

Why does the brain fill in?

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When a visual stimulus impinges on the retina, it triggers a sequence of neural activations at subcortical and cortical sites. Although we have witnessed great advances since the seminal work of Hubel and Wiesel in the 1960s, fundamental questions remain to be answered. In particular, we still have only cursory knowledge of how the neural substrate – which involves more than 30 visual areas – forms the basis of our perceived world.

A key property of visual physiology is selectivity: cells are found that are tuned to orientation, wavelength, and direction of motion, among other attributes. They also respond to stimulus contrast, with larger responses being elicited by larger contrast steps. But how these individual cell responses help code for our perception of the world is unknown. Consider the simple property of objects that we call 'brightness', which varies from 'dim' through 'gray' to 'bright'. Although brightness depends on contrast (which drives cell responses), the neural-perceptual mapping is subtle and complex, as the consideration of a few visual illusions demonstrates. For example, in Fig. 1A, one perceives a central bright triangle, although the white of the page is uniform¹. In Fig. 1B one perceives a series of bright and dark bars, each of roughly uniform brightness, although the stimulus luminance (Fig. 1E) is the same everywhere apart from in the vicinity of the edges (where 'cusp' edges are present); the so-called Craik-O'Brien-Cornsweet effect (COCE) (K. Craik, PhD thesis, University of Cambridge, 1940; O'Brien²; Cornsweet³). Both stimuli are examples of situations in which stimulus regions somehow 'inherit' border-contrast information. Thus, the 'pac-men' inducers (the three circles with notches taken out) in Fig. 1A lead to an 'illusory figure' that is completed when the inducing parts of the figure are present (Fig. 1D). In Fig. 1B, the contrast at the edge is used to 'fill in' the rectangular regions (Fig. 1E).

These two illusions are examples of what visual scientists refer to as 'filling-in' or the 'perceptual completion' phenomena: situations in which subjects report that something is present in a particular region of visual space when it is actually absent from that region, but present in the surrounding region. Another example is shown in Fig. 1C. After a few seconds fixating off the center of the figure, the texture present in the surround (but missing in the center) can be seen at the center also, indicating that the texture information in the surround 'fills in' the center square (Fig. 1F).

Perceptual filling-in can be used as an effective tool to probe the character of visual representations. For example, does perceptual filling-in imply that the brain 'reconstructs' the visual scene, thus supporting the percept reported by subjects? For instance, is the bright triangle perceived in Fig. 1A caused by an associated pattern of firing in topographically organized visual areas, such as cortical area V2? Or are more 'cognitive' or symbolic processes (which are, to be sure, also associated with underlying neural processes) involved? For instance, in Figs 1B and 1C are our percepts the result of mechanisms that simply tag an entire region with a 'more-of-the-same' label? A careful examination of the data shows that no general inferences are possible⁴. Nevertheless, as we now discuss, some completion phenomena speak in favor of 'active' spreading processes in topographically organized areas early in the cortical visual pathway.

Brightness filling-in

Davey *et al.*⁵ have recently investigated the temporal properties of the COCE. The starting point of the investigation is the observation that if the COCE relies on neural-spreading processes it should proceed at a finite pace, and thus exhibit characteristic temporal properties. Suppose a COCE pattern is presented to an observer who fixates at an inspection point. If spreading processes are involved, brightness changes will depend on the spreading rate and on how far the inspection point is from the (cusp) edge. If the edge contrast is reversed such that a dark-light transition is changed to a light-dark transition, a reversal in brightness should occur some time later at the inspection point. Now, if the edge contrast is continuously reversed, we should observe the concomitant continuous brightness reversal. A faster rate of contrast reversal should produce a faster rate of brightness reversal. However, if the contrast reversal rate is increased further, there will be a point at which the brightness changes will cease to occur. This is because the contrast signal that spreads from the edge will be opposed by the next reversal of edge contrast (before the spreading activation has reached the inspection point). Consequently, no brightness change is observed. The temporal frequency of the stimulus when induction ceases to occur is called the cut-off frequency.

In one experiment Davey *et al.* asked subjects to match square-wave gratings (in which physical luminance differences do exist between bright and dark re-

gions) to COCE gratings. Their main finding was that induced brightness in the COCE gratings was stronger and persisted until higher temporal frequencies for higher spatial frequencies (see Fig. 2). In other words, for smaller regions (narrower bars), the modulation in brightness can be perceived until higher rates of contrast reversal of the edges; conversely, for larger regions, only slow temporal changes in contrast produce brightness changes. These results are suggestive of lateral spreading processes. To appreciate this, consider the fact that the higher the spatial frequency of the stimulus, the smaller the individual stimulus regions will be and the smaller the cortical distance over which spreading must occur. A reduced distance implies that spreading will take less time to have an effect on the inspection region. Consequently, the spreading process that produces visible brightness changes is better able to keep up with the contrast changes at the edge when the COCE regions are small (i.e. for a high-spatial-frequency stimulus). In all, a higher cut-off frequency should be observed.

