ISSN 0042-6989
Volume 34 Number 24
December 1994

Vision Research

An International Journal for Functional Aspects of Vision

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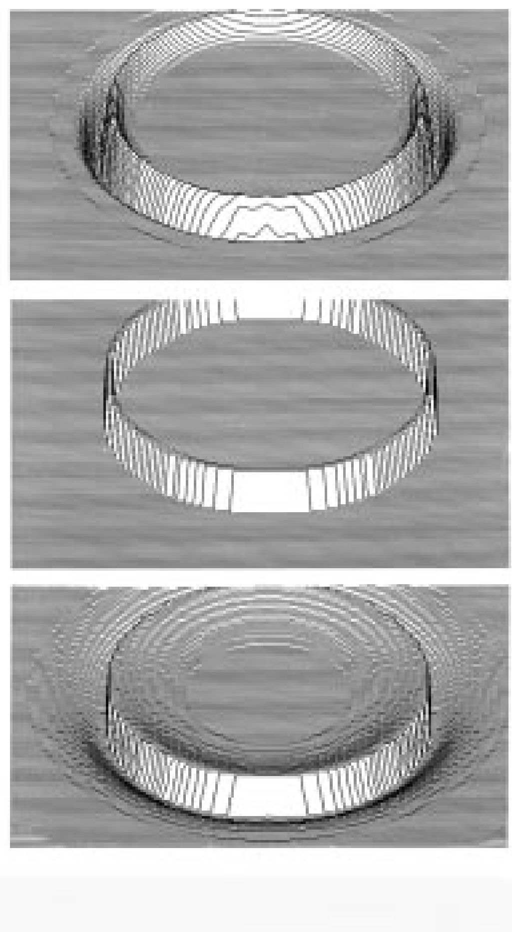

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Vision Res. Vol. 34, No. 24, pp. 3371–3387, 1994
Elsevier Science Ltd. Printed in Great Britain

0042-6989(94)00121-9

The Temporal Dynamics of Brightness Filling-in

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Received 2 April 1993; in revised form 25 March 1994

The temporal dynamics of brightness filling-in were studied through neural network simulation experiments conducted under visual masking stimulus conditions. Grossberg *et al.* have specified a filling-in model called the Boundary Contour System/Feature Contour System (BCS/FCS). The BCS generates boundary segmentation, while the FCS fills-in surface feature within these segmentation boundaries. Simulation experiments demonstrate that the model accurately predicts that area-suppression follows a U-shaped function of forward masking and demonstrate that the psychophysical findings of Paradiso and Nakayama [(1991) *Vision Research, 31,* 1221–1236] which they regarded as being against the BCS/FCS model, actually support the model.

Neural network   Brightness   Filling-in   Masking   Area-suppression

1. INTRODUCTION

Since the time of Kuffler and Ratliff it has been understood that the information sent from the retina to the brain is primarily about luminance and color contrasts rather than about uniform luminance and color areas. This however raises an interesting problem: why is our visual experience of object surfaces, not just of their edges? One explanation that has gained much attention recently is that the edge information flows across the area that corresponds to uniform surface, filling it in with feature. There are several functional advantages to a filling-in process. Because stabilized images tend to fade, this process will tend to fill-in over shadows of retinal veins, scotomas, the blind spot, and the blue insensitive fovea.

Numerous examples of filling-in phenomena and completion phenomena appear in the clinical literature; for example from retinal scotomas (Gerrits & Timmerman, 1969) and homonymous hemianopia (Gassel & Williams, 1963). Lashley (1941) described completion in his personal experience of migraine scotoma. He became aware of his scotoma when he glanced to the right of a friend's face and noticed that his friend's head had disappeared and was replaced by the vertical stripes in the wallpaper behind him that seemed to extend down to the neck-tie. Lashley concluded that the filling-in of a blind spot and the completion of migrainous scotoma must represent some intrinsic organizing function of the cortex (Gassel & Williams, 1963). Walls (1954) carried the idea further by proposing that filling-in is a normal part of the functioning of the visual system, rather than merely a pathological condition.

Filling-in phenomena have been studied more systematically in experimental work using stabilized images. Normally the eye jitters (microsaccades) in its orbit, thereby keeping the retinal image in continual relative motion with respect to a scene, which preserves the neural edge response. The neural response to an edge quickly fades if the edge is not moving across the retina. By using contact lenses, part of a scene can be artificially stabilized on the retina. Using this technique it can easily be demonstrated that as the edge percept of a figure fades, the color outside the figure is perceived to flow in over the interior of the figure and fill it in (Krauskopf, 1963; Gerrits, de Haan & Vendrik, 1966; Yarbus, 1967). When viewing a stabilized image, the target looks very sharp and clear when it is first turned on, but then it rapidly fades out and disappears. Stabilized patterns can fade from perception in less than a second. If the stabilized image slips on the retina, it will reappear and quickly disappear again.

