas?

What is the presumed relationship between different types of filling-in? By answering these questions, we will be better able to understand how the brain represents the illusory experiences of filling-in, and we might gain insights into the way in which visual experience is represented in the brain.

Here, I summarize recent advances in this field, beginning with an introduction to examples of filling-in events. Psychophysical studies are summarized that provide converging evidence that some neural computation occurs in the brain when filling-in occurs, and recent neurophysiological and neuroimaging experiments are described that indicate that neural activation in early visual cortical areas is involved in many types of filling-in. These neural events must be distinguished from topographic remapping — another possible mechanism of filling-in. I then try to combine pieces of empirical evidence to suggest a possible neural mechanism of filling-in. The model is still preliminary, and it is possible that different types of filling-in involve separate mechanisms. Nonetheless, such an attempt is timely and should be useful in providing pointers when considering the next direction of exploration in this field. In the final section, filling-in is viewed in the context of general mechanisms of surface perception.

Phenomenology of filling-in

Filling-in occurs in a variety of situations. Some of these situations have common characteristics, and here I describe a range of filling-in events, classifying them into three main groups.

National Institute for
Physiological Sciences
and Graduate University
for Advanced Studies
(SOKENDAI), Myodaiji,
Okazaki, Aichi, Japan.
e-mail: komatsu@nips.ac.jp
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Deficits of visual inputs. One situation in which filling-in occurs is when some region of the visual field is deprived of visual input — for example, filling-in at the blind spot or at a scotoma^{5–8}. The blind spot is the region of the visual field that corresponds to the optic disc in the retina. Because there are no photoreceptors at the optic disc, where the optic nerve leaves the retina, there is no visual input. However, we still perceive the same colour or pattern as the surround within the region of the visual field that corresponds to the blind spot (FIG. 1a). The blind spot is a physiological structure that reflects the normal development of the visual system. Circumscribed damage to some part of the visual system eliminates visual input from a certain region in the visual field. Such a region is called a scotoma. Filling-in of colour or pattern is also reported to occur at the scotoma^{5,7}. Patients with scotoma often do not realize that such damage exists until an objective test is performed⁹. This is because filling-in occurs at the scotoma, so no odd region is perceived in the visual field.

Steady fixation and stabilized retinal image. Filling-in also occurs in the normal visual field where there is no deficit of visual inputs. In one example, stabilization of the border of a surface on the retina causes filling-in. For instance, when steady fixation is maintained, the contrast of an object in the peripheral visual field gradually decreases, and the object finally becomes invisible. When this happens, the part of the visual field that was originally occupied by the object is filled in with the visual features of the surround. This is known as the Troxler effect^{10–12}. A similar type of filling-in occurs in a small region surrounded by a texture consisting of a large number of elements. When steady fixation is maintained, the originally empty region is perceived as having the same texture as the surrounding field^{5,13,14}. This phenomenon is often referred to as filling-in at an artificial scotoma, but I regard this term as being too general and potentially confusing, so here I refer to it as texture filling-in. This type of filling-in does not happen instantaneously; it usually takes several seconds or longer for filling-in to occur. Eye movements break the filling-in, and the original percept is restored.

An extreme case of this type of filling-in is the stabilized retinal image^{15–17}. If the contour of an object is stabilized on the retina using a specially designed device to eliminate the effect of involuntary small eye movements, fading of the object and the resulting filling-in is facilitated. In one such experiment, Krauskopf presented a visual stimulus consisting of a red disc surrounded by a green annulus, and stabilized the border between the red and green regions on the retina¹⁶. He reported that the inner boundary, which is stabilized, disappeared, the central disc took on the colour of the annulus, and the subject saw a large uniform green disc. A remarkable fact common to both the Troxler effect and the stabilized retinal image experiments is that although an object is present continuously in the scene, visual features at the surround occupy the visual field corresponding to the object.

Neon colour spreading and other illusions. Filling-in occurs in a variety of well-known illusions, three of which are described here. In these cases, filling-in occurs in the normal visual field and does not require prolonged fixation. In FIG. 1b, line ends of coloured parts of the circles are aligned to form the contour of an illusory figure, and the same colour spreads faintly across the illusory figure. This is known as neon colour spreading^{18–21}. The region where neon colour spreading occurs tends to appear transparent.

In FIG. 1c, the region between two vertical lines appears darker than the regions outside the lines. Actually, the luminance in the middle of the central region is the same as that at the right and left margins of the figure. This is known as the Craik–O’Brien–Cornsweet illusion^{22,23}. A rapid change in luminance occurs at the two vertical lines, and on either side of the lines the luminance gradually changes to the constant level. Our visual system is sensitive to the rapid change but is insensitive to the gradual change. Luminance contrast information detected at the border is used to interpolate the brightness of the surface between the borders, and brightness filling-in occurs.

In FIG. 1d, vertical achromatic gratings are separated by a horizontal dark band. However, it is perceived as if an illusory grating crosses the gap to connect the upper and lower gratings. This is known as a phantom illusion^{24,25}. The phantom is perceived more clearly when the two gratings are moving coherently, and is most clearly observed when the luminance of the gap is the same as the maximum or minimum of the gratings. In various filling-in phenomena, filling-in commonly occurs more easily when the boundary contrast decreases.

The main topic of this review is the neural mechanisms of perceptual filling-in. Different types of filling-in might have different underlying mechanisms, or there might be some general mechanism. One extreme possibility is that no active neural processing is necessary to explain the phenomenon. Our visual system might simply ignore the lack of visual input, and filling-in might be a passive outcome of this. However, various psychophysical experiments suggest that active processes are involved in filling-in, and these are described below.

Involvement of active processes in filling-in

Aftereffect and afterimage. The results of several studies have shown that there are functional consequences of filling-in. In one study, motion aftereffect was generated after filling-in of motion at the blind spot²⁶. In human participants, Murakami presented a moving grating on the right eye’s blind spot for 30 s to cause adaptation. Each subject then viewed a smaller grating that was contained in the visual field corresponding to the right eye’s blind spot through his left eye. Clear motion aftereffect was observed even though only filled-in motion, not real motion, existed at this part of the visual field. This result indicates that filled-in motion and real motion share the same neural mechanisms and that sharing occurs at a relatively early stage, when there is retinotopic information, but beyond the stage of binocular convergence of visual signals in the primary visual cortex (V1). It has also been

Luminance

The intensity of light emitted from a light source or reflected from a surface that can be measured objectively.

Achromatic grating

A visual stimulus consisting of alternating light and dark bars in shades of grey.

Motion aftereffect

Also known as the waterfall illusion. Prolonged observation of a moving stimulus leads to an aftereffect in which stationary objects appear to move in the opposite direction.

Retinotopic

If a two-dimensional array of neurons in a given area corresponds topographically (in spatial arrangement) to those on the retina, this area is said to have retinotopic organization. Early visual areas have retinotopic organization with different degrees of precision.

