Quick guides

Visual filling-in

Stuart Anstis

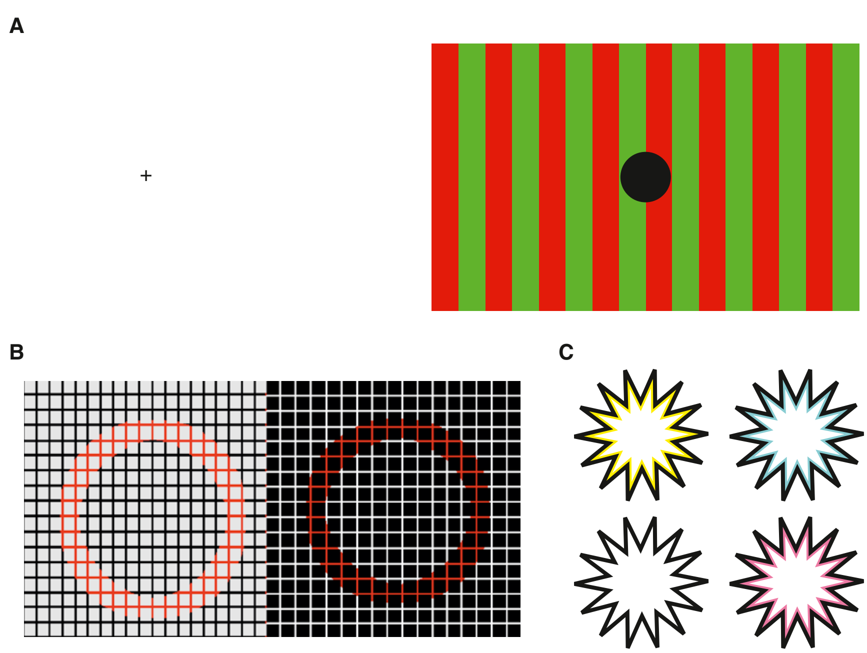
What is filling-in? It is the phenomenon in which an empty region of visual space appears to be filled with the color, brightness or texture of its surround. The brain is capable of filling-in the blind spot, borders, surfaces and objects. To explain each case there are two main types of theory, suggesting that filling-in is either isomorphic or symbolic.

How is the blind spot filled in? The natural blind spot is a retinal region devoid of photoreceptors, where the head of the optic nerve joins the retina (Figure 1A). Close your left eye and extend your right arm straight in front of you. Spread your fingers wide, palm down, and gaze at your thumbnail. Now wiggle your little finger. It will fall on your blind spot and you will be unable to see it! The blind spot is quite large, about 6° in diameter — large enough to hold a dozen moons side by side. So it makes a big hole in the visual field — yet we do not see a hole. It is true that the retina of the other eye covers this area, but even with the other eye closed the area of the blind spot looks ‘filled-in’ with the color or texture of the surround. If the surround is red or black or striped, then the region of the blind spot appears to be filled in with red or black or with stripes. Also, traumatic damage to the retina, or the slow degeneration caused by glaucoma, can result in a blind spot or scotoma: a scotoma is also perceptually filled-in, so effectively that the patient is often not aware of it, which can lead to undesirable delay in seeking medical treatment.

Why do peripheral objects fade? If the eyes fixate a point very steadily, small objects in peripheral vision often fade out from view and disappear. This was first reported by Troxler in 1804. This process is accelerated if the edges of the object are blurred, and is even faster and more complete if these edges are stabilized against the jitter caused by small eye movements by means of special lenses. If a red disk is surrounded by a green annulus, and the border of the red disk, but not of the green annulus, is retinally stabilized, then the red disk is gradually filled-in perceptually with the green color of the annulus, and the whole field looks green. Although the red disk is still present in the field, it becomes invisible.

Consider a large field filled with twinkling noise, like the snow on a detuned TV set, with a fixation point at its center and a small embedded window that is viewed peripherally. During prolonged fixation on the center, the window and its contents gradually disappear. If the window is filled with random dots that drift to the left (with the window’s edges remaining stationary), or simply with grey, then the window fades out from view within 5–20 seconds. The smaller and more peripheral the target, the faster it disappears. When the display is abruptly replaced by a uniform grey field, the area of the window appears to be filled with an aftereffect: respectively, a motion aftereffect apparently drifting to the right, or an aftereffect of apparent twinkle.