Examples of filling-in come not only from clinical and experimental results, but can also be easily seen (or rather not seen) in more everyday situations. One stabilized image that is rarely seen is the shadow of the retinal blood vessels. This extensive network of vessels that lies in a layer just over the photoreceptors can easily be made visible however, simply by moving a spot of light on the sclera (Cornsweet, 1970). Another easily observed stabilized image effect is the Troxler (1804) effect: when contrast is low, prolonged steady staring can result in a reduction of the perceived contrast and even in stimulus fading and disappearance (Fiorentini, Baumgartner,

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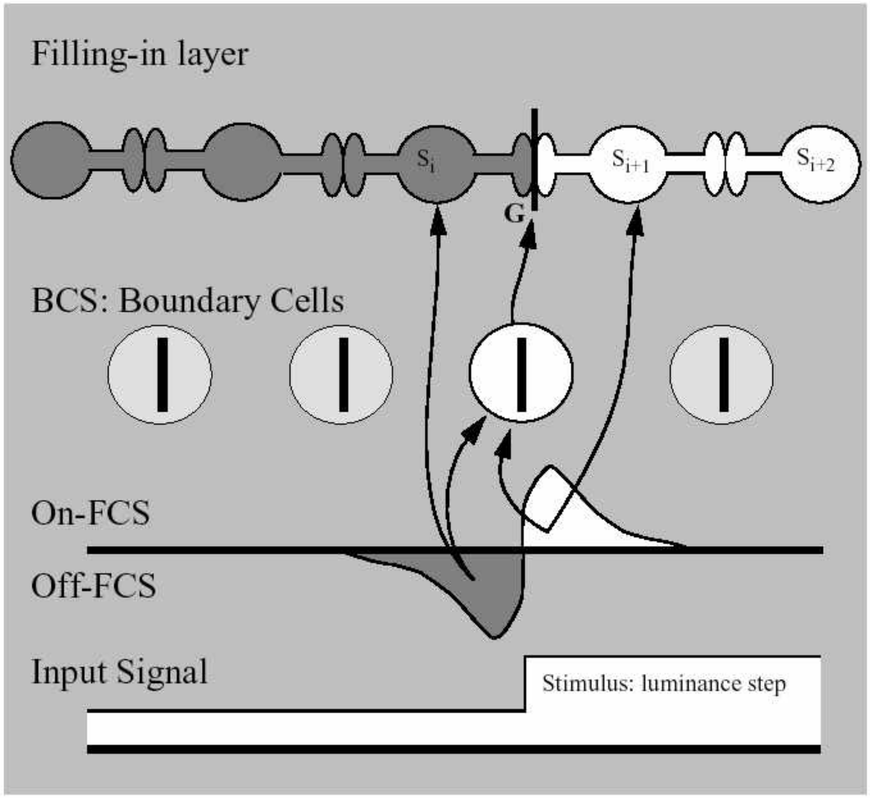


FIGURE 1. Filling-in of FCS signals within BCS boundaries. The BCS/FCS system response to a luminance step increase. The ON-channel FCS response is plotted at the right of the contour in white as a positive (upward) deflection from the baseline and the OFF-channel FCS response is plotted at the left of the contour in dark gray as a negative (downward) deflection. The activated BCS cells are highlighted in white; they are insensitive to direction of contrast. These BCS complex cells create high resistance gates, G, which impedes diffusion. The ON-FCS signal and OFF-FCS signal are input to the filling-in layer where the feature signals diffuse until they are stopped by a boundary.

Magnussen, Schiller & Thomas, 1990, p. 138; Cornsweet, 1970, p. 409).

Gerrits and Vendrik (1970) were apparently the first to develop a filling-in theory that qualitatively modelled the phenomenon by specifying a filling-in process that works in parallel with a filling-in-barrier mechanism. According to their filling-in theory, the ON-responses and the OFF-responses, which peak on opposite sides of a contour edge, fill-in over areas that correspond to uniform regions of the stimulus. Mixing of the antagonistic activities is prevented by a boundary, or barrier, that is created at the locations where contrast is high (edges). Filling-in theory clarifies how a neural representation of visual surface information matches our visual percept of surfaces.

The existence of a neural filling-in process has also been supported by the masking experiments of Stoper and Mansfield (1978). They were apparently the first to study* the distinction between "contour-suppression" and "area-suppression" masking effects. Contour-suppression has been assumed to be the mechanism responsible for brightness suppression in traditional metacontrast experiments where, for example, a disk target is followed by a larger annulus mask with an inside diameter the same as the diameter of the disk. The ON-to-OFF response to the contour of the disk is suppressed by the OFF-to-ON response to the contour of the annulus. This type of masking shows relatively no forward masking effect (Alpern, 1953, p. 650; Kolers & Rosner, 1960, p. 18). Area-suppression differs from contour-suppression in that it occurs away from contour edges in areas corresponding to uniform surface and that it follows a U-shaped function of stimulus onset asynchrony (SOA) for forward masking, which is equal to those obtained for backward masking. They proposed an explanation for this in terms of interference with a filling-in process, as had been described by Gerrits and Vendrik (1970). Stoper and Mansfield (1978) conjectured that contour-suppression is mediated by a fast low-level system while area-suppression is mediated by a more sluggish high level system.

Grossberg *et al.* (Grossberg, 1983; Cohen & Grossberg, 1984; Grossberg & Todorović, 1988) have mathematically specified a filling-in model called the Boundary Contour System/Feature Contour System (BCS/FCS) model. The BCS and FCS systems work in parallel: the FCS discounts variable illumination and the BCS generates an emergent boundary segmentation of a

*Werner (1935) noted an area suppression effect that occurred under metacontrast with incomplete masks.

