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Perceptual Fading of Visual Texture Borders

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A light gray square was displayed on a background of dynamic two-dimensional noise. After 10 sec of steady eccentric fixation, the square disappeared completely and the region corresponding to it was "filled in" by dynamic noise from the surround. Furthermore, when the whole display was switched off, a persisting patch of dynamic two-dimensional noise was seen in the region corresponding to the gray square. This persistent patch could be seen for almost 10 sec on some trials, suggesting that a dynamic neural representation of the surrounding "twinkle" is being created in this region. The fading of the square was especially pronounced in peripheral vision. Also, displacing the square by a small distance was usually sufficient to restore its visibility but this distance increased with eccentricity. This may be a consequence of the progressive increase of receptive field size with eccentricity that has been noted in both area 17 and MT. The perceptual fading and "filling in" that we report concurs with the recent physiological observations of Pettet and Gilbert [(1991) *Society for Neuroscience Abstracts*, *17*, 1090] and Gilbert and Wiesel [(1992) *Nature*, *356*, 150–152] in area 17 of cats and primates.

Filling-in Perceptual fading Receptive field dynamics Visual texture

INTRODUCTION

Most object boundaries in the real world are defined by a luminance difference across their border. However, in exceptional cases edges can be defined without such luminance differences, and these equiluminous edges have interesting properties. Examples include: an equiluminous chromatic edge, where two areas of the same luminance but different hues meet; or a texture edge, such as the border between fine and coarse textures of the same mean luminance; or a kinetic edge such as the border between two random-dot textures which are identical save that they are drifting in different directions, or that one is moving and the other is stationary.

While viewing displays containing kinetic edges we noticed that they had a strong tendency to fade completely on steady fixation (Ramachandran & Kleffner, 1989; Ramachandran & Gregory, 1991; also see Spillmann & Kurtenbach, 1992). The significance of this effect derives from the fact that, unlike classical "Troxler fading" (Troxler, 1804), it cannot be explained by local adaptation to luminance edges. The fading is *selective*; in that it affects only the kinetic edges. The elements that define the edge do not fade since they are being continuously refreshed on the screen, and so at the eye.

A similar fading effect can also be observed if a homogeneous gray or a pink square is displayed on dynamic "snow" (Ramachandran & Kleffner, 1989; Ramachandran & Gregory, 1991). Using displays of this kind (Fig. 1) we made several new observations. First, when the square disappeared the region corresponding to it appeared to be "filled in" by the dynamic noise from the surround. Second the fading was especially pronounced with eccentric viewing, and third, when we switched off the display after viewing it for a few seconds, we noticed a curious visual after effect; a patch of dynamic noise was seen in the region corresponding to the gray square (Ramachandran & Gregory, 1991). Our purpose in this paper is to explore the spatial and temporal characteristics of these illusions and to suggest possible physiological correlates based on the recent work of Fiorani *et al.* (1992), Gilbert and Wiesel (1991, 1992) and Pettet and Gilbert (1991).

EXPERIMENT 1: PERCEPTUAL FADING IS ENHANCED IN PERIPHERAL VISION

Stimuli were displayed on a monitor screen, 25° wide × 18° high, under the control of a microcomputer and viewed from a distance of 57 cm in a dimly lit room. The entire screen was filled with small, twinkling dots of eight different gray levels with each dot (pixel) subtending 4.7 min arc visual angle. The flicker rate of each dot was 12 Hz. A central fixation spot was provided and subjects were asked to fixate the spot binocularly. A small (1 × 1°) gray square was displayed on the screen (Fig. 1) and its eccentricity was varied by randomizing its position from trial to trial. The mean luminance of the square (6 cd/m^2) was the same as that of the dynamic noise background.

Four naive subjects were used in the experiment and they were asked to simply press a button as soon as the square had disappeared completely. The results of this

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FIGURE 1. Stimulus used to study perceptual fading and "filling in" (after Ramachandran & Gregory, 1991). The background consisted of twinkling spots of eight different gray levels. The square subtended 1.0 × 1.0° and it had the same mean luminance (60 cd m^{-2}) as the twinkling texture. The fixation spot was about 12° away from the border of the square. On steady fixation the square vanished in about 5 sec and was filled in by the twinkling noise from the surround. A similar fading and filling in of texture was originally described by Ramachandran and Kleffner (1989) but in their stimulus the square was a "window" filled with horizontally moving dots rather than a homogeneous gray. Also, we found that if the square was very small ($<0.2°$) it could be seen to vanish even if it was very bright or dark, that is non-equiluminous with the surround. (The effect could then be seen even if the fixation spot was only 2° from the square.) The fading occurred even more quickly (<2 sec) if the square was in a different stereoscopic plane (nearer or further) than the twinkling texture. This was confirmed by four subjects.

experiment are shown in Fig. 2. (Each datum point represents the mean of four subjects × ten trials = 40 trials.) Notice that the square fades more readily on eccentric viewing than when it is near the center of gaze.