This is not simply adaptation to luminance edges of the window — they are constantly refreshed by the twinkling dots that alter the contrast of the edges. Even a flickering spot on a plain grey surround gradually fades out, and to keep it visible the amplitude of flicker must be increased steadily over time. Wiggly lines gradually look straighter. All these cases show a gradual loss of visual information in the peripheral visual field, occurring in two stages; at first the borders of the patch act like a dam that initially erodes gradually over time; and then the surround floods in rapidly like water over the dam, actively filling-in the patch until it is invisible. This competition between two surfaces, in which the surround surface gradually wins, may not be the same process as filling-in of the blind spot, which is instantaneous; nobody knows.



Current Biology

Figure 1. Filling-in of the blind spot and of surfaces.

(A) The blind spot. Close your left eye, gaze at the cross, and move the page toward you. At some point the black spot will disappear because it lands on your retinal blind spot. However, the red and green stripes perceptually fill into the blind space. (B) Neon spreading. The thin red lines are perceptually filled in to form an illusory pink annulus. Both rings are the same red, but they average together with their white or black backgrounds to look light or dark pink. (C) Pinna’s water color illusion. The colored lines appear to fill-in and tinge the entire regions with color.

How are surfaces filled in? If the intersections of a mesh of thin black lines are colored, say red, then each red intersection seems to expand into a pink disk. This bleeding of color, which resembles diffusion, is called neon spreading. It is strongest if the grey surround has the same luminance as the red color, and is weakened if a thin white gap (not shown) is left between each red cross and the black lines aligned with it. In Figure 1B, the red crosses seem to amalgamate and form a complete pink annulus.

In Pinna's water color illusion, a shape is drawn with a wiggly black outline (Figure 1C). Running along just inside the black is a wiggly colored line, say yellow, which makes the whole shape appear to be tinged with yellow. This effect was well known to early cartographers, who tinted coastlines blue in their maps to suggest the blue of the ocean. Watercolor and neon colors spread, provided they are equiluminous with their surround, in a visual process analogous to physical diffusion, until they encounter a luminance contour that acts as a barrier and prevents further spreading.

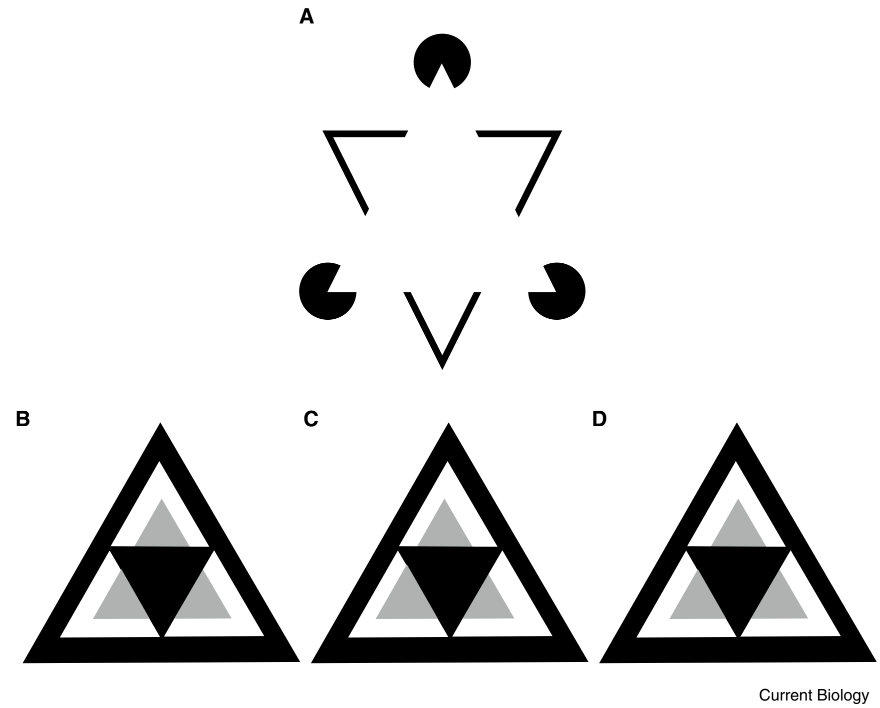


Figure 2. Modal and amodal completion.