Texture filling-in

De Weerd *et al.*⁶ have recently performed a detailed investigation of texture filling-in (Fig. 1C) as studied by Ramachandran and Gregory⁷. Two aspects of their study are particularly important. The first is the evidence for the chief involvement of topographically organized, early cortical areas on the effect. Larger squares take longer to fill in (Ref. 5, Experiment 1). However, the critical factor determining the time to complete was found to be the cortical projection area. Therefore, it is 'cortical size', that is, the size of the cortical area stimulated taking into account the human cortical magnification factor⁸, rather than physical size that matters (Ref. 5, Experiments 5 and 6). Squares of very different retinal size showed similar filling-in times if their cortical projection areas were similar (by viewing them at different eccentricities). In fact, cortical projection area provided an accurate linear fit to time to fill in, with a regression $r^2=0.83$ ($P<0.01$), if the cortical magnification of area V3 in humans is considered.

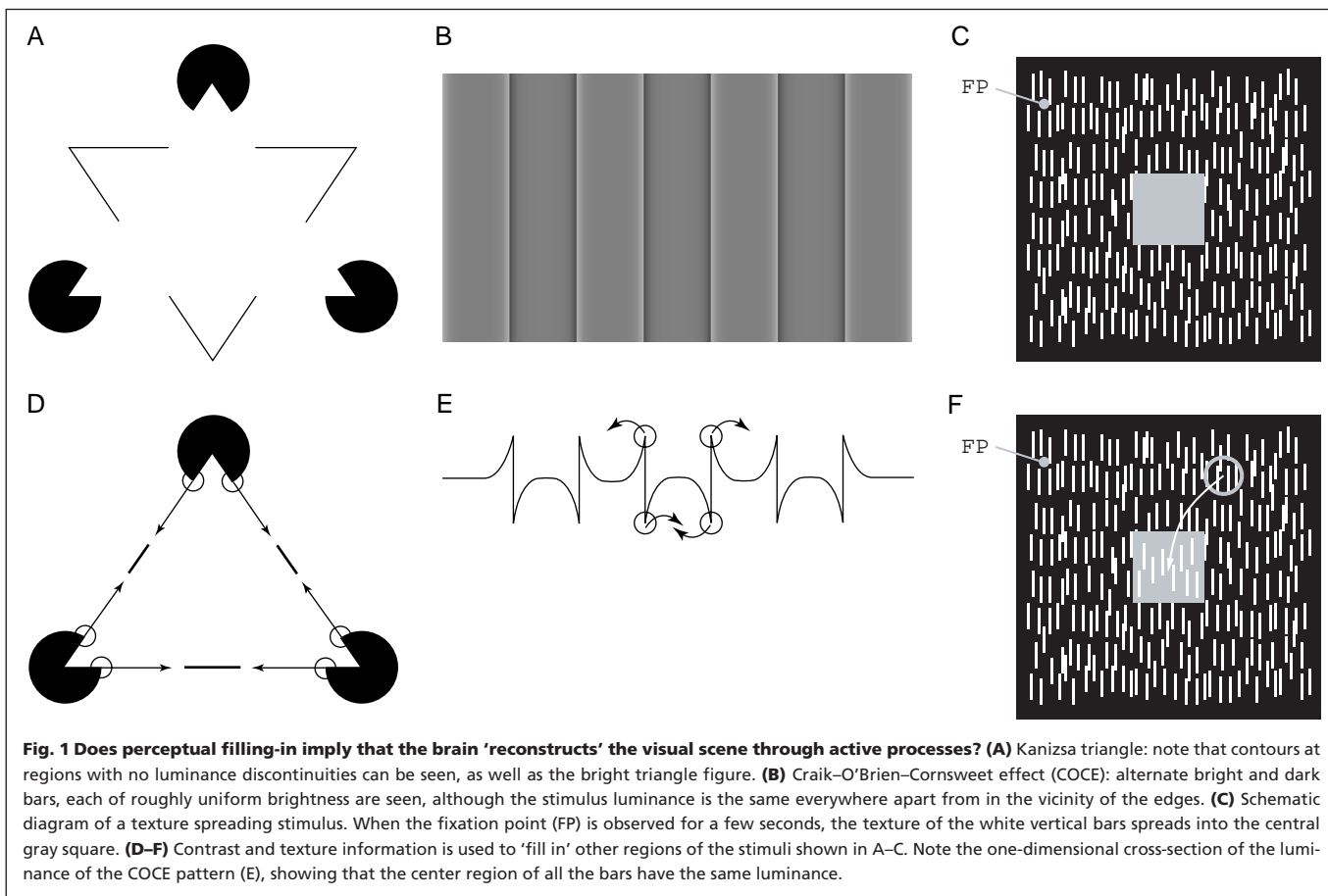
The second important point of De Weerd *et al.*'s study is that the time course of filling-in is compatible with normal surface perception. The slow timescale of texture filling-in (3–6 s) does not reflect a slow filling-in process (that would not be part of normal vision, but only a laboratory curiosity, as some have suggested⁹), but rather the long time it