Primary visual cortex

(Also known as V1 or the striate cortex). The cortical area that is the main recipient of visual information from the retinae (by way of the lateral geniculate nucleus).

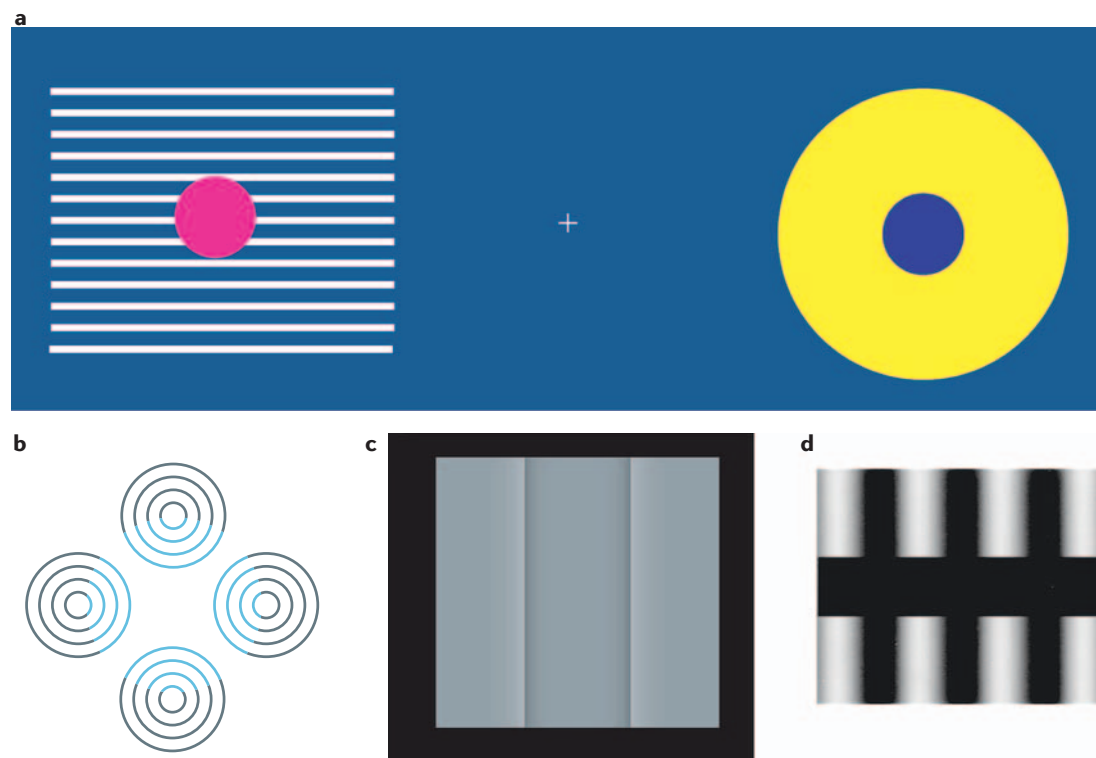


Figure 1 | Examples of various stimuli that induce filling-in. **a** | Filling-in and completion at the blind spot. When the reader's gaze is fixed on the cross at the centre, cover the left eye. If the distance between the printed page and the face is adjusted to an appropriate distance (~15 cm), the smaller blue disc disappears. This is because the smaller circle is contained completely within the blind spot of the right eye. At the same time, a large yellow disc is seen. This is an example of filling-in at the blind spot. When the right eye is covered, the uniform horizontal grating can be seen even though the middle part of the stripes is inside the blind spot. This is due to the pattern filling in on the left eye's blind spot. Such an event is also called perceptual 'completion'. **b–d** | Other examples of filling-in. A faint blue circle in **b** (an example of neon colour spreading), a central dark band in **c** (Craik–O'Brien–Cornsweet illusion) and black stripes crossing the gap in **d** (phantom illusion) are all seen as a result of filling-in. Parts **b–d** can be viewed either monocularly or binocularly. Part **b** modified from REF. 21.

shown that a moving phantom illusion generates motion aftereffect at the visual field where filling-in occurred²⁷.

Shimojo and colleagues have shown that prolonged viewing of a neon colour spreading stimulus generates a negative afterimage of the filled-in coloured surface²⁸. If the inducers (for example, the coloured parts of the concentric rings in FIG. 1b) are presented at different times, neither neon colour spreading nor the afterimage is generated. This indicates that some global processing beyond the simple summation of local effects by each inducer is involved in the generation of neon colour spreading.

It has been reported that when the stimulus is turned off after certain types of filling-in, such as texture filling-in or stabilized retinal image, are established, the filled-in percept of texture or colour is maintained for a short period, then gradually decays^{5,17}. This suggests that some active process with a buffering function is involved in this type of filling-in.

Spread of attention. Many studies have shown that when attention is cued to one part of a surface, attention tends to spread across the entire surface. Davis and Driver investigated whether or not spread of attention differs between 'modal' and 'amodal' completion²⁹. Modal completion means that an illusory surface is perceived with vivid

sensation as if it really exists as part of a certain feature; amodal completion means that the presence of an illusory surface or contour is realized even though it is invisible and it lacks vivid sensation. Filling-in is, by definition, modal. Davis and Driver²⁹ prepared a figure in which a bar was superimposed on an ellipse, and measured the spread of attention between the bar and ellipse. They manipulated the depth order of the bar and the ellipse by changing the binocular disparity of the stimulus. In one situation, the ellipse was perceived to be in front of the bar, and the ellipse was modally completed. In the other situation, the bar was perceived to be in front of the ellipse, and the ellipse was amodally completed behind the bar. One target character and one distractor character were presented either on the bar or on the ellipse. Spread of attention was measured as the amount of interfering effect of the distractor on the discrimination of the target character. They found that the interference between two characters was larger when the ellipse was modally completed compared with when it was amodally completed. This can be regarded as another example in which filling-in is accompanied by a functional consequence. In other words, filling-in not only produces phenomenal illusions, but can also have some impact on other perceptual or cognitive processes.

