What gets filled-in during filling-in?

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In a recent review, Komatsu[1] concluded that there is substantial evidence for neural mechanisms underlying the filling-in of visual properties such as contours, texture, brightness and colour. Komatsu[1] stressed, however, that the evidence for filling-in depends on the details of the experiment and the type of filling-in phenomenon under investigation. We suggest here that recent human functional MRI (fMRI) studies provide a key to understanding what is and what is not filled-in during filling-in. In agreement with previous neurophysiological studies that failed to find evidence for neural surface filling-in[2,3], these fMRI studies did not provide evidence that activity in the early visual cortex corresponds in a topographic (isomorphic) manner with illusory surface regions[4,5]. These recent findings conflict with some other fMRI reports in favour of isomorphic surface filling-in[6,7] and with various studies of surface filling-in observed at the level of single neurons in monkey and cat visual cortices[8–14].

How might these various findings be reconciled? Cornelissen *et al.*[5] recently reported that fMRI activity elicited by luminance and colour edges is accurately modelled by assuming a linear combination of short-range (~1 mm along cortical surface) and long-range (> 15 mm) responses (FIG. 1a,b). Both short- and long-range responses are symmetrical (Gaussian) with respect to the inducing edge and therefore neither corresponds topographically with surface brightness and colour. The long-range component of these responses — which extend up to 5 degrees away from the stimulus edge, similar to the non-classical receptive field properties of single neurons — calls into question the validity of positive fMRI and neurophysiological reports of cortical surface filling-in. Stated plainly, many positive reports of surface filling-in can be understood as an artefact of long-range cortical responses to edge stimuli. The fMRI activity maps of Sasaki and Watanabe[6], for example, are qualitatively more consistent with long-range edge-centred responses than uniformly filled-in surface responses (FIG. 1c). Recent modelling of the responses of single neurons of the primary visual cortex to stimuli that induce illusory brightness contrast[8] supports the notion that long-range cortical responses are unrelated to surface filling-in in most surface responsive neurons[15].

Future studies of filling-in also need to distinguish between the filling-in of contour and surface information. For example, Meng *et al.*[7] showed that the perception of illusory visual phantoms is correlated with fMRI activity in the primary visual cortex. The authors' stimuli induce the perception of strong illusory contours, along with a weaker surface filling-in effect. Although we do not question the evidence for the completion of illusory contours in the visual cortex, we do emphasize that the case in favour of cortical surface filling-in is weakened by recent findings.

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Figure 1 | **Long-range symmetrical responses to edge stimuli may explain previous reports of cortical surface filling-in. a** | fMRI activity in the primary visual cortex during brightness changes elicited in disc-surround stimuli by either luminance modulation of the central disc (open circles) or induced by modulating the surround (filled circles)[5]. Responses were strongest at the transition between the central disc and surround (0 mm), and decreased with increasing distance from this edge. **b** | Responses could be accurately modelled with a linear combination of short- and long-range Gaussian edge responses and a small luminance response (see inset). The long-range edge response extends over several millimetres of cortical surface (full-width half-maximum > 15 mm) and is symmetrical around the edge. Model results are shown for luminance modulation of the central disc. **c** | Cortical responses to stimuli eliciting neon colour spreading. Note that responses are evidently strongest near illusory edges (dotted lines indicated by white arrows) and decrease with distance from the edge. We suggest that such responses are better understood in terms of long-range Gaussian responses than uniform filled-in surface responses. Panels **a** and **b** reproduced, with permission, from REF. 5 © (2006) Society for Neuroscience. Panel **c** reproduced, with permission, from REF. 6 © (2004) National Academy of Sciences.