(A) Modal completion: Kanisza's illusory triangle. This appears to occlude the pacmen and thin black lines. It seems to float in front and be slightly brighter than the background. (B–D) If you cross your eyes and fuse C and D together binocularly, a grey triangle is visible lying in depth behind the three portholes. This is amodal completion: the hidden part of the triangle is not assigned a particular color. But if you fuse B and C together, the grey triangle now floats in depth above the portholes — and modal completion fills-in its ghostly grey center that floats above the surround.

What are 'modal' and 'amodal' completion? Objects in the visual world are often partly covered or partly visible, so we need to be able to fill in the gaps and perceive the whole object. If a target is partly covered by an occluder, 'amodal completion' refers to completing the perception of the hidden parts that lack any visible attributes (color, texture and so on). On the other hand, Kanisza's triangle (Figure 2A) produces 'modal completion' in front of the supposedly occluded pacmen. The illusory triangle looks slightly brighter than the surround, and in front of it, though there are no corresponding luminance edges present. These illusory contours are modal, being perceptually salient and appearing to belong to the triangular figure rather than the ground.

The illustrations in Figure 2B–D bring out the subjective difference between modal and amodal completion. By crossing one's eyes in free fusion it is possible to combine C and D. The disparities are arranged so that a grey triangle appears to lie in depth behind three triangular portholes. The grey triangle is amodally complete — it looks like a single triangle, not like three unrelated segments — but the brightness of its hidden parts is not perceptually represented. If one binocularly combines B and C, however, one sees in stereo the grey triangle lying in depth in front of the three portholes. Now the ghostly middle of the grey triangle is perceptually — modally — filled-in, in front of the black surround.

What causes filling-in? Edges and contours are important in the filling-in of colors, brightness and textures into surfaces. There are two theories of how this might be done: isomorphic or neural filling-in, and symbolic filling-in.

According to the isomorphic theory, a surface to be filled-in is represented in the brain by a two-dimensional array of neurons, and these actually fire under the influence of excitation spreading in from the edges. It is suggested that color signals spread in all directions until they are stopped by a luminance border that acts as a barrier. This process is thought to be analogous to physical diffusion.

By the alternative theory, symbolic filling-in, there is no spread of activity within the surface. Instead, visual properties of the surround, such as texture, contrast polarity and color, are tagged and applied to the enclosed surface. This process is sparse and economical and resembles the vector graphics method of representation. It is not clear how this would be implemented in the nervous system. On some minimalist version of symbolic filling-in, little implementation is needed; thus, the retinal blind spot might be ignored, as the gap behind our heads is ignored, since after all there are no neurons in the brain devoted to seeing the blind spot.

What is the evidence for isomorphic filling-in? Strong support comes from motion aftereffects around the blind spot. It is known that, if one first inspects a striped moving pattern, then when the motion is stopped the stripes appear to move back in the opposite direction. This motion aftereffect can be built up to one eye and elicited from the other eye. Murakami aimed an annular stimulus containing drifting stripes at the blind spot of the right eye. Filling-in made this look like a complete striped disk. He then tested with a small striped disk, smaller than the hole in the annulus, and viewed by the corresponding intact retina of the *left* eye. Observers reported a motion aftereffect. This suggests that the motion was actively filled into the blind spot of the right eye.

Further support comes from filling-in of a large disk. A large white disk was flashed up on a black surround, followed 50–100 milliseconds later by a white outline circle of about half the diameter. Observers reported that the interior of the outline circle looked black. If the circle was smaller, the optimal time gap was longer. This suggests that a brightness signal propagates inward from the circumference at an estimated speed of 110–150° of visual angle per second, and is arrested by the barrier of the outline circle. This is supported by experiments on simultaneous contrast. A static grey disk appears to brighten and dim when its surround respectively dims and brightens, but this process breaks down at repetition rates exceeding 2.5 Hz, suggesting also a spreading process at a finite speed. Similar effects have been shown for the filling-in of texture.