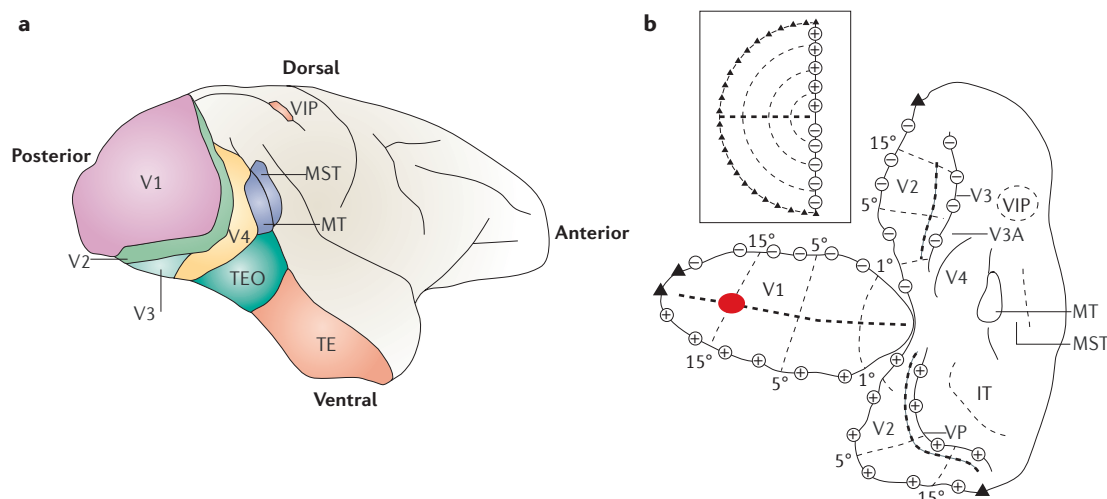


Figure 2 | Visual cortical areas of the macaque monkey. Schematic illustration of several visual areas of the macaque monkey and their retinotopic organization. **a** | Lateral view of the cerebral cortex of the monkey. V1 (primary visual cortex), V2, V3, V4, the inferior temporal cortical areas TEO and TE, MT (middle temporal area), MST (medial superior temporal area) and VIP (ventral intraparietal area) are different visual areas, and the approximate positions and extents of these areas are indicated. **b** | Two-dimensional flattened map of the visual cortex. Boundaries of each area are shown. The large ellipse on the left represents V1. For V1, V2 and V3, a retinotopic map that represents the visual field is shown on the right. The meaning of each symbol can be seen in the inset (upper left), which illustrates a half visual field: black triangles represent the peripheral visual field; the thick broken line represents the horizontal meridian; minus symbols indicate the lower vertical meridian; plus symbols indicate the upper vertical meridian. The red spot in V1 indicates the region corresponding to the blind spot. Part **b** modified, with permission, from REF. 101 © (1983) Society for Neuroscience.

Other examples. If filling-in of a region is achieved by ignoring that region, the contents of the filled-in percept should simply reflect — be the same as — those in the surrounding visual field. Ramachandran and Gregory found that this is not the case for texture filling-in⁵. Subjects viewed a visual stimulus that contained a grey square on a pink background. The square region and background had different textures. Steady fixation resulted in filling-in of the grey square region in two steps: first, only the colour filled in the square region, then the texture filled in. The percept at the first stage does not correspond to any stimulus on the retina, and this contradicts the idea that filling-in is achieved by ignoring that region. Instead, this observation suggests that the filled-in percept is actively constructed by neural processes in the brain.

Parametric studies of filling-in have also shown that the strength of filling-in gradually changes depending on the stimulus parameters^{14,30}. It is hard to explain this parametric nature of filling-in if the visual system simply ignores the scotoma.

Although the studies and observations mentioned above are clearly incomplete, these and other similar examples suggest that filling-in is not a result of merely ignoring some region of the visual field; instead it involves active neural processes.

Activities of early visual areas during filling-in

In the past decade, several studies examining neural activities related to filling-in have emerged and are summarized in this section. These studies had a common strategy: they investigated whether neurons are activated in the region of the retinotopic map of early visual areas representing the interior of the surface where filling-in occurs (FIG. 2). This

is similar to the approach pioneered by von der Heydt and Peterhans in their study of neural responses to illusory contours³¹. It is conceivable that higher areas are also involved, but no attempt has yet been made to study the role of these areas in filling-in. The same strategy used in early visual areas cannot be readily used in higher areas where neurons have large receptive fields and complex stimulus selectivity. Here, I first describe single-neuron recording experiments in monkeys, and then review functional MRI (fMRI) experiments in humans.

Neurophysiological experiments. Neuronal activities in the visual cortex that are related to filling-in at the blind spot were first revealed by Fiorani and colleagues³². They recorded neuronal activity from the V1 region that represented the visual field corresponding to the blind spot (the BS region) of anaesthetized *Cebus* monkeys. When a long moving bar crossed over the blind spot, some neurons were activated in the BS region of V1. In some of their trials, responses were weak when the bar stimulated only one side of the blind spot, and the response to the long bar stimulating both sides was larger than the sum of responses to bar stimuli applied to either side of the blind spot separately. The researchers could sometimes infer the extent of the receptive field in the blind spot by using two orthogonal bars, and these receptive fields were arranged regularly along the retinotopic map of V1. Fiorani *et al.* also found that when the V1 receptive field was covered by an opaque mask in the normal visual field, neurons were activated when a long bar moved across the mask. This is a situation in which amodal completion occurs. However, because the monkey was paralysed and there was little eye movement, the contrast of the mask

Receptive field

The area of sensory space in which stimulus presentation leads to the response of a particular sensory neuron.

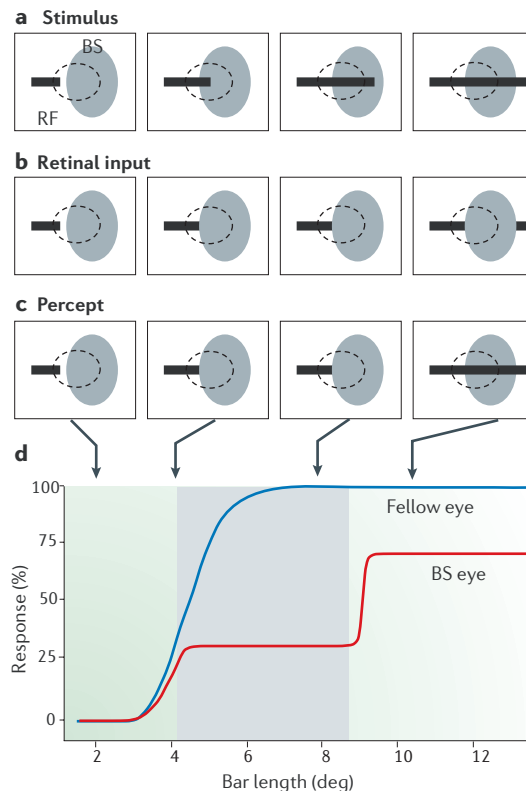


Figure 3 | Neuronal activities that correlate with perceptual completion at the blind spot. Schematic illustration of an experiment³³ designed to study neural responses in relation to the completion of bar stimuli at the blind spot (BS) region of area V1 (primary visual cortex).

a | Examples of bar stimuli. The grey oval represents the blind spot, and the dashed circle is an example of the receptive field (RF). One end of the bar stimulus was fixed at a position outside the blind spot, and the position of the other end was varied. **b,c** | Retinal input generated by each bar stimulus (**b**), and the resulting percept (**c**). As long as one end of the bar was inside the blind spot, the perceived length remained constant, whereas when the bar exceeded the blind spot, perceptual completion occurred, and the perceived bar length increased substantially. Some V1 neurons located in deep layers showed a significant increase in their activity when completion occurred, even though the retinal stimulation increased only slightly. **d** | Schematic example of the responses of such neurons. The red line is the response obtained through the eye that provides the blind spot (BS eye), and the blue line is the response of the same neuron obtained through the opposite (fellow) eye. The pale grey region in **d** represents the visual field that corresponds to the blind spot.