What causes the square to fade?* The effect cannot be due to *local* adaptation (e.g. in the retina) to the luminance edges that define the square since these edges are being constantly refreshed on the screen. We would argue, instead, that the fading is caused by selective adaptation or "fatigue" of neural detectors that are specialized for extracting texture borders and kinetic edges. Such neurons have been described in both cat V1 (Hammond & Smith, 1984) and primate MT (Albright, 1992; Allman, 1985).

This hypothesis would also explain why fading occurs more readily with eccentric viewing. Since receptive field sizes in primate area MT increase progressively with retinal eccentricity (Albright & Desimore, 1987), a smaller eye movement would be required to restore the visibility of the square near the center of gaze than in peripheral vision. Since it is difficult to keep the eyes perfectly steady, it must follow that statistically speaking the square would tend to take less time to fade when it is in the periphery.

Consistent with this line of reasoning, we found that after the square had faded, its visibility could be restored by switching it off and displacing it by a small distance so that a new set of receptive fields was stimulated. Our

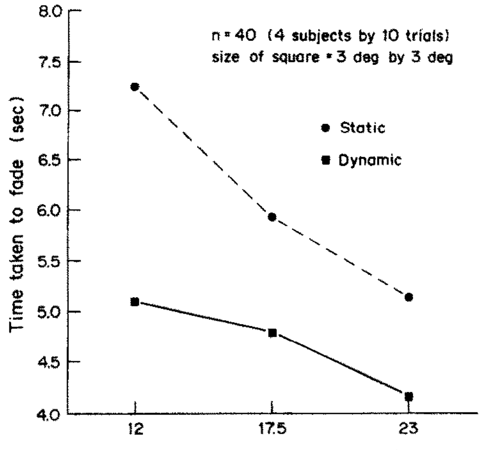

FIGURE 2. Effect of eccentricity on perceptual fading. The stimulus was identical to (Fig. 1) except that the square was presented at various randomly chosen eccentricities on different trials. Notice that the square takes longer to fade near the center of gaze. (Each datum point represents the mean of 40 trials: four subjects × ten trials each.)

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*We are happy to acknowledge that a similar fading of kinetic edges has also been independently observed by Spillman and Kurtenbach (1990), although their interpretation is somewhat different from ours.

next question is: how much must the square be displaced in order to restore its visibility? And does this distance vary with eccentricity?

EXPERIMENT 2: DISPLACEMENT THRESHOLD FOR RESTORING VISIBILITY OF THE SQUARE

The stimulus used in this experiment was identical to the one used in Expt 1 (Fig. 1). The square was presented at a given fixed eccentricity (e.g. 10°) and after it had faded completely we displaced it by different amounts (on different trials) to determine the displacement threshold for restoring visibility of the square. The displacement was always done diagonally—so that none of the borders of the square coincided with original locations of these borders. The subject's task was to simply report whether the square had reappeared or not after a given displacement. Four naive subjects were used, and they were unaware of the purpose of the study.

In Fig. 3 we plotted the displacement threshold against eccentricity (each datum point represents the mean of four subjects × ten trials = 40 readings). Notice that the displacement required to restore visibility increases monotonically with eccentricity as predicted by the "neural fatigue" hypothesis.

EXPERIMENT 3: DYNAMIC NOISE BACKGROUND ENHANCES PERCEPTUAL FADING

Preliminary observations (Ramachandran & Anstis, 1987; Ramachandran & Kleffner, 1989; Ramachandran & Gregory, 1991; Spillman & Kurtenbach, 1992) suggested that the perceptual fading observed in these dynamic displays was more striking and took less time than in more conventional static displays. To confirm this, we repeated experiment described above using a static noise background instead of dynamic noise. Notice that fading still occurs but that the whole graph is shifted upwards (Fig. 2) suggesting that at any given eccentricity fading occurs more readily in dynamic displays than in static ones. This is somewhat counterintuitive since the luminous edges are actually being continuously refreshed when dynamic noise is used and one might therefore expect it to take *longer* to fade. The fact that it fades more quickly suggests once again that the effect occurs due to fatigue of neural detectors that are specialized for extracting kinetic edges.