Where can I find out more?

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Tudor domain

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What is the Tudor domain? The Tudor domain was first identified as a segment of approximately 60 amino acids that is present in 11 repeated units in the *Drosophila* protein of the same name. *Drosophila tudor* was first identified genetically, in a large-scale screen for maternal-effect lethal mutations that affected embryonic development. Several complementation groups of such mutations were identified in which homozygous females produced embryos that failed to specify primordial germ cells, and these were named after extinct European royal families (*tudor*, *vasa*, *valois*, and *staufen*). Since that time, over 200 Tudor-domain containing proteins have been identified from essentially all varieties of eukaryotes, including plants, animals, and fungi, but not from prokaryotes. Tudor domains are related to Chromo, MBT, PWWP, and Agenet-like domains, which are implicated in chromatin binding. The core Tudor domain forms a β-barrel like core structure that contains four short β-strands followed by an α-helical region (Figure 1). In different types of Tudor-domain containing proteins, the core Tudor domain or domains can be flanked on the amino-terminal side with other conserved motifs.

What is the function of the Tudor domain? Four types of Tudor domains can be distinguished based on their flanking sequences. The original germ-line type Tudor domain binds to proteins with dimethylated arginine or lysine residues. Work in mammals and *Drosophila* is consistent with a model that arginine methylation of Piwi-type proteins, and their consequent binding to Tudor proteins, is necessary to

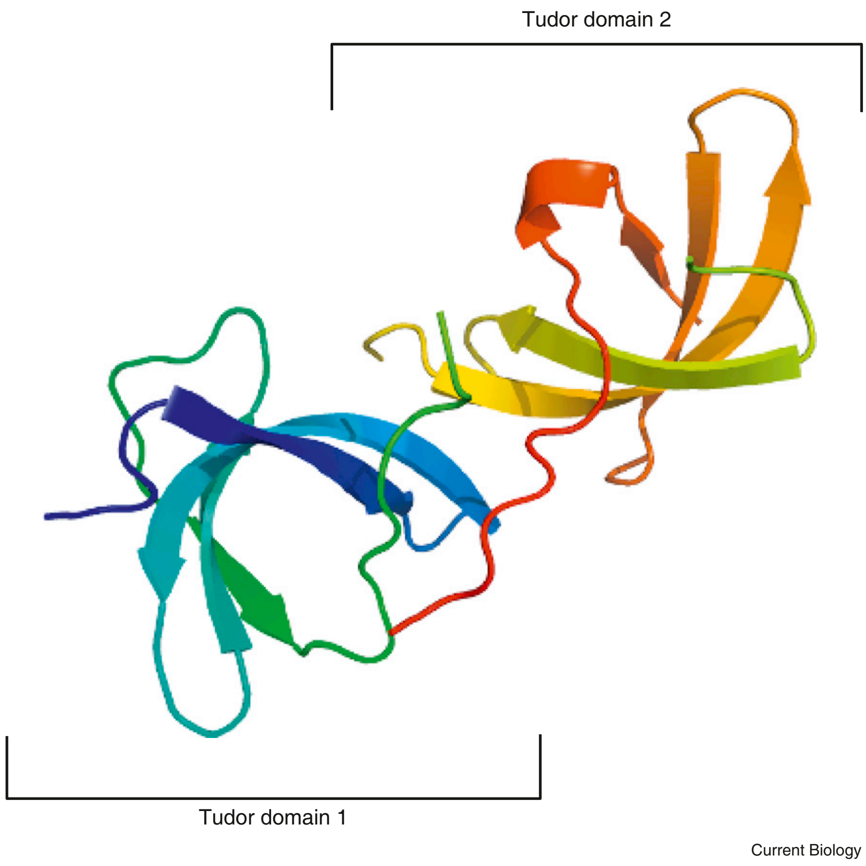

Figure 1. The Tudor domain.

Schematic representation of the structure of the two Tudor domains of the human fragile X mental retardation protein FXR2 (PDB: 3H8Z). The structure was generated by the Structural Genomics Consortium (www.thesgc.org) and placed in the public domain. Each Tudor domain contains four β-strands (depicted by broad colored arrows) that form a barrel structure.