†Gerrits and Vendrik (1970), p. 418, made it clear that they believed that the filling-in process is most probably located beyond V1, because, for example, of the completion of geometric figures and observations of migraine scotomas.

scene. The signals from these two systems interact to create visible percepts by filling-in surface features within segmentation boundaries. In the BCS/FCS theory, in Visual Area One† (V1) the FCS is associated with the blobs that are reported to contain cells selective for color contrasts (Livingstone & Hubel, 1984) and the BCS is associated with the simple and complex cells that are reported to respond to edges or oriented contrasts (Hubel & Wiesel, 1968). In the BCS/FCS model, filling-in is hypothesized to occur via electrotonically coupled syncytia and it is instantiated as a passive diffusion of activation across nearest neighbor cells.* Figure 1 schematically illustrates the model.

Paradiso and Nakayama (1991) have recently published the results of masking experiments that attempt to catch brightness filling-in "in the act", at various stages of the filling-in process, by systematically varying the shape and spacing of mask contours. First they used a straight line mask that produced a gradual shading, or roll-off, of brightness from the light target edge to the dark mask edge. Next they compared the effects of the straight line mask to a mask line bent into a C-shape. The latter showed darkening of the inside corners of the C-shape, which may suggest a blocking of brightness or a trapping of darkness. In another set of experiments they used an annulus with gaps cut in as the mask. Gap size was varied to examine how mask contour continuity affects brightness suppression. The results showed that target brightness varied monotonically with gap size.

Based on their psychophysical results the authors expressed doubts as to the ability of the BCS/FCS model to make the correct brightness predictions for their experiments. "The first problem is that diffusion continues until it is stopped by shunting inhibition. This suggests that there should be sharp edges to filled-in areas corresponding to the sites of shunting inhibition. This is inconsistent with our observation indicating that in many cases brightness gradually rolls off near masking lines. A second difficulty results from the feature that diffusion continues until an equilibrium state is reached. It isn't obvious how such a process could account for the significant masking observed with line segments in (Expt 4, shown here in Fig. 2). The model seems to incorrectly predict that brightness would diffuse around the edges of the masking segment and fill-in the center of the target." (Paradiso & Nakayama, 1991, p. 1235).

These comments of Paradiso and Nakayama (1991) apparently derive from the earlier publications of simulations of the BCS/FCS brightness predictions, all of which were at steady state. In the context of normal vision, the filling-in process is very fast. Nevertheless, in the context of masking experiments, where the stimuli are presented so close together that the visual system cannot resolve them as distinct perceptual events, the visual system is hardly at steady state. Under masking conditions we must also look at the transients of the model, rather than simply at the steady state solution.

This paper examines the temporal dynamics of the BCS/FCS model under various masking conditions. The psychophysical experiments and theoretical concerns of Paradiso and Nakayama (1991) are examined in simulation experiments one through four. Simulation experiment five studies how well the model predicts the forward-masking effects observed under the area-suppression paradigm used by Stoper and Mansfield (1978).

*In the filling-in theory developed by Grossberg, the cortical syncytia are hypothesized to be encephalizations of ancestral retinal syncytia and the electrotonic coupling is considered to be formally analogous to the interactions in H1 horizontal cells of turtle retina (Grossberg, 1987).

2. METHODS

The simulations use the simplest version of the BCS/FCS model that is sufficient to examine the issues of interest in this paper. The neural network model consists of five two-dimensional layers: an input layer, $I_{ij}(t)$, where the "visual" masking stimuli are presented and four neuronal layers, one each for the center-surround contrast sensitive cells, $x_{ij}^{(ON)}$ and $x_{ij}^{(OFF)}$, one for the boundary cells, B_{ij}, and one for the filling-in layer cells, S_{ij}. The filling-in layer is the output layer for the model, it shows the brightness predictions. The activation of the neurons are determined by differential equations, as described below.

The network equation used to model the retinal ganglion cells, x_{ij}, is shown in equation (1) (Grossberg, 1983). Parameters P_x, D_x, and H_x are the passive decay rate, depolarization limit, and hyperpolarization limit of the neuron, respectively. Variables e_{ij} and i_{ij} are the total excitatory and total inhibitory inputs to the neuron, respectively.

$$\frac{dx_{ij}^{(ON)}}{dt} = -P_x x_{ij}^{(ON)} + (D_x - x_{ij}^{(ON)})e_{ij} - (x_{ij}^{(ON)} + H_x)i_{ij}, \quad (1)$$

$$\frac{dx_{ij}^{(OFF)}}{dt} = -P_x x_{ij}^{(OFF)} + (D_x - x_{ij}^{(OFF)})i_{ij} - (x_{ij}^{(OFF)} + H_x)e_{ij}, \quad (2)$$ (Corrected)

$$e_{ij} = C \sum_{p,q} \Psi_{pqij}^{(center)} I_{pq}(t), \quad (3)$$

$$i_{ij} = E \sum_{p,q} \Psi_{pqij}^{(surround)} I_{pq}(t). \quad (4)$$

In equations (3) and (4) the kernels, $\Psi^{(w)}$, are Gaussian distributions that specify the center and surround receptive fields, which compose the difference of Gaussians (DOG) receptive field. Equation (5) specifies the Gaussian distribution that determines the spatial bandwidth of the receptive field

$$\Psi_{pqij}^{(w)} = \exp\{-\lambda_w[(p-i)^2 + (q-j)^2]\}. \quad (5)$$

The spatial constants, $\lambda_{(w)}$, of the center and surround areas were of ratio 1:2. Each of the Gaussians was numerically normalized such that the sum of the kernel elements equals unity. The remaining parameters in the equation were chosen such that spatially uniform stimuli yield a zero response, specifically $(D_x C - H_x E) = 0$.

