Response from Maddess, Srinivasan and Davey

Pessoa and Neumann[1] 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 observations[6,7], 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[1], 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[10]. 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[11] than it is to the COCE.

The phenomenon that propagates illusory edges, illustrated in Fig. 1A and 1D of Pessoa and Neumann[1], 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[1]. 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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that region might reveal interpolation mechanisms intervening in normal surface perception.

The mechanisms underpinning those interpolation mechanisms have long remained elusive. Psychophysical experiments (e.g. Refs 2,3) have shown that filling-in of brightness, though fast, requires time, suggesting that an active neural process is involved. A recent experiment by Davey *et al.*[4] showed that the speed of brightness filling-in is compatible with a constant propagation velocity across the cortex in visual areas early in the pathway. On the basis of these data, Pessoa and Neumann suggest that the filling-in of brightness could be described mathematically as a diffusion process in retinotopically organized visual areas.

Experiments such as those of Paradiso and Nakayama[2] and Davey *et al.*[4] measured the speed of filling-in from the outer edge of a surface inwards, as it might occur during normal surface perception. As expected, filling-in took place at a very fast speed (within milliseconds), immediately after stimulus onset. In the experiments we performed[5], perceptual filling-in was induced under observation conditions that bear little resemblance to normal perception. While maintaining fixation, subjects were presented with a gray square away from fixation, embedded in a textured surface. Only after prolonged peripheral fixation, subjects reported that the square was filled in by the surrounding texture. The delay of the filling-in was of the order of seconds, and we found that it was related to the total length of the square's boundary representation in early visual cortical areas. These data suggested that the filling-in of the square depended on how quickly adaptation of the square's boundary occurred, which takes more time for longer boundaries. Thus, only after the boundary representations obstructing the filling-in of the texture were 'removed' by adaptation did the texture 'flow' into the region previously occupied by the square. The psychophysical results taken together suggest that both the neural filling-in process and the adaptation of boundaries preventing filling-in depend upon early (retinotopically organized) visual areas.

From this perspective, it can be easily seen why Pessoa and Neumann's statement – that our study provided evidence 'that the time course of filling-in is compatible with normal surface perception' – is a little misleading. Introspective reports from our subjects indicated that the actual filling-in of the square, which took place after several seconds of maintained fixation, was indeed experienced as a fast event, compatible with the idea that this visual illusion is relevant for normal surface perception. However, we made no attempt to measure the velocity of the (unobstructed) filling-in process, as Davey *et al.*[4] did. Rather, we measured the time before a figure became filled-in by its background, and found that this time interval is related to the time required for boundaries to adapt and figure/ground segregation to fail, but unrelated to the speed of the filling-in process itself.

Furthermore, while it may be feasible to describe filling-in of brightness mathematically as a process of diffusion in a single area[6], this might be less feasible for the filling-in of texture. The stimulus we used was a dynamic texture containing several features, such as the brightness of the background and line elements, orientation, spatial frequency, and random motion. To the extent that the structure of the texture is preserved during perceptual filling-in, it seems unlikely that diffusion processes will be sufficient to describe the filling-in, and more complex interpolation processes are likely to be involved. In addition, the fact that we[7] found a neural correlate of perceptual filling-in in visual areas V2 and V3 of the monkey does not imply that the filling-in of texture takes place exclusively within those two areas, as Pessoa and Neumann seem to suggest. Indeed, we do not know which features in the stimulus drove the neural responses recorded in V2 and V3 during filling-in, and it is entirely possible that these responses, while tightly correlated with the percept, might not represent the percept completely. Thus, visual areas other than V2 and V3 might contribute to the filling-in of dynamic texture.

In summary, we are gaining insight into why the brain fills in, and into some fundamental aspects of the mechanisms underlying filling-in. In particular, evidence is emerging that processes in retinotopically organized visual areas contribute to some types of filling-in, and that filling-in cannot necessarily be reduced to a 'symbolic' completion operation in higher-order areas of the visual system[8]. However, more detailed insights into the mechanisms of the different types of filling-in await further experimental investigation.

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