V2

The second tier of visual cortical areas, which is adjacent to V1. V2 consists of three compartments that can be visualized by cytochrome oxidase staining: thick stripe, thin stripe and interstripe.

V2 thin stripe

One of three compartments in V2 where many neurons have sensitivity to the colour or brightness of a visual stimulus.

V3

The third tier of visual cortical areas, which receives its main visual input from V1 and V2. V3 can be divided into two areas because dorsal and ventral parts of V3 have different connections and cell properties.

fields that extended outside the blind spot. To study whether the activities of these neurons correlate with perception, responses to bar stimuli with various lengths were compared (FIG. 3). One end of the bar was fixed at a position outside the blind spot, and the position of the other end was varied. As long as one end of the bar stayed within the blind spot, the perceived length remained constant, whereas when the bar exceeded the blind spot, perceptual completion occurred, and the perceived bar length increased substantially. Some V1 neurons located in deep layers showed a significant increase in activity when completion occurred, even though retinal stimulation increased only slightly. The response increase was much larger than would be expected from simple spatial summation. These neurons tended to be preferentially activated by long bar stimuli.

In another study, we found neurons in the BS region of V1 that were activated when a large uniformly painted surface was presented on the blind spot³⁴. Most of these neurons also had large receptive fields that extended outside the blind spot, preferred large surface stimuli, and were located in deep layers. These neurons seem to carry signals closely related to the filled-in percept. To encode the presence of a uniform surface covering the blind spot, two sets of information need to be represented. One is the presence of large stimuli of certain colour and brightness. The other is the absence of small stimuli, such as line terminations and local contrast, within this region of the visual field. The observed activity of V1 neurons during filling-in at the blind spot clearly carries the first set of information. During filling-in, cells in this region tuned to smaller sizes were silent. So, both sets of information required for filling-in seem to be represented in the BS region in V1.

Neuronal activities related to retinal scotoma, where, as in the blind spot, there is no visual input, have been studied extensively from different perspectives, and these studies are described below.

Neural responses related to the Craik-O'Brien-Cornsweet illusion were recently reported by Roe and colleagues³⁵. They used anaesthetized macaque monkeys, and recorded neurons from areas of V1 and V2 with receptive fields inside the region where illusory brightness is induced. No neurons were activated in the superficial layer of V1, but there were neurons in thin stripes of V2 that were activated when the illusory brightness was modulated. The same neurons were also activated when they were stimulated by real luminance change. Neurons responsive to the luminance change of the surface covering the receptive field have been reported in V1 (REFS 36–39), and some of these also show response change correlated with the brightness induction^{38,39}. The results of Roe and colleagues suggest that the neural mechanism involved in processing brightness of real surface and the illusory brightness filled in from the contrast border share the same neural mechanisms at the level of the V2 thin stripe.

De Weerd and colleagues investigated the responses of V1, V2 and V3 to stimuli that induce texture filling-in⁴⁰. When a monkey was performing a visual fixation task, they presented dynamic texture background in which

border should have been reduced, and it is possible that modal completion occurred. Interestingly, responses to the completed bar stimuli were observed only in layers 4Cα, 4b and 6.

We recently reported a quantitative analysis of responses to bar stimuli on the blind spot in the awake macaque monkey performing a visual fixation task³³. We also found neurons in the BS region of V1 that are activated by a long bar crossing over the blind spot. In contrast to the report of Fiorani *et al.*, these neurons had receptive

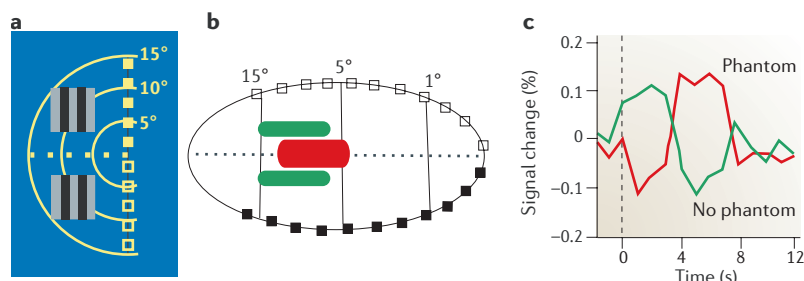


Figure 4 | Neural activation during filling-in of a phantom illusion. Schematic illustration of a functional MRI (fMRI) experiment used to study activity relating to a phantom illusion in the human visual cortex⁴². In this experiment, two moving gratings that were separated by a gap were presented to the upper and lower visual fields. **a** | The positions of two gratings in the visual field. When two vertical gratings were presented, a phantom grating was perceived to extend through the gap region, whereas when horizontal gratings were presented, no phantom illusion occurred. Activity in the cortical region corresponding to the gap when the vertical gratings were presented was compared with activity when the horizontal gratings were presented. **b** | The regions corresponding to the gap (red) and gratings (green) are indicated on the retinotopic map of area V1 (primary visual cortex). Filled squares represent the upper vertical meridian; open squares represent the lower vertical meridian. Activation consistent with phantom perception was observed in V1 and V2. **c** | When a pair of vertical gratings was presented to one eye and a pair of horizontal gratings was presented to the other, binocular rivalry was perceived, and a phantom illusion appeared and disappeared alternately. When fMRI signals were aligned at the time of the alternation of perception, the activity in the gap region increased after the phantom was perceived, and decreased when the phantom disappeared. Part c modified, with permission, from REF. 42 © (2005) Macmillan Publishers Ltd.

many short white line elements were moving randomly on a black background. Within the background there was a grey square region without texture. The researchers investigated what happened when a neuron's receptive field was placed in the grey region, and found that many neurons in V2 and V3 gradually increased their activity several seconds after stimulus presentation. This time course is similar to that of the filling-in documented when humans observed the same stimulus. The response increase was stronger in V3 than V2, and was not clear in V1.

von der Heydt and colleagues examined neural response change associated with colour filling-in in the Troxler effect¹¹. When a monkey was fixating, it was presented with a concentric stimulus that had a central disc of one colour and a surrounding annulus of a different colour. When steady fixation was maintained for several seconds, the central disc became blurred, and this region was filled in with the colour of the annulus. The monkeys were trained to report the change in perceived colour. von der Heydt *et al.* then examined the activities of neurons in V1 and V2 that had receptive fields inside the central disc and that responded to the uniform disc (surface cell). They observed no clear change in the activities of surface cells in either V1 or V2. By contrast, responses of edge cells that respond to the contrast at the border gradually decreased during fixation. This indicates that surface cells signalled the disc colour presented to the retina regardless of whether filling-in occurred or not. In this experiment, V1 neurons were recorded from superficial layers.