The FCS output signal for each channel (c) is the half-wave rectified cell potential of that channel,

$$X_{ij}^{(c)} = \max(x_{ij}^{(c)}, 0). \qquad (6)$$

That is, the cell fires at a rate proportional to the depolarization level, but is silent when the cell is hyperpolarized. The parameters for the ON- and OFF-channels were identical, such that a stimulus edge would produce ON- and OFF-FCS activations equal in strength, though opposite in sign, as shown in Fig. 1.

The outputs, $X_{ij}^{(ON)}$ and $X_{ij}^{(OFF)}$, from the center–surround shunting network are the inputs to the second stage, the BCS, that generates emergent boundary segmentation of a scene. The boundary system has been greatly simplified to increase simulation speed and to allow a focus on the filling-in dynamics that are the issue here. The boundary signals are created at locations where ON- and OFF-activations are spatially adjacent

$$B_{ij} = \max\left(\left(\sum_{(p,q)\in N_{ij}} X_{pq}^{(ON)}\right)\left(\sum_{(p,q)\in N_{ij}} X_{pq}^{(OFF)}\right) - L, 0\right). \qquad (7)$$

Parameter L specifies how much contrast is required before a boundary signal is created.

Finally, the FCS and BCS provide parallel input to the filling-in layer. The ON- and OFF-activations flow into each other and cancel except where flow is impeded by high resistance boundary signals. The FCS signals, $X_{ij}^{(ON)}$ and $X_{ij}^{(OFF)}$, which are only active at locations immediately adjacent to stimulus contrasts, are fed into the filling-in layer where the activity freely spreads across neighbor cells. This diffusive filling-in process is impeded by high resistance gating signals, G_{pqij}, between locations (i, j) and (p, q) that are activated by BCS boundaries. In general this gated diffusion process* is specified by

$$\frac{dS_{ij}}{dt} = -P_S S_{ij} + (X_{ij}^{(ON)} - X_{ij}^{(OFF)}) + F_{ij}, \qquad (8)$$

where P_S is the passive decay rate constant, the $X_{ij}^{(c)}$ terms are the direct input and the F_{ij} term is the diffusion (filling-in) term

$$F_{ij} = \sum_{(p,q)\in N_{ij}} [(S_{pq} - S_{ij})G_{pqij}]. \qquad (9)$$

In the simulations the term $(X_{ij}^{(ON)} - X_{ij}^{(OFF)})$ was replaced by $x_{ij}^{(ON)}$, such that

$$\frac{dS_{ij}}{dt} = -P_S S_{ij} + x_{ij}^{(ON)} + F_{ij}. \qquad (10)$$

This is essentially the same† because the latter depolarization and hyperpolarization values correspond to the ON- and OFF-responses and they are already together in one variable.

Notice that the term $(S_{pq} - S_{ij})$ in equation (9) is a discrete approximation to the Laplacian diffusion operator, since the set N_{ij} of locations comprises only the lattice of nearest neighbors of (i, j)

$$N_{ij} = \{(i, j-1), (i-1, j), (i+1, j), (i, j+1)\} \qquad (11)$$

(Grossberg & Todorović, 1988). The diffusion gating coefficients, G_{pqij}, that regulate the lateral spread of activation, depend on the spatially adjacent boundary contour signals, B_{ij} and B_{pq}, as follows

$$G_{pqij} = \frac{\delta}{1 + \epsilon(B_{pq} B_{ij})}. \qquad (12)$$

Parameter δ controls the rate of diffusion. A large value will allow rapid diffusion from the edges across uniform areas, which results in a smoother appearance. A smaller value will cause input activation to accumulate where it is input near the boundaries, because it cannot diffuse away fast enough. Parameter ϵ controls the diffusion across boundaries. A large value allows little diffusion across boundaries. Both δ and ϵ should be positive so that G_{pqij} remains positive. In the simulations $\delta = \epsilon$.

Examination of the filling-in layer, equation (8), shows that cell activation is the result of two mechanisms: direct input $(X_{ij}^{(ON)} - X_{ij}^{(OFF)})$ (the fast component) and diffusion from nearest neighbors, F_{ij} (the slow component). The dynamics resulting from these two components may be considered to correspond to the fast and slow components supposed by Stoper and Mansfield (1978) to account for their psychophysical results (this idea will be developed further in the General Discussion section). The simulations will clarify how the two processes act on different time scales to produce the brightness percept under area-suppression masking conditions. Equilibrium is restored by two processes, passive decay and mutual annihilation of ON- and OFF-signals as they flow into one another after boundary activations fade.

The simulations were performed on the Connection Machine® using the C* (parallel C) programming language. The input layer, I_{ij}, and the neural fields for the FCS channels, $x_{ij}^{(ON)}$ and $x_{ij}^{(OFF)}$, the BCS, B_{ij}, and for the filling-in layer, S_{ij}, were all 128×128 processing units wide. The diameter of the target disk stimulus was 80 units in each simulation. The parameters‡ were the same in all simulations in this paper.