EXPERIMENT 4: A NEW AFTEREFFECT INDUCED BY 2-D VISUAL NOISE

When we viewed a display such as Fig. 1 for a few seconds and then switched it off, we noticed a striking new visual aftereffect. The region that was originally occupied by the gray square was now occupied by dynamic twinkling noise whose spatial and temporal characteristics resembled the noise in the surround (Ramachandran & Gregory, 1991). Curiously, no aftereffect was seen in the surround area where the snow had actually been displayed.

We showed this display to six naive subjects. After the display had been viewed for 20 sec, it was switched off and they were simply asked whether (a) they saw anything in the region originally occupied by the square and (b) whether anything was seen in the surrounding area. All six subjects responded that they saw a persistent patch of twinkling noise in the region of the gray square but that nothing was visible in the surround. We then repeated the experiment with static rather than dynamic noise and found that none of the six observers could see the patch of noise. And lastly, it is worth noting that the effect was seen only when the square was viewed with eccentric fixation. When viewed directly using foveal vision, none of the six subjects reported an aftereffect.

Next, we measured the persistence of the aftereffect after the display had been viewed for 20 sec. Subjects were simply asked to start a stopwatch as soon as the display was switched off and then stop it as soon as the persistent twinkling patch could no longer be seen. The mean persistence time was ($N = 24$ trials) 8.6 sec. The aftereffect was usually reported to be spatially heterogeneous and dynamic, i.e. it was seen to twinkle. There was, however, some variability in this percept since one of our subjects reported that on some trials a static patch of noise was seen instead of a twinkling patch. If static noise was used (instead of dynamic noise) as inducing stimulus, on the other hand, none of our subjects ever saw a persisting patch of noise.

CONCLUSION

We have studied three main effects in this paper: (a) a gray square displayed on a twinkling noise background tends to fade completely after a few seconds of steady fixation (Ramachandran & Anstis, 1987; Ramachandran & Gregory, 1991; Spillman & Kurtenbach, 1992); (b) the region occupied by the square gets "filled in" by the twinkling noise from the surround; and (c) when the entire display is switched off subjects see a persisting patch of noise in the region corresponding to the gray square. We will now consider each of these effects in turn and discuss possible physiological correlates.

The fading of the gray square is, of course, vaguely reminiscent of the perceptual fading effect that was originally described by Troxler (1804) who found that small, eccentric, low-contrast test spots could be made to disappear completely as a result of steady, prolonged fixation. The key difference is that our effect is selective, i.e. only the *square* fades but the elements that define it remain visible. Indeed, since the elements that define the square edge are by continuously refreshed one might have expected fading to take longer in this display than in more conventional static displays, but, as we have seen, the opposite is true (Fig. 2). We may therefore conclude that the fading observed in our displays probably occurs due to selective fatigue of neurons that are specialized for extracting texture borders and kinetic edges. The existence of such neurons has been established both in cat V1 (Hammond & Smith, 1984) and higher extrastriate areas such as MT

(Allman, 1985; Albright, 1992). The observation that smaller displacements of the square can restore its visibility near the center of gaze than in the periphery (Fig. 3) is also consistent with this hypothesis since receptive field sizes are known to increase progressively with eccentricity.

Why does fading occur more readily when the background is dynamic than when it is static (Fig. 2)? One simple possibility is that neurons that extract kinetic edges, for some reason, become more easily "fatigued" than ones that extract static texture borders (or alternately, their receptive fields may be larger and consequently, less steady fixation may be needed to fatigue a given neuron). A second, more farfetched possibility is that the dynamic noise background excites the magnocellular pathway and in some way actively inhibits the "form" of the square that may be represented in a different visual area such as V4.

When the square disappears it obviously does not leave a gap or hole behind. What subjects report, instead, is that the region occupied by the square gets apparently "filled in" by the dynamic noise from the surround. Does the filling of this "artificial scotoma" involve creating an actual neural representation of the surrounding texture in the region corresponding to the scotoma or does the visual system simply ignore the absence of signals from this region—just as we ignore the back of our head? This question has been considered in detail elsewhere by Ramachandran and Gregory (1991) who showed that the visual system does indeed create an actual neural representation of the surround in the region corresponding to the scotoma (see also Ramachandran, 1992, 1993).

The most striking effect reported in this paper is the persisting patch of dynamic noise that is observed when the whole display was switched off (Ramachandran & Gregory, 1992). What is truly surprising about this aftereffect is that it is spatially heterogeneous (i.e. it mimics the "grain" of the inducing texture) and that it is actually seen to twinkle. One wonders whether the numerous reciprocal cross connections that are known to exist between different extrastriate visual neurons (Van Essen, 1979) are somehow involved in maintaining this dynamic percept.