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takes for figure-ground segregation to fail, after which a fast completion process ensues (Ref. 5, Experiment 2). In other words, after the contours between the textured and untextured regions adapt (see Fig. 1C), they no longer contain the fast spreading process that results (see also Ref. 10). Thus, in everyday perception, contours antagonize the perceptual completion of texture information, but weak boundaries can be overcome and produce fast perceptual completion.

Filling-in for signal integration

The visual system in its early stages acquires reliable *local* estimates of visual attributes, such as motion, orientation, and disparity. However, given the spatially confined profiles of receptive fields in these areas, such estimates are ambiguous with respect to the larger global context. For example, although at the retinal level cells encode stimulus contrast, these local estimates do not reliably predict object properties, such as lightness, because identical 'luminance steps' can be associated with different surface gray values (e.g. a dark-gray to middle-gray transition might have the same edge contrast as a middle-gray to light-gray transition). As another example, consider the orientation-selective responses of cells in cortical area V1. Because of image degradation and occlusion (which is a prevalent condition in the natural world), these local responses do not uniquely determine the orientation of more extended object outlines,

or contours. Therefore, to fulfill its general action-guiding role, the visual system must integrate the available early information. By doing this, reliable lightness values can be computed and object contours determined, for example.

We propose that neural filling-in in topographically organized areas is an effective way for the visual system to accomplish the integration of early information. In the case of brightness we suggest that this is accomplished through 'neural spreading processes'. Functionally, this is equivalent to a diffusion process that uses local contrast signals as initial estimates that are diffused. Formally, we have:

$$\frac{dv(x)}{dt} = -v(x) + c(x) + \nabla \cdot (\rho(x)\nabla v(x))$$

where *v* is the cell's potential (for spatial location *x*), *c* is the contrast estimate, and $\nabla \cdot (\rho\nabla v)$ specifies a diffusion term in which local contrast information modulates the rate of lateral diffusion (the modulation function is denoted by ρ). Its magnitude is typically low when a boundary separates two positions (so that regions become independent units that are 'colored' with a given level) and high when no boundary is present (so that within regions, positions may freely influence each other). These ideas were introduced by Fry and others¹¹⁻¹³ and culminated in the formalization above by Cohen and Grossberg¹⁴.

We have proposed that filling-in should be viewed as a form of surface property determination (Ref. 15 and other, unpublished results). From sparse, local measurements, the visual system generates the most likely 'hypothesis'