3. RESULTS AND DISCUSSION

The first set of psychophysical experiments and results that are modeled here are schematically illustrated in Fig. 2. This figure is adapted from a figure in the original publication of Paradiso and Nakayama (1991) that shows the percepts reported by their subjects in each case. Each row of the figure illustrates one experiment. In each experiment the target, t (shown in the first

*According to the theoretical description of the BCS/FCS model there is a diffusive syncytia, $S^{(c)}$, for each spatial scale, chromatic-channel, and ON- and OFF-channel.

†The comparability of equation 8 and equation 10 will be reduced at stimulus contrast ratios much higher than those used here; if such high contrasts are to be employed, be sure to use equation 8. Equation 10 was used here because that is what was used by Grossberg and Todorović (1988).

‡$P_x = 0.1$, $D_x = 6.25$, $C = 0.5$, $H_x = 2.5$, $E = 1.25$, $\lambda_{(center)} = 2$, $\lambda_{(surround)} = 4$, $L = 0.1$, $P_s = 0.5$, $\delta = \epsilon = 40{,}000$.

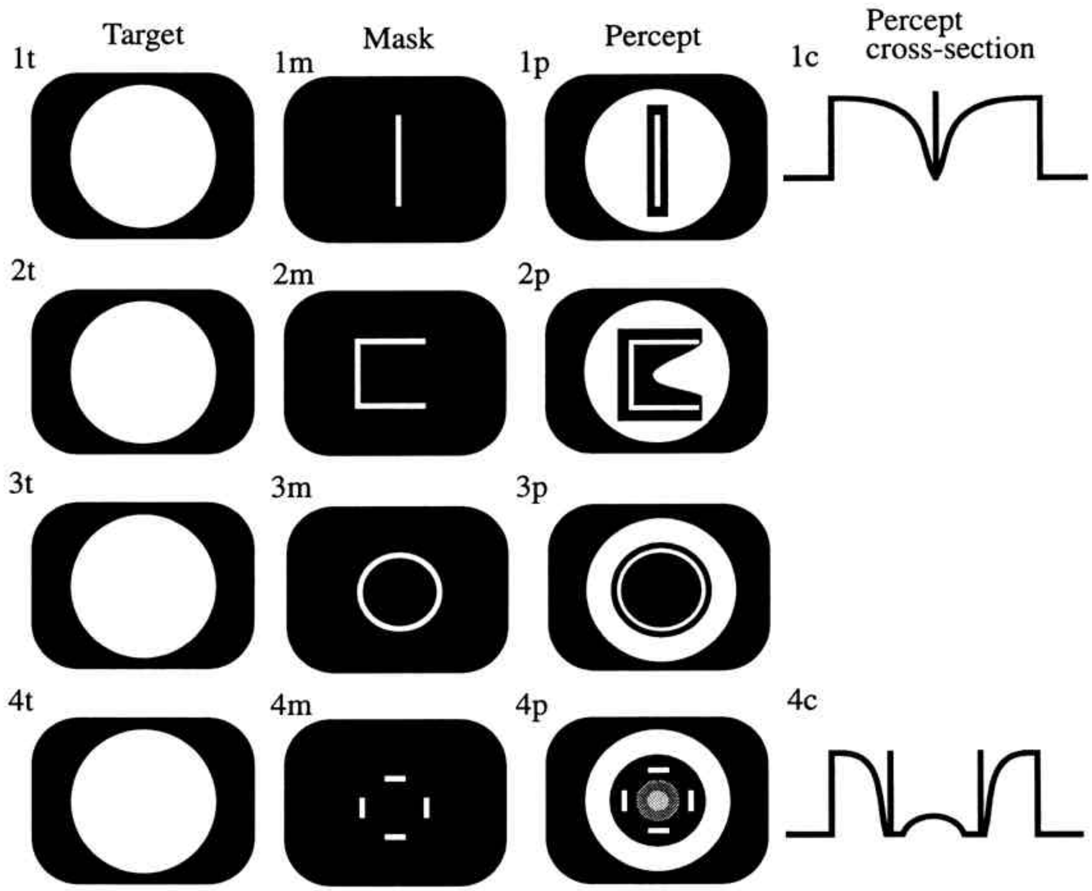


FIGURE 2. Four masking experiments done by Paradiso and Nakayama. The frames are labeled with reference to row and column. Each row, numbered 1–4, schematically illustrates one type of experiment. The first column shows the target, t, a luminous disk against a dark background, which was the same for every experiment. The second column shows the type of mask, m, that was employed, which is what defines the experiment. The third column shows the brightness percept, p, and the last column shows the cross-section, c, of the brightness percept. Cross-section (1c) was not published but is inferred from (4c) that was part of the published data. Adapted from Paradiso and Nakayama (1991).

column) is a luminous disk against a darker background. The mask, m, is one of the types shown in the second column. Each is a bright shape against a darker background. The first mask (illustration 1m) is a single luminous line; the second mask (2m) is a C-shape. The third and fourth masks (3m and 4m) are an annulus and an annulus with gaps cut into it, respectively. The latter illustration is representative of a set of masking experiments that involve parametrically changing the gap-size, which are considered in Expt 4.

Analysis of the model will begin by examining the concerns raised by Paradiso and Nakayama (1991).

3.1. Experiment 1: gradual roll-off near masking lines

The first concern raised by Paradiso and Nakayama (1991) has to do with the ability of the BCS/FCS to predict the gradual roll-off of brightness near the edges of masking stimuli. This objection is refuted immediately by the simulation of the first experiment illustrated in Fig. 2 (row 1). The simulation results are shown in Fig. 3 where it is easy to see that brightness does gradually roll off near the masking line. The degree of roll-off (the shading effect) is a function of the diffusion parameter, δ, as described in the Methods. A spatio-temporal plot of the simulation results of Fig. 3(a) is shown in Fig. 3(b).