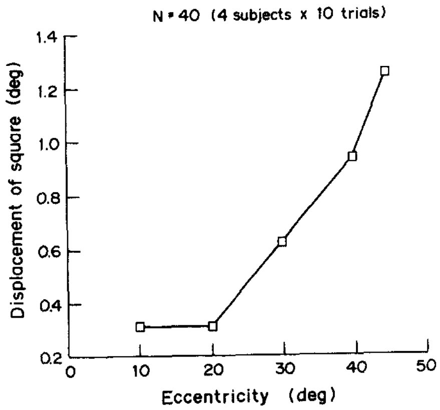

FIGURE 3. Displacement thresholds for restoring visibility of the square as a function of eccentricity. Notice that smaller displacements will restore visibility near the center of gaze than in peripheral vision. (Each datum point represents the mean of 40 trials: four subjects × ten trials each.)

There are at least two plausible interpretations of this aftereffect that are not mutually exclusive. First, it is possible that whatever neural process initiated the "filling in," continues to remain active even after the display is switched off. In other words, the aftereffect might represent a persistence of the neural representation corresponding to the "filling in." A second, more parsimonious interpretation would be that the dynamic noise creates a peculiar state of adaptation in the surround which subsequently "induces" a twinkling patch of noise in the region of the square. Even so, whatever neural process causes this induction is unlikely to be very different from whatever process caused the "filling in" in the first place. (Also, this account doesn't explain why no aftereffect is seen in the surround!) In any event, whatever the ultimate interpretation of these findings, they imply that the "filling in" of artificial scotomas involves more than just ignoring the absence of signals from this region of the visual field. On the contrary, the process is likely to involve creating a dynamic neural representation in the region corresponding to the scotoma (Ramachandran & Gregory, 1991). And the same principle seems to hold for the "filling in" of the natural blind spot (Ramachandran, 1993) and of scotomas of cortical origin (Ramachandran, 1992).

What is the neural locus of the aftereffect? Our preliminary observations using twinkling lines (i.e. one-dimensional instead of two-dimensional noise) suggests that the effect is orientation selective; subjects tend to report a persistent patch of twinkling "streaks" or lines in the region of the artificial scotoma. Since cells in the retina and in the LGN are not orientation selective, this observation would imply a cortical locus for the aftereffect. Additional evidence for this view comes from some recent experiments we did on two patients who had retinal scotomas produced by laser. These patients were asked to view our twinkling noise display for 20 sec and then transfer their gaze to a homogeneous gray screen. Without prompting, each patient reported seeing a persisting patch of twinkling noise whose shape almost exactly matched the shape of his scotoma as measured by conventional perimetry. The mean persistence time of this patch of twinkling noise was 9.4 sec ($n = 16$; two subjects and eight trials each). Since there is no retina corresponding to the twinkling patch, we conclude from these experiments that the aftereffect is probably cortical in origin.

What are the actual physiological mechanisms underlying the "filling in" of artificial scotomas? Our experiments suggest that filling in occurs fairly early in visual processing and must involve creating an actual neural representation of the surround in the region of the scotoma. This view is consistent with a remarkable series of physiological experiments performed recently by Gilbert and Wiesel (1991, 1992). They destroyed a small patch of retina and recorded from the area of visual cortex to which this patch would normally project. These cells were initially silent, of course, as one would expect, but the researchers found that within a few minutes the same cells now had receptive fields that were outside the zone of lesion; they could be excited by visual stimuli that lay outside the scotoma! More recently, they tried repeating these experiments using an artificial scotoma instead of a real one (Pettet & Gilbert, 1991). Instead of destroying retinal receptors they used a display similar to Fig. 1. To their surprise they found that cells that initially had receptive fields within the gray square now had receptive fields that were much larger and included regions outside the square. These rapid changes in receptive field organization may provide an explanation for some of the perceptual "filling in" effects that we have described in this article. Since these cells were originally responding to stimuli inside the scotoma, patterns immediately outside the scotoma would tend to be mislocalized so that they are now seen inside it and this would correspond roughly to what we call "filling in." Furthermore, these results imply that receptive fields are not fixed anatomical entities formed by retinal receptors funneling information on to single cells in the cortex. They suggest, instead, that the classical receptive field may be just the tip of an iceberg. Each cell may have thousands of silent synapses that can be reactivated or inhibited—perhaps in seconds—in response to ongoing visual stimulation and this can manifest as dynamic changes in receptive field organization. Studying these dynamic changes may give us novel insights into neural mechanisms underlying perception.

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