How Does the Brain Fill-in the Visual World?

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Our awareness of the visual environment comes to us from the pattern of light on the retina. But this pattern is an incomplete record of the visual scene, because many pieces of the scene fall on the blind spot or are obscured by retinal vessels. This loss of information can be worsened by disease-induced retinal damage, or when cortical injury following stroke damages areas of visual cortex corresponding to parts of the visual field. Yet healthy people and most patients are largely unaware of this missing or incomplete information. Instead, we see the visual scene as though it were complete because the brain 'fills-in' the missing information. The neural mechanisms involved in such perceptual 'filling-in' can tell us a great deal about normal visual processes, and are also likely to be involved when parts of the visual system are damaged and more extensive filling-in takes place.

Filling-in at the blind spot

Although the blind spot is devoid of photoreceptors and carries no visual information from the corresponding region in visual space, when we view the world through one eye, we don't see a blank patch: the visual system fills-in the missing information from the surrounding colour or pattern (Figure 1). Behavioural studies in healthy people suggest that filling-in at the blind spot is a rapid, preattentive process that occurs early in the visual system. For example, if several rings are viewed, but with one positioned in the visual field so its retinal projection lies just around the blind spot, then this particular ring will 'pop out' of the group as it is perceived not as a ring, but as a filled-in disc among the other rings that do not lie over the blind spot.[1] Even an extremely narrow border (0.05 deg) surrounding the blind spot, will generate the appearance of uniform colour filling-in the blind spot,[2] consistent with the theory that such filling-in depends on local processes generated at the edge of the blind spot representation in primary visual cortex. Single cell recordings from anaesthetised monkeys show that when filling-in takes place at the blind spot, neural responses are generated at the retinotopic representation of the blind spot in primary visual cortex.[3,4] However, the precise mechanism by which perceptual filling-in across the blind spot occurs is still unknown. The two main theories are that it involves lateral propagation of signals from the edge of the blind spot, or is due to remapping of receptive fields of surrounding neurons into the blind spot region.[5]

Filling-in after prolonged fixation

Filling-in also takes place in normal vision during prolonged fixation. For example, a figure viewed in the periphery on a bland and featureless background will seem to disappear after a few seconds of prolonged fixation, to be replaced by the background (see Figure 2a). This type of filling-in is known as Troxler fading.[6] A similar but more striking effect is seen if the featureless background is replaced by a dynamic texture, similar to the static on a television set. This dynamic background promotes rapid filling-in of even quite salient figures placed on top of the background, and the resultant effect is described as an 'artificial scotoma' because the figure becomes invisible and 'filled in' by the textured background[7] (see Figure 2b). These 'artificial scotomas' may be associated with similar neural processes that lead to the filling-in which takes place when targets are stabilised on the retina, as eye movements disrupt the artificial scotoma.[8] Behavioural studies suggest that the filling-in associated with an artificial scotoma takes place in early retinotopic cortex as it is influenced by low-level sensory factors such as eccentricity and boundary length of the figure that 'fills-in'.[9,10] This is consistent with single cell studies in monkeys[11] and neuroimaging reports in humans.[12,13] However, recent work suggests that higher cognitive factors may also play a role, as directing spatial attention to the peripheral figure makes it

Figure 1: Examples of perceptual filling-in at the blind spot. Hold the page approximately 15 cm from your face, close your right eye and fixate the cross with your left eye while attending to the horizontal bars. Move the page gently closer and/or further away from you until the green disc falls into the blind spot. When the green disc falls across the blind spot, it will disappear and the space it occupies will be perceptually filled-in by the horizontal bars. Now close your left eye and fixate the cross with your right eye while attending to the pink and yellow target. Again, move the page closer and further away until the target falls into the blind spot. When the yellow disc falls across the blind spot, the appearance will be of a large pink circle, with the yellow disc disappearing and becoming filled-in by the surrounding pink. Similar to example shown in Komatsu, H. Nature Reviews Neuroscience, 2006;7:220-31.

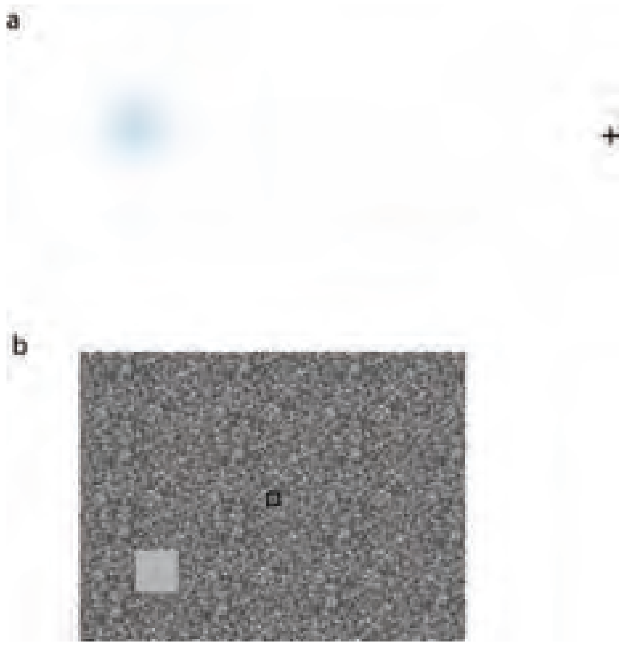

Figure 2: Filling-in after prolonged fixation. (a) Example of Troxler fading.[7] Hold the page 20cm away from your face, fixate the cross with both eyes open, after a few seconds, the blue pattern will fade and disappear.
(b) Example of an artificial scotoma. A square figure is placed in the near periphery on the background of dynamic twinkling noise. Participants fixate centrally and the square figure gradually fades and disappears.