The brightness perception in this masking experiment is influenced by the introduction of an FCS dark-edges signal in response to the mask-edge. Because the interaction between the ON- and the OFF-percept is typically presumed to be an *additive interaction* (Gerrits & Vendrik, 1970, p. 423), it is convenient to represent the "percept" of the combined ON- and OFF-activations as the positive and negative deflections from zero baseline. This zero baseline corresponds to the gray that is perceived when the eyes are closed, which is usually referred to as *Hering gray*, or *Eigengrau*. Note that the Eigengrau is not as dark as the black that is generated from contrast.

This particular experiment does not involve obstruction of diffusion, whereas the subsequent masking experiments do.

*The threshold level for the binary image was taken very close to the zero (Eigengrau) level; the C-shape actually moves out during the time course of the masking simulation, so any degree of concavity could be easily obtained at most any threshold level near zero, i.e. the C-shape is very robust. Though the similarity to the published figures is exciting, it should be remembered that the psychophysical percept is actually of a gradually shaded area, consequently the real power of the model in capturing the psychophysical percept is represented in the contour plot, not in the binary threshold figure.

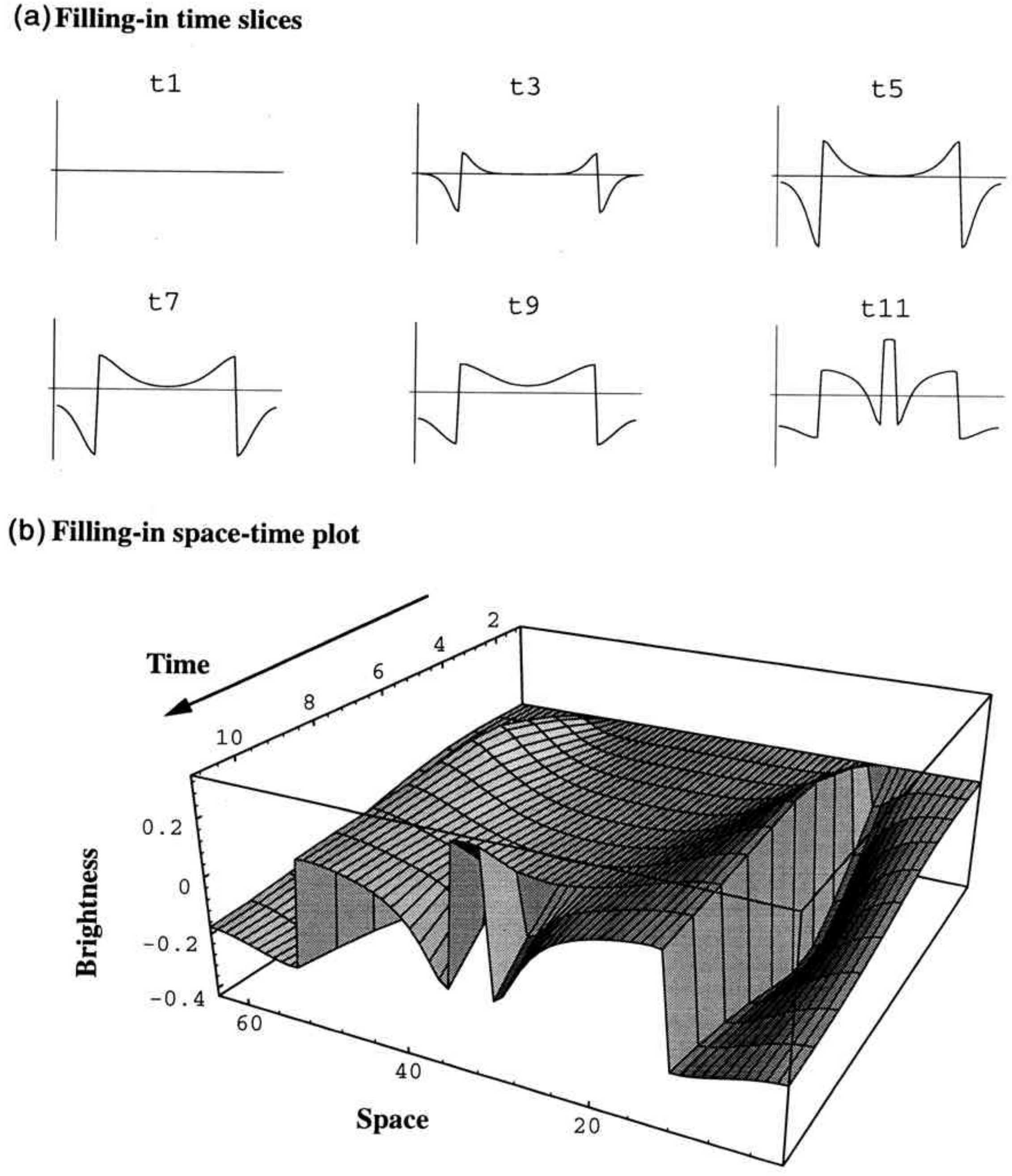
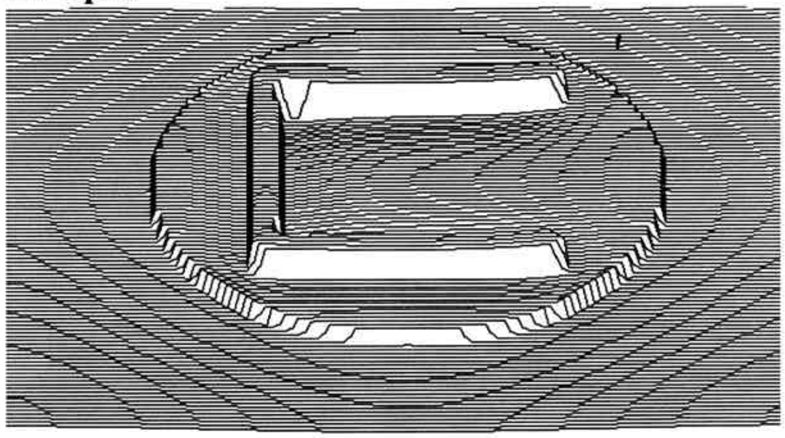


