Response from Maddess, Srinivasan and Davey

Pessoa and Neumann' summarize our results well and the comparison made with the results of De Weerd et al.[2] is interesting, provocative and worthy of experimental testing. They don't mention that, like De Weerd et al., we also find that cortical measures determine the speed of construction of illusory brightness. We showed that our observed flicker fusion frequencies for 'Craik–O'Brien–Cornsweet effect' (COCE) gratings of different stripe widths could most simply be understood if one assumed a constant cortical propagation velocity, calculated as either 155 or 205 mm.s⁻¹ depending on whether V1 or V2 was involved. Other authors have reported that illusory brightness and actual brightness perception also take time and may involve a filling-in process[3,4].

At the same time we feel that it might be premature to accept that a filling-in process happens *per se.* Our results could accommodate versions of the 'interpretive' hypothesis of Campbell and Robson[5]. Under this hypothesis, the brain 'recognizes' (in some way) that it can't see the low-spatial-frequency components of a low-contrast square wave and so it interprets all objects having higher spatial-frequency components consistent with a low-contrast square wave as square waves. Our findings could support versions of the interpretive hypothesis where the time required for the recognition process depends on the spatial frequency. This could be a natural consequence of the wavelet-like transform performed in early visual processing, where information about progressively lower spatial frequencies is processed over progressively greater cortical distances. So, for example, the rate-limiting process might be the speed at which the brain recognizes that low spatial frequencies in the image have unreliably low contrasts, this recognition being processed over longer cortical distances for broader gratings. This example is perhaps a little contrived but it illustrates that we have not demonstrated that filling-in occurs in a literal sense.

One thing is clear: the construction of the illusory brightness in COCE gratings continues at contrasts well above the threshold for seeing the fundamental spatial frequency of the equivalent square wave, and this finding runs contrary to the original interpretive hypothesis. Several authors have made related observation+, however, Moulden and Kingdom[8] have proposed versions of the interpretive hypothesis that might account for the brightness induction. The diffusion model of Cohen and Grossberg[9] discussed by Pessoa and Neumann provides an intriguing, testable, formal framework for discussion of filling-in effects. In short, more experiments are needed to resolve conclusively the issue of filling-in in relation to the COCE.

Even if literal filling-in does indeed occur in all three examples discussed by Pessoa and Neumann, it may be somewhat premature to assume that precisely the same phenomenon operates in all three instances. The texture filling-in phenomenon, illustrated in Fig. 1C and 1F of Pessoa and Neumann', causes the perception of texture to spread inwards to fill in the blank area. The COCE phenomenon, on the other hand, is driven solely by the presence of edge information (i.e. by the presence of a high spatial derivative), and it propagates *opposing* kinds of information on either side of the edge. That is, if a COCE-type process were operating at the boundary between the textured and the blank areas in Fig. 1C, it would act to ensure that the blank area stayed blank and the textured area remained textured, or at least, perhaps, that the blank area was perceived as having a lower textural density. Indeed, a textural density equivalent of the COCE has been reported'". This is contrary to the findings of De Weerd et al.[2] who report that the blank area is filled in with the surrounding texture. The phenomenon described by Pessoa and Neumann is perhaps more akin to the so-called 'neon colour spreading' effects" than it is to the COCE.

The phenomenon that propagates illusory edges, illustrated in Fig. IA and 1D of Pessoa and Neumann', seems to be different again. In this case the gaps between 'real' edges are bridged by illusory contours and, unlike the COCE, filling-in here occurs *along* the direction of the edges, rather than in an orthogonal direction. Furthermore, the filling-in by the illusory contours occurs only when the real contours are parallel and co-linear, or nearly so[12]. Clearly, the filling-in process is much more selective with illusory contours than it is with the COCE or the neon colour spreading phenomena.

Given these differences between the three phenomena discussed by Pessoa and Neumann, we feel that more experiments are necessary before one can be sure that the same process underpins all of them.

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Response from De Weerd, Desimone and Ungerleider

Pessoa and Neumann suggest that 'filling-in' is a strategy that the visual system uses to turn the sparse, local measurements of brightness, orientation, and other features into an integrated percept of contours, surfaces and, ultimately, objects, that is useful for guiding our actions in the world. It has been suggested before that the perception of illusory contours in two-dimensional displays (as in a Kanizsa-triangle figure) reveals mechanisms of normal contour perception, necessary for the completion of the partly occluded contours of interposed objects in the three-dimensional world'. Similarly, the illusion that under particular conditions a region of an image is filled in by a percept for which the physical evidence exists only around

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