So, the results of single-unit recording experiments are diverse: neural responses during filling-in at the blind spot have been observed in V1, whereas those

occurring during the Craik–O'Brien–Cornsweet illusion and texture filling-in were observed in V2 or at a later stage. No response change related to the filling-in of the Troxler effect was observed in either V1 or V2 regions representing the interior surface where filling-in occurred. These differences might reflect diversity in the underlying neural mechanisms. They might also be related to differences in the stimuli used: the experiment for filling-in at the blind spot used simple coloured surface or bar stimuli — quite different from the stimuli used for the texture filling-in experiment. Furthermore, differences in the recording layer must be considered: neural responses related to filling-in at the blind spot were observed in deep layers of V1, but the recordings using the Craik–O'Brien–Cornsweet illusion and the Troxler effect were concentrated in the superficial layers of V1, so we cannot tell what is happening in the deep layers of V1. This point is considered in a later section.

Neuroimaging experiments. In recent years, several studies have examined the brain activities of healthy human participants during filling-in using fMRI. The basic strategy of the experiment is similar to the single-unit recording experiments described above: first, to determine the retinotopic map of the early visual areas and identify the region of the visual field where filling-in occurs; then, to investigate activation of this area when filling-in occurs.

In one of these studies, Sasaki and Watanabe examined activation during neon colour spreading, and found that the V1 region corresponding to the interior of the filled-in surface is activated⁴¹. Interestingly, similar activity was not observed in extrastriate areas corresponding to the filled-in surface.

Meng and colleagues investigated activity associated with a phantom illusion⁴² (FIG. 4). In their experiment, two moving gratings were presented in the upper and lower visual fields, and were separated by a gap. When two vertical gratings were presented, a phantom was perceived to extend through the gap region, whereas when horizontal gratings were presented, no phantom illusion occurred. They identified the cortical region corresponding to the gap and compared the activity recorded when vertical gratings were presented with that obtained when horizontal gratings were presented. Activation consistent with phantom perception was observed in V1 and V2. When a pair of vertical gratings was presented through one eye and a pair of horizontal gratings was presented through the other eye (dichoptic presentation), the phantom was perceived across the gap in one eye, and no phantom was perceived in the other. This caused binocular rivalry, and the phantom illusion appeared and disappeared automatically every few seconds. When fMRI signals were aligned at the timing of the alternation of perception, the activity in the gap region increased when the phantom was perceived, and decreased when the phantom disappeared. This indicates that even when retinal stimulation is constant, V1 activity changes in close correlation with perception.

Tong and Engel looked at activity in the BS region of V1 using binocular rivalry⁴³. They presented pattern stimuli on the blind spot of one eye or to the corresponding visual field of the fellow eye. In these cases, although

Extrastriate areas

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

Binocular rivalry

A phenomenon that occurs when each of a subject's eyes is shown a different image. This results in a bistable visual experience. For example, perception of horizontal or vertical bars spontaneously alternates when the two bar types are viewed through different eyes simultaneously.

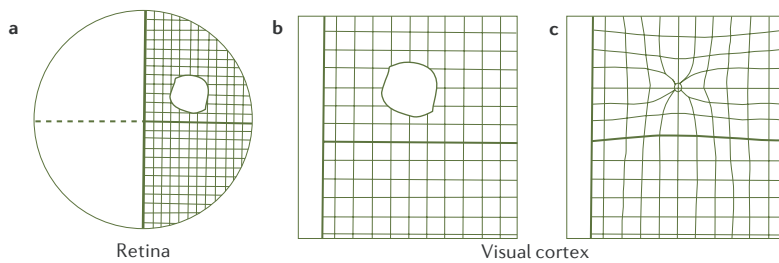


Figure 5 | Cortical reorganization due to retinal scotoma. Schematic illustration of the reorganization of the retinotopic map of the visual cortex following a binocular retinal lesion. **a** | Schematic illustration of a retinal lesion (white patch) on the visual field map (grid) projected onto the retina. A retinal lesion at the same visual field location is also made in the opposite eye. **b** | Retinotopic map of the visual cortex immediately after the binocular retinal lesion. A silent region appears (white patch) that corresponds to the binocular scotoma, and neurons in this region are not responsive to any visual stimuli. No clear distortion of the retinotopic map is observed. **c** | Retinotopic map of the visual cortex several months after the retinal lesion. Neurons in the originally silenced region are responsive to stimuli presented around the scotoma, and there is clear distortion of the retinotopic map. Parts **a–c** modified, with permission, from REF. 49 © (1993) Oxford University Press.

the percept is the same, the activation caused by the same pattern stimulus is much stronger when it is presented through the fellow eye. This is because the BS region in V1 is basically a monocular region dominated by the input through the fellow eye. They used this fact to examine the activity change associated with filling-in at the blind spot. They dichoptically presented a green horizontal grating or a red vertical grating either on the blind spot of one eye or to the corresponding visual field of the other eye. In this situation, the filled-in grating on the blind spot and the orthogonal grating viewed through the fellow eye caused binocular rivalry, and the perception of the green horizontal grating and the red vertical grating automatically alternated. When fMRI signals were aligned at the time of perceptual alternation, the signal strength increased when the grating presented through the fellow eye was perceived, and decreased when the filled-in grating was perceived. Although the activation associated with filling-in is not shown directly, this result clearly indicates that the activity at the BS region of V1 closely correlates with perceptual alternation at the blind spot.

Morrone and colleagues⁴⁴ examined activity associated with the Craik–O’Brien–Cornsweet illusion by comparing fMRI signals associated with a Craik–O’Brien–Cornsweet stimulus with those in response to a line stimulus with matched contrast that did not induce brightness filling-in. They found responses selective to the Craik–O’Brien–Cornsweet illusion in two higher associative areas but not in early visual areas, which appears to contradict the results of a unit recording experiment. The reason for this discrepancy is not clear.

To summarize, recent studies using fMRI in humans and single-unit recording experiments in primates have commonly, although not always, found activation associated with filling-in in early visual areas. fMRI studies in particular have demonstrated V1 activities that correlate with perception in three phenomena tested — filling-in at the blind spot, neon colour spreading and visual phantom illusion.

Cortical reorganization and filling-in

Another type of neural event associated with filling-in that must be distinguished from those described above — topographic remapping — is considered in this section.