FIGURE 3. Dynamic simulation of case 1, using the BCS/FCS. A sequence of uniform time slices from a dynamic simulation of the BCS/FCS model when presented with the first masking experiment that was schematically illustrated in Fig. 2 (top row). In each time slice in (a) the abscissa is space and the ordinate is the filling-in layer activity. The horizontal line is the baseline, *Eigengrau*, brightness level: at t_1 the brightness is at the Eigengrau. At t_3 the response to the target is just beginning; at t_5 the activation has increased and the beginning of filling-in is evident; at t_7 the target stimulus is removed, the peaks begin to subside but filling-in continues; t_9 is a snapshot during the inter-stimulus interval; finally, at t_{11} we see the effect of the mask that has become active. Compare t_{11} here to Fig. 2 (1c). The time indices in (a) correspond to those in (b) that shows the spatio-temporal dynamics in three dimensions.

3.2. Experiment 2: C-mask

Gradation of brightness is even more apparent in Fig. 4(a) that shows a simulation of the second masking experiment that uses a C-mask, as illustrated in Fig. 2 (m). The equal-activity contours in Fig. 4(a) clearly show the light-edge activity filling-in toward the interior of the C-shape. The binary threshold* of Fig. 4(a) is shown in Fig. 4(b). It is almost identical to the figure published by Paradiso and Nakayama (1991), which is reproduced in Fig. 2 (2p). It shows the same asymmetric brightness suppression where the brightness of the disk is considerably darker inside the "C" than outside. The brightness percept from this C-mask stimulus involves both obstruction of the disk light-edge response diffusing toward the center of the disk, as well as the introduction of mask

(a) C-mask surface plot



(b) Binary threshold

FIGURE 4. C-mask simulation. Filling-in layer activation after the C-shaped mask-stimulus [see Fig. 2 (2m)] was presented. (a) A surface representation and (b) a binary threshold version of these activations. This compares very favorably to the percept illustrated in Fig. 2 (2p).

dark-edge signal into the filling-in layer. This combined effect becomes even more apparent with the annulus-mask stimuli that are examined next.

3.3. Experiment 3: masking with annulus and annulus-segments

In this next set of experiments the masking-stimulus is an annulus or an annulus with gaps in it, as schematically illustrated in Fig. 2 (3m and 4m). The question is "whether continuity is essential for a contour to have a suppressive effect on brightness" (Paradiso & Nakayama, 1991, p. 1224). In Fig. 5(a) the target-stimulus, and Fig. 5(b) the masking-stimulus are shown in a surface representation of luminance. In the psychophysical experiments the gap-size is varied parametrically and the brightness percept at the center of the disk is evaluated in a brightness matching paradigm. In the simulation experiments the brightness percept is taken from the filling-in layer activation at the center of the disk.

Figures 6–8 are snapshots of the activations of the FCS ON-response, the BCS and the filling-in layer at three different epochs during the temporal evolution of the masking experiment. The next three subsections explain what is happening in each of these snapshots.

3.3.1. Epoch 1: target stimulus. Figure 6(a) shows the transient response of the model system just after the target stimulus (disk) is presented. The surface in Fig. 6(a) shows the FCS ON-response and Fig. 6(b) shows the BCS response to the target disk. In Fig. 6(c) the beginning of the filling-in response is shown: the FCS light-edge response, which is injected into the filling-in layer, flows toward the center of the disk, while the dark-edge response flows outward away from the disk.*

3.3.2. Epoch 2: annulus-segments masking stimulus. Figure 7 shows the responses at a time immediately after the masking-stimulus has come on. The surface in Fig. 7(a) shows that the FCS response to the disk is in the process of decaying away, only a residual neural trace is still apparent. Even though the FCS signal† is low, it is still sufficient to maintain a boundary signal, as can be seen in Fig. 7(b). The FCS response to the mask-stimulus is growing; it too generates a boundary signal during this phase. In Fig. 7(c) the filling-in response shows progress toward a well formed disk,‡ and the effects of the mask

*See General Discussion section on darkness filling-in.

†The boundary threshold and the boundary response function are model parameters.

‡The slight tooth-like glitches at the edge of the disk are an implementation-specific behavior and not a property of the model, per se.