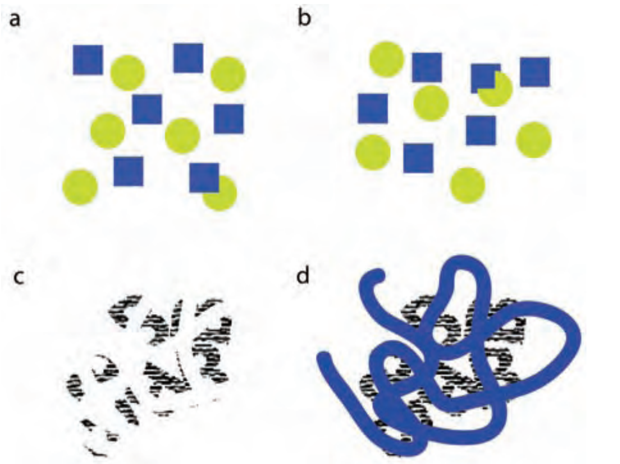

Figure 3: Occluded objects (a,b) Visual search with for amodally completed target. Identifying the notched circle is harder in (A) as it is amodally completed and perceived as a circle among the other circles. In (B), the notched circle 'pops out'. Search display similar to those used in[15] (c,d) Depth cues to identify occluded objects. The left-hand image (c) is difficult to interpret. (d) Adding a blue snakelike occluder helps to define the occluded figures as uppercase Bs. Similar to example shown in Nakayama et al., 1989.[16]

more likely to 'fill in' and disappear.[14] Thus, although filling-in may be generated by low-level, early retinotopic neural processes, it is also modulated by higher cognitive factors.

Filling-in behind occluders

The world is very cluttered and most objects do not present themselves in isolation but are seen at least partially occluded by other objects. Yet we do not have the impression of being surrounded by fragmented objects. The brain 'fills-in' the missing information and our impression is the familiar one of viewing complete objects. This type of filling-in of objects behind occluders is also known as amodal completion and seems to occur at slightly later stages of visual processing than the filling-in of artificial scotomas and the blind spot.The effects of amodal completion can be seen when subjects are asked to search for a notched circle in an array of circles and squares. If the notched circle abuts the edge of one of the squares so that it seems to be occluded by it, the notched circle takes longer to find (see Figure 3a)[15] as it is perceived as a complete circle in a sea of complete circles. Occluded objects are also easier to recognise than those with the equivalent portions deleted (see Figure 3b)[16,17] suggesting that inferred depth is used to inform the visual system of object boundaries, as objects are far more likely to be partly occluded than have bits missing. This would suggest some involvement of object related areas in identifying occluded items. Indeed, a recent neuroimaging study showed increased activity during presentation of occluded objects in the lateral occipital complex (LOC), a region known to be involved in object processing; and in the posterior intraparietal region.[18,19] The process of filling-in behind occluders is likely to involve a large number of information processing steps such as distinguishing between the boundaries of the occluded and the occluding object, assigning each of the resulting partial views a surface and then filling-in the missing information of each part[17] using clues from depth disparity and colinear edges.

> *Understanding the processes involved in filling-in in the healthy brain can provide insights into filling-in following visual loss*

Filling-in as a response to disorders of vision

Patients with retinal scotomas due to macular degeneration and toxoplasma also experience perceptual filling-in.[20-22] This can be problematic, especially in age-related macular degeneration, as early detection of the macular disease is essential to preserve foveal function with newer treatments[23] and when patients fill-in across their scotomas they are unaware of their visual field deficits.

The mechanisms of filling-in across retinal scotomas are still debated. In monkeys, cells within primary visual cortex representing the lesion expand their receptive fields within minutes after inducing a retinal lesion[24] and several months after the lesion, the receptive fields have expanded and shifted to outside the lesion. Similar reports of receptive field reorganisation in V1 (primary visual cortex) have been shown in retinal lesions in cats[25,26] and following cortical lesions in kittens.[27] In humans, reports are less consistent. Visual cortex (including V1) deprived of retinal input due to macular degeneration shows increased activation with functional MRI to stimuli outside the corresponding region in visual space.[28-30] Reorganisation also occurs following loss of visual input due to optic radiation damage following stroke.[29] However, other studies have failed to find consistent evidence for cortical reorganisation in macular degeneration[31] and a recent study suggests that large scale cortical reorganisation may only occur with complete absence of functional foveal vision.[30] The processes underlying this cortical reorganisation remain unknown. One possibility is that it arises from disinhibition of pre-existing long-range horizontal connections in V1,[32] but this would require connections longer than those known to occur in primate V1.[33] Alternatively, new horizontal connections might be formed.[34] A third possibility is that reorganisation occurs due to new or unmasked feedback projections from higher visual areas with larger receptive fields (see also reference 35 for an example).[35]

Conclusion

Perceptual filling-in, in many different forms, plays a critical role in completing missing information in normal human vision and is also a consequence of visual loss. The mechanisms are likely to differ between the various types of filling-in but may be important in designing treatments to encourage cortical reorganisation following damage to visual structures. ◆

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