The basic strategy common to physiological studies summarized in the previous section is the examination of activity in the cortical region that topographically corresponds to the visual field where filling-in occurs. This strategy is based on the premise that the cortical region has a normal topographic map of the visual field. However, this premise does not hold for binocular retinal scotoma. When retinal lesions are made at corresponding positions in both eyes (binocular retinal scotoma), the region in the visual cortex retinotopically corresponding to the scotoma is deprived of visual input. As a result, this region becomes silent and neurons in this region do not respond to any visual stimulus for some time. However, neurons in this region gradually restore responses to stimuli presented around the scotoma, and if the scotoma is not too large no silent region remains several months after the retinal lesion^{45,46}. At that time, neurons located in the cortical region that corresponds to the scotoma have receptive fields around the scotoma. This means that reorganization of the retinotopic map of the visual cortex has occurred and the region around the scotoma is distorted (FIG. 5), although this might not always happen⁴⁷.

What would be the perceptual consequence of such reorganization? One possible scenario is that the neurons in higher cortical areas receiving the signal from the reorganized V1 region interpret it according to the original retinotopic map and treat it as if the signal originated from visual input within the scotoma^{48,49}. In this case, the subject would perceive as though the visual features present at the surround of the scotoma also exist within the scotoma. Such mislocalization of visual signals might cause perceptual filling-in at the binocular scotoma. It is reported that similar, although much less extensive, reorganization also occurs for monocular retinal lesions⁵⁰. In human patients with macular degeneration, a large degree of reorganization of the retinotopic map in the visual cortex has been observed using fMRI measurements⁵¹. Therefore, distortion of the visual space accompanying the reorganization of the cortical retinotopic map is probably related, at least in part, to the filling-in at the scotoma.

Can filling-in at the blind spot be explained by a similar scenario? The blind spot resembles a monocular scotoma because both form a monocular region in the cortical retinotopic map. However, it is highly unlikely that a similar mechanism is involved in both. At the BS region of V1, no neuron has been found whose receptive field is displaced to the outside of the blind spot in only one eye. Although there are binocular neurons in this region, the part of the receptive field that extends out of the blind spot largely matches between the two eyes³⁴. Psychophysical experiments examining the spatial distortion around the blind spot failed to detect clear distortion⁵², although some studies claim the opposite⁵³. A recent fMRI study investigating this question also

Macular degeneration

A disease of the retina in which the macula, the central part of the retina, degenerates.

failed to find distortion in the retinotopic map around the blind spot⁵⁴. Therefore, neural mechanisms of filling-in at the blind spot cannot be explained by the distortion of the retinotopic map, and we need to consider other mechanisms. Likewise, for various filling-in phenomena besides that at the retinal scotoma, there seems no reason to assume that distortion of the retinotopic map is involved.

Possible neural mechanisms of filling-in

As described above, neurophysiological and neuro-imaging studies have shown that in most situations in which filling-in occurs, early visual areas are activated. Especially important is the fact that neurons are activated in the region of the retinotopic map of early areas representing not only the boundary of the surface but also the interior of the surface. These neural activations correlated with perception. On the basis of these empirical findings, we can now consider the neural mechanisms of filling-in.

Symbolic or cognitive theory. Two different ideas about the neural mechanisms of filling-in have been considered. One of these is known as the ‘symbolic’ or ‘cognitive’ theory^{4,11}. According to this theory, early visual areas extract only the contrast information at the surface border, and the colour and shape of the surface are reconstructed in higher areas on the basis of this information. A blind spot or scotoma does not generate border signals by itself, but the surface covering these regions generates contrast information at its border. Higher areas use this information to represent the entire surface, filling in the blind spot or scotoma. In the Troxler effect and stabilized retinal image, border signals of a surface that is stationary on the retina diminish and the strong signal from the unstabilized outer border is used to construct the entire surface, resulting in the perceptual filling-in of visual features from the unstabilized border. According to this theory, there is no need for the activity change to occur in the surface region where filling-in of visual features is perceived.

However, experimental results described above indicate that various types of perceptual filling-in, such as filling-in at the blind spot, the Craik–O’Brien–Cornsweet illusion or neon colour spreading, accompany neural activation as early as V1 or V2, and this contradicts the prediction of symbolic theory. So far, only the experimental results of the Troxler effect appear to be consistent with this theory.

Isomorphic theory. Another idea about the mechanisms of filling-in is known as the ‘isomorphic’ theory. This theory assumes that when perceptual filling-in occurs, spread of activation occurs across the retinotopic map of the visual cortex from the border to the interior of the surface, and a two-dimensional array of neurons with a pointwise representation of visual features, such as colour or brightness, is activated in early visual areas^{2,4,55–57}. One premise of this theory is that a similar two-dimensional array of feature-sensitive neurons is activated when the real surface is perceived in the normal visual field, and this

has been confirmed by several recent studies^{38,39,58}. So, can we observe the activities of such two-dimensional arrays of feature-sensitive neurons when perceptual filling-in occurs at a certain region in the visual field? The results of neural recordings are different from the prediction of the isomorphic theory in several ways. The fact that neurons activated during filling-in at the blind spot are observed in the BS region of V1 seems to be consistent with isomorphic theory. However, the activated neurons were located in the deep layer — activation was not observed in the superficial layer of V1 — and they tended to have large receptive fields extending outside the blind spot³⁴. When a uniform surface presented in the normal visual field is viewed or when a surface covering the blind spot is viewed through the fellow eye, neurons in the superficial layer and those with small receptive fields are also activated. In this regard, the experimental findings are different from those that isomorphic theory would predict. Experiments examining the Craik–O’Brien–Cornsweet illusion and texture filling-in found neural activation in V2 or V3 regions corresponding to the surface^{35,40}. These examples suggest the possibility that the perception of real surface and that of filled-in surface share the same neural processes at some stage beyond V1. On the other hand, fMRI studies in humans have usually found activity of V1 correlating with perception at the region corresponding to the filled-in surface^{41–43}.

Several psychophysical experiments have shown that apparently instantaneous surface perception actually takes time, depending on the spatial extent of the surface^{59–62}. These results were taken to indicate the propagation of signals across the spatially arranged array of neurons and are thought to be evidence of isomorphic theory. However, other scale-dependent, long-range interactive processes in which time needed for neural computation depends on the spatial extent might also explain these observations, even if the process is dissimilar to that assumed by isomorphic theory. Below, I consider a possible neural mechanism of filling-in from a different perspective, on the basis of the characteristics of neural responses observed in V1 during filling-in at the blind spot.

A scale-sensitive mechanism in deep layers. We recorded neurons from the BS region in V1 that responded when a uniform surface was presented to the blind spot³⁴. We examined the selectivity of these neurons to the surface size in either binocular or monocular viewing using only the fellow eye and found that all of these neurons preferred large surface size. We have also found that neurons whose responses are enhanced at the completion of the bar stimulus in the blind spot have a preference for long bar stimuli³³. In both studies, these neurons were recorded mainly from deep layers and were not observed in superficial layers. These results suggest that when perceptual filling-in occurs at the blind spot, different sets of neurons in deep layers are selectively activated depending on the stimulus to be filled in. When a uniform coloured surface is filled in, neurons in deep layers that prefer a large surface with a particular colour are

Pointwise representation
One way to represent surface attributes such as colour is to activate colour-selective neurons that have a small receptive field at each point on a surface. This is an example of pointwise representation.