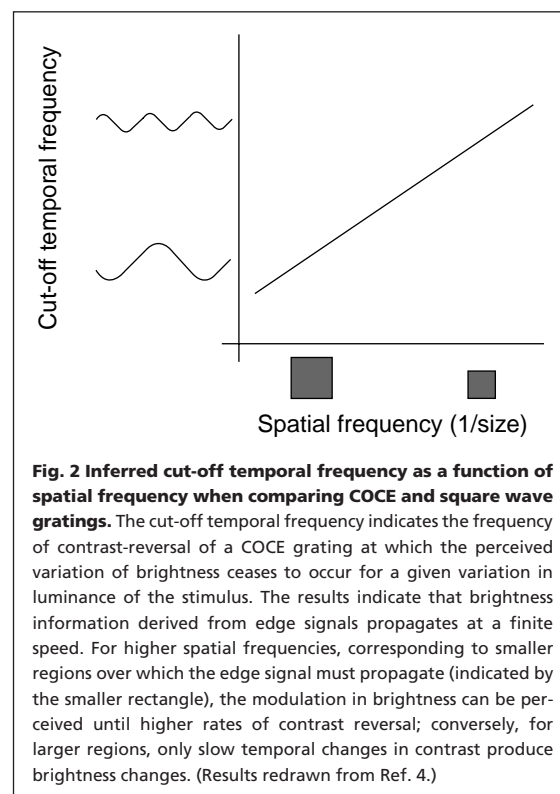
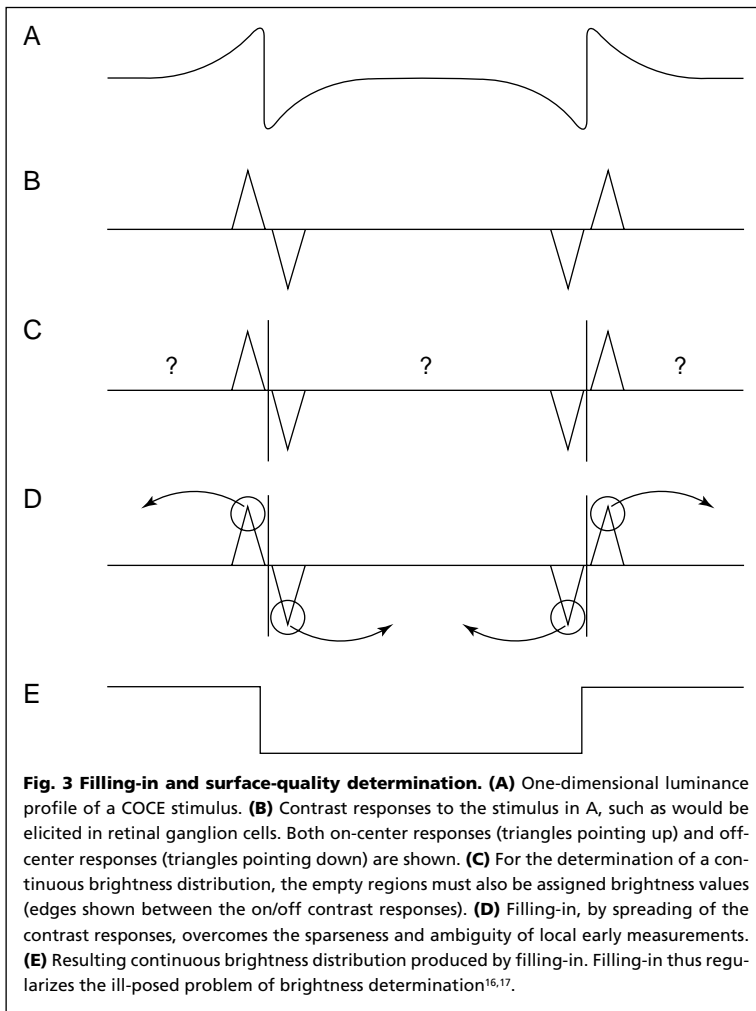


Fig. 2 Inferred cut-off temporal frequency as a function of spatial frequency when comparing COCE and square wave gratings. The cut-off temporal frequency indicates the frequency of contrast-reversal of a COCE grating at which the perceived variation of brightness ceases to occur for a given variation in luminance of the stimulus. The results indicate that brightness information derived from edge signals propagates at a finite speed. For higher spatial frequencies, corresponding to smaller regions over which the edge signal must propagate (indicated by the smaller rectangle), the modulation in brightness can be perceived until higher rates of contrast reversal; conversely, for larger regions, only slow temporal changes in contrast produce brightness changes. (Results redrawn from Ref. 4.)



consistent with them. In this context, it is useful to employ the formalism of regularization theory employed in computer vision. Brightness determination can be described as the problem of finding a solution (how brightness varies across space) given only local contrast estimates. The sparseness of the contrast measurements (which are reliably obtained only at contrast edges) poses an especially acute challenge to the visual system, which must somehow use them to determine the continuous variation of brightness across the visual field. This 'inverse problem' is classified as 'ill-posed'¹⁶ because, formally, the uniqueness of a solution is neither given by the data (the local contrast measures) nor is it continuously dependent on the data, as the input can be noisy^{16,17}. The solution has then to be 'regularized', that is, constraints must be imposed on the possible set of candidate solutions. We have shown that filling-in as instantiated by the diffusion equation above is, in fact, a form of regularizing the determination of brightness. In other words, it is a means of obtaining a unique, smooth brightness distribution from the set of local contrast measurements (Fig. 3).

Conclusions

Perceptual filling-in reflects, in many cases, the active neural processes of

surface attribute determination (such as brightness and texture). These processes make effective use of the topographically organized circuits of early cortical visual areas. They should not be viewed as redundant processes of 'painting an internal screen' (e.g. Refs 18,19) but as critical mechanisms of the integration of local (ambiguous) measurements of visual attributes. As such they form an integral part of the processes that allow us to perceive the rich world around us. The neural mechanisms that instantiate such integration processes remain unclear at present²⁰. In the case of brightness, filling-in may occur as early as the striate cortex²¹, while for texture, V2 or V3 are more likely substrates²². The precise determination of the neural circuits underlying completion in general is of paramount importance for the elucidation of the substrates of visual perception.

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