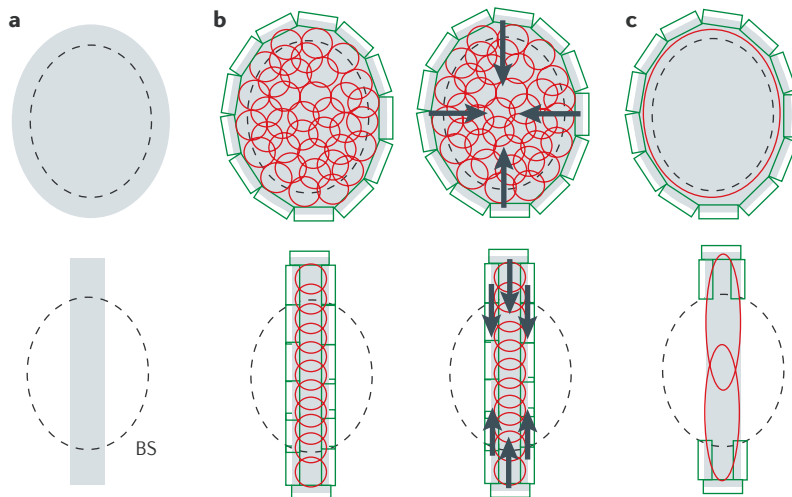


Figure 6 | Possible neural mechanisms of filling-in at the blind spot. Neural events predicted by 'isomorphic' theory and actually observed events in the blind spot (BS) region of area V1 (primary visual cortex) when perceptual filling-in of a uniform surface (top row) or completion of a bar stimulus (bottom row) occurs at the blind spot. **a** | Stimuli that induce filling-in and completion, respectively, at the blind spot (dashed line). **b** | Neural events predicted by isomorphic theory. Rectangles indicate edge cells, which are sensitive to the orientation of the edge and extract the contrast signal at the edge. Red circles indicate surface cells, which can code the surface colour at each point. The size of each circle is the average receptive field size of superficial cells in the BS region of V1. According to this theory, the contrast signal detected at the edge is spread across a two-dimensional array of feature-sensitive neurons as indicated by arrows. **c** | When a uniform coloured surface is filled in, neurons in deep layers that prefer a large surface are selectively activated; when a bar stimulus is completed, neurons preferring long bars are selectively activated. These neurons tend to have large receptive fields (indicated by red ellipses) that extend outside the blind spot. This selection of particular types of neuron in V1 deep layers might be important in the process of filling-in.

selectively activated; when a bar stimulus is completed, neurons preferring a stimulus elongated along a given orientation are selectively activated (FIG. 6). Similarly, when a texture pattern with elements of a certain size fills in the blind spot, neurons in deep layers that prefer that size might be selectively activated.

It has been shown that there is an orderly map representing various spatial frequencies in the superficial layer of V1 (REFS 63–66), but there appear to be neurons that prefer various stimulus sizes in the deep layers as well⁶⁷. Studies systematically investigating the receptive field sizes in different layers have shown that the mean size is largest in V1 layer 6 (REF. 68) and in layer 5 of area MT (REF. 69), and that the variation of the receptive field size tends to be quite large in these deep layers. Presumably, spatial scale is represented separately in both superficial and deep layers, and the representations might be functionally quite different. Selection of neurons in deep layers that represent a particular spatial scale and that are sensitive to particular features might be important in filling-in⁷⁰. Inputs to deep-layer neurons carrying signals for filling-in can be given by the horizontal connection in V1, and feedback projection from the extrastriate cortex.

The above argument is based on studies of the BS region in V1. Neuronal activities in deep layers of V1 have not been investigated in physiological experiments

studying different types of filling-in phenomena, and we do not know whether or not similar neuronal activities occur in deep layers. Although uniform colour or brightness can be processed in V1, coding texture might be possible only at a stage beyond V1 with large receptive fields that can extract some statistical property of the image. Neon colour spreading seems to require object representation based on a global configuration of elements and formation of an illusory figure, and higher cortical areas need to be involved⁷¹. However, even in these cases, V1 might be activated by feedback projection if its retinotopic map is important to filling-in. If so, it is possible that a common mechanism involving deep layers of V1 is shared by various types of filling-in.

If the Troxler effect is mediated by a similar mechanism, dissociation might occur between the superficial and deep layers of V1 regions representing that area such that the superficial neurons code retinally given colour whereas the neurons in deep layers code perceived colour. Neurons in deep layers of V1 project intracortically, as well as subcortically, to several structures such as the pulvinar and the lateral geniculate nucleus (LGN) of the thalamus, the superior colliculus and the claustrum. Neuronal activities of these structures have not been studied in relation to filling-in. Of these structures, it is suggested that the pathway through the pulvinar carries one of the main driving signals to the extrastriate areas⁷². One study suggested that a feedback connection from V1 to the LGN is involved in grouping spatially separate parts into single objects by synchronizing spike discharges of LGN neurons that are activated by different parts of stimuli⁷³. Because filling-in and grouping share some functional similarities, they might share some underlying mechanisms⁷⁴. In addition, recent neuroimaging studies have shown that the LGN shows activation that correlates with perception in binocular rivalry^{75,76}.

Symbolic theory and cognitive theory are the two most extreme theories of filling-in. Neither one of these theories seems entirely consistent with empirical findings of brain activation related to filling-in. The actual mechanism of filling-in might be quite complex, and there might be more than one filling-in process. One mechanism that incorporates empirical findings involves the selective activation of feature- as well as scale-sensitive neurons in deep layers of V1.

General mechanisms of surface perception

Filling-in is thought to be related to the function of surface interpolation based on border contrast information⁷⁷. Why did our visual system evolve such a function? One likely explanation is that this function is deeply related to adaptation to life in a three-dimensional world, in which various objects are placed in space and occlude each other. Unless the occluding object is transparent, only the nearest surface is visible, and its features are perceived. If, however, some parts of the occluded surface are seen, the object can be reconstructed by combining incomplete contour segments. The nearest surface is modal, whereas other surfaces hidden behind are amodal. However, it has

Spatial frequency

A variable determined by the width of stripes on a grating. A grating with low spatial frequency has thick stripes, whereas a grating with high spatial frequency has narrow stripes.

Pulvinar nucleus

The pulvinar is a complex of several nuclei in the thalamus that have strong connections with many visual cortical areas.

Lateral geniculate nucleus (LGN)

The LGN is a nucleus in the thalamus that acts as a major relay station for visual signals from the retina to area V1. The LGN also receives a massive feedback projection from V1.

Qualia

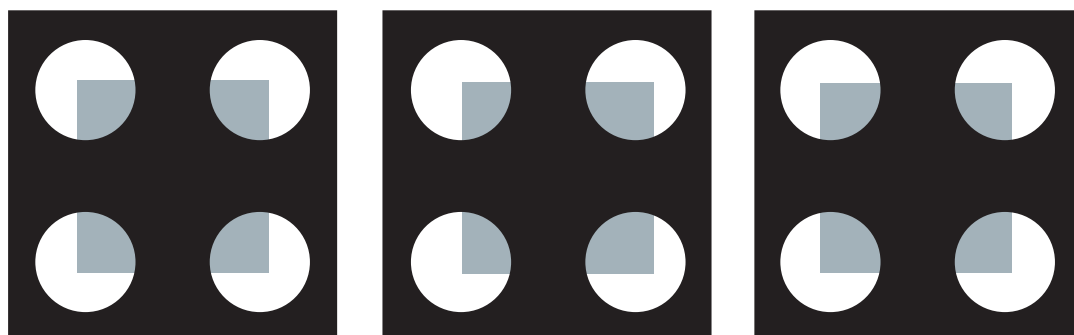
Qualities of conscious perceptual experience, or the 'raw' feel of sensation, such as the 'redness' of the colour red.

Depth assignment

When a retinal image contains multiple surfaces, the depth order of the surfaces is derived by using various monocular as well as binocular visual cues in the image.

Stereo-image

A set of two images — one of which is presented to the right eye and the other to the left — that contain binocular stereo-disparity. Different parts of the stereo-image appear to be at different depths.

Box 1 | Influence of three-dimensional interpretation of the scene on filling-in

Nakayama and colleagues⁸³ have shown that there is a close interaction between depth assignment and filling-in. In the panel, the central image can be fused with either the left or the right image to generate two stereo-images by converging or diverging the two eyes. In one of these, an illusory square is seen floating in front of the circles. In the other, an illusory square is seen behind the circles. In the former case, the square is 'modally' completed and clear neon colour spreading is perceived. By contrast, in the latter case, the square is 'amodally' completed and there is no spreading of colour at all; the front surface appears opaque. This demonstrates that the occurrence of neon colour spreading is closely related to the three-dimensional interpretation of the scene. In other words, neural mechanisms of filling-in are strongly affected by the neural processes used to analyse the depth structure of a scene. Image modified, with permission, from REF. 83 © (1990) Pion Limited, London.

been shown that visual features of amodally completed surfaces are internally represented, although they do not generate vivid sensation^{78,79}. Therefore, at each point of the visual field, our visual system might have many representations of surfaces and their features. Depth order of objects is judged by different mechanisms that process binocular disparity signals and monocular depth cues, such as junction and line termination^{80,81}.

Among the many represented surfaces in a given direction in visual space, only the one judged to be the nearest becomes modal and gives rise to conscious perception. An exception is when transparency occurs, so that two objects can be perceived in the same location. Filling-in might be regarded as a special example of a process in which an illusory surface judged to be the

nearest one becomes modal. Close interaction has been shown between depth assignment and filling-in^{82–84}, and a dramatic example was provided by Nakayama and colleagues⁸³ (BOX 1). This and other demonstrations indicate that the occurrence of filling-in is closely related to the three-dimensional interpretation of the scene.

To summarize, surface perception includes two different processes. One process constructs the surface based on available contour information and the interpolation of incomplete data. The underlying mechanism of this process has been studied extensively, and both early visual areas and higher areas are probably involved^{31,71,85–88}. Processes related to contour formation, such as contextual modulation of contours^{89,90} and border ownership assignment, have been shown to be formed in early visual areas, and neural responses related to figure-ground segregation have been observed in both early and late areas^{91–96}. This process occurs for any surface, regardless of whether it is modal or amodal. As a result, many representations of surfaces emerge in each direction in visual space, and these might be maintained through a recurrent feedforward-feedback loop between early and late visual areas^{97–99}.

The second process gives visible features, such as colour, brightness and texture, to a surface that was assigned the top priority position in the depth order (nearest surface) as a result of the first process. A possible neural mechanism of filling-in (discussed in the previous section) should relate mainly to this process, which generates modal perception of the surface. In the process of filling-in, visual signals transmitted through horizontal connections in V1 or through feedback projection from higher areas selectively activate specific neurons in deep layers of V1, and modal surface perception is experienced. In this regard, the question of the neural mechanisms of filling-in should be tightly related to the question of how qualia emerge.

Box 2 | Relationship between filling-in and attention

A number of recent functional MRI (fMRI) studies in humans and some single-unit recording experiments in awake, behaving primates have shown that attention modulates the activation of visual areas including V1. When filling-in occurs at a region in the visual field, the filled-in attributes, such as colour or pattern, may draw the attention of the subject to this part of the visual field. This might cause some modulation of neural activity in the early visual cortex. However, it has been shown that the activity associated with filling-in in early visual areas is observed even when the effect of attention is controlled. In the fMRI experiments by Sasaki and Watanabe⁴¹ and Meng *et al.*⁴², the attention of subjects was controlled by asking them to perform a demanding task unrelated to filling-in at a different part of the visual field. Activation of early visual areas was clearly observed under such conditions. They also presented the same filling-in stimuli when attention was not controlled. Interestingly, in both studies, activation was observed in extrastriate areas such as V3 in the uncontrolled condition, although these areas were not activated when attention was controlled. Stronger effects of attention in extrastriate areas are consistent with the findings of unit recording experiments in primates. These results indicate that the activation observed in V1 is genuinely related to filling-in and is not the result of attention. It has also been shown psychophysically that 'modal' and 'amodal' completion occur before attention is allocated to a given stimulus^{6,100}. Presumably, filling-in and attention are processed using quite separate neural mechanisms in the brain.

Concluding remarks

We can now assert that filling-in is perceived as a consequence of neural computation in the brain. Activity of neurons in early visual areas commonly seems to be involved in the representation of filled-in surface. This is different from the attentional modulation of neuronal activities observed in the visual cortex (BOX 2). Details of the neural interactions in early visual areas and between higher and lower areas are the important questions to be studied. Specifically, it is important to know how the signals that code contours and those that code features interact with each other. Rapid development of techniques for imaging neural activities may allow us to know, in the near future, the spatial distribution

and dynamics of neural activation within an area and between areas during the process of filling-in.

It is commonly believed that surface perception resulting from perceptual filling-in and ordinary surface perception share common underlying neural mechanisms somewhere in the course of visual processing. Clearly, the mechanisms involved are different at the receptor level, so at which stage in visual processing do they start to share common mechanisms? This might be the critical stage at which subjective visual experience emerges. In this regard, understanding in detail the neural mechanisms of perceptual filling-in will eventually answer this crucial question on visual perception.

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Competing interests statement

The author declares no competing financial interests.

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