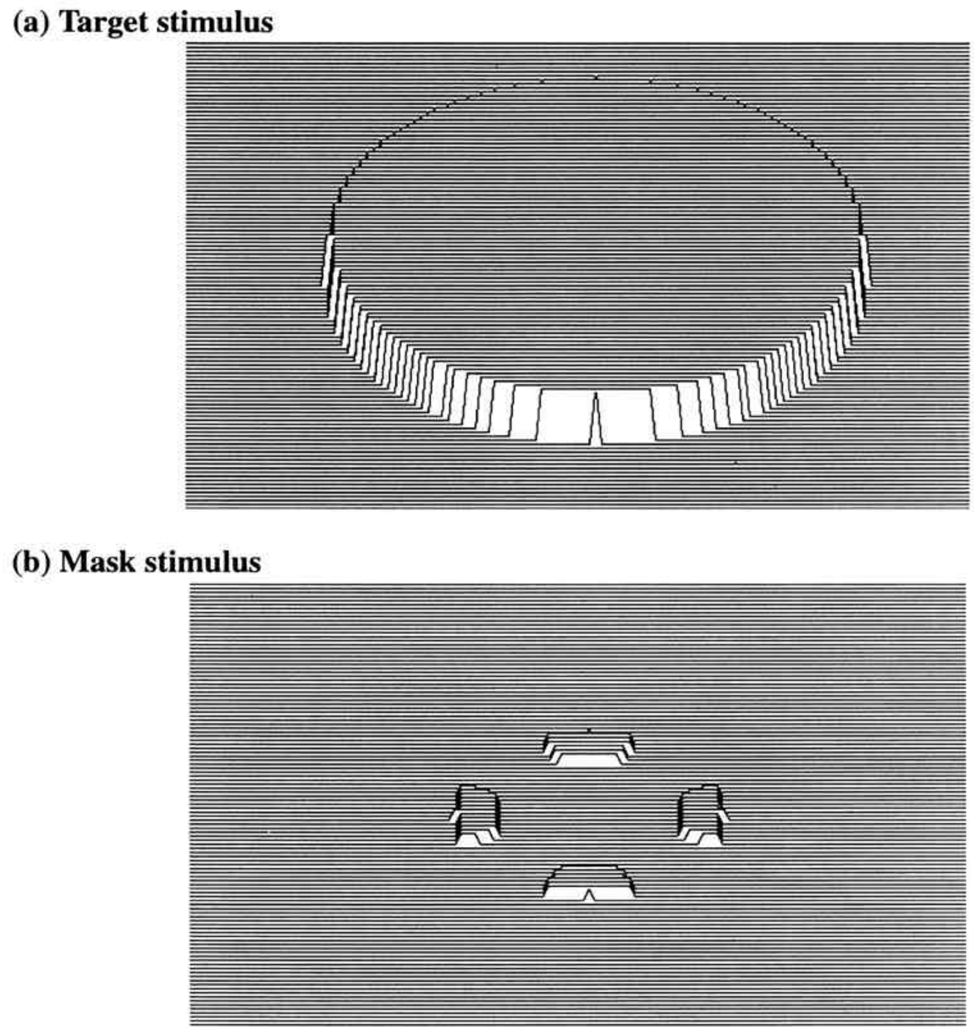


FIGURE 5. Target stimulus and annulus-segments masking stimulus. The masking experiment comprises the rapid succession of two stimuli. (a) The target-stimulus, and (b) the masking-stimulus are shown in a surface representation of brightness. The gap-size in the annulus-segment mask (b) are varied parametrically.

BCS-response impeding the flow of the disk light-edge signal, as well as the new dark-edge FCS-signals introduced by the mask. Figure 7(c) shows a dome-shaped brightness percept inside the mask. Compare this to the reported percept that is illustrated in Fig. 2 (4c).

3.3.3. Epoch 3: decay phase. Figure 8 shows the responses at the end of the stimulus presentation sequence, after the mask-stimulus has gone off. The FCS response [Fig. 8(a)] to the disk has vanished and the FCS response (magnified) to the mask is decaying. The BCS signal [Fig. 8(b)] to the target-stimulus has completely vanished and the BCS response associated with the mask has decayed below the level where it can hold the mask contour in the filling-in layer [Fig. 8(c)]; the ON- and OFF-activations quickly neutralize* one another and reinstate the baseline activation that forms the Eigengrau percept. The next section examines how the brightness percept in the center of the annulus varies as the annulus gap-size varies.

*Barlow (1961) suggested that rapid neutralization was one of the design benefits of a network with parallel ON- and OFF-systems.

3.4. Experiment 4: variation of gap-size

By varying the annulus gap size, it is possible to parametrically vary the masking effect. Recall that the second objection made by Paradiso and Nakayama (1991) was that the diffusion within the disk would continue to equilibrium through any gaps in the segmented annulus mask and fill-in the center to generate an incorrect brightness prediction. The refutation of the second objection is related to that of the first. Again, even though diffusion is very fast, it does require some time to equilibrate. Just as in the psychophysical results, if the SOA is sufficiently small that the FCS light-edge response has not already filled-in to form a uniform brightness percept, then the mask will impede flow of the light-edge signal, as well as introduce mask dark-edge FCS signals. Introduction of the dark-edge signal additively reduces the interior brightness, as a function of the total mask perimeter.

Figure 9 illustrates the effect of varying the annulus gap-size. Four different gap sizes were chosen: 10, 30, 50, and 70 deg per quadrant, which correspond to $10/90 = 11\%$, $30/90 = 33\%$, 55%, and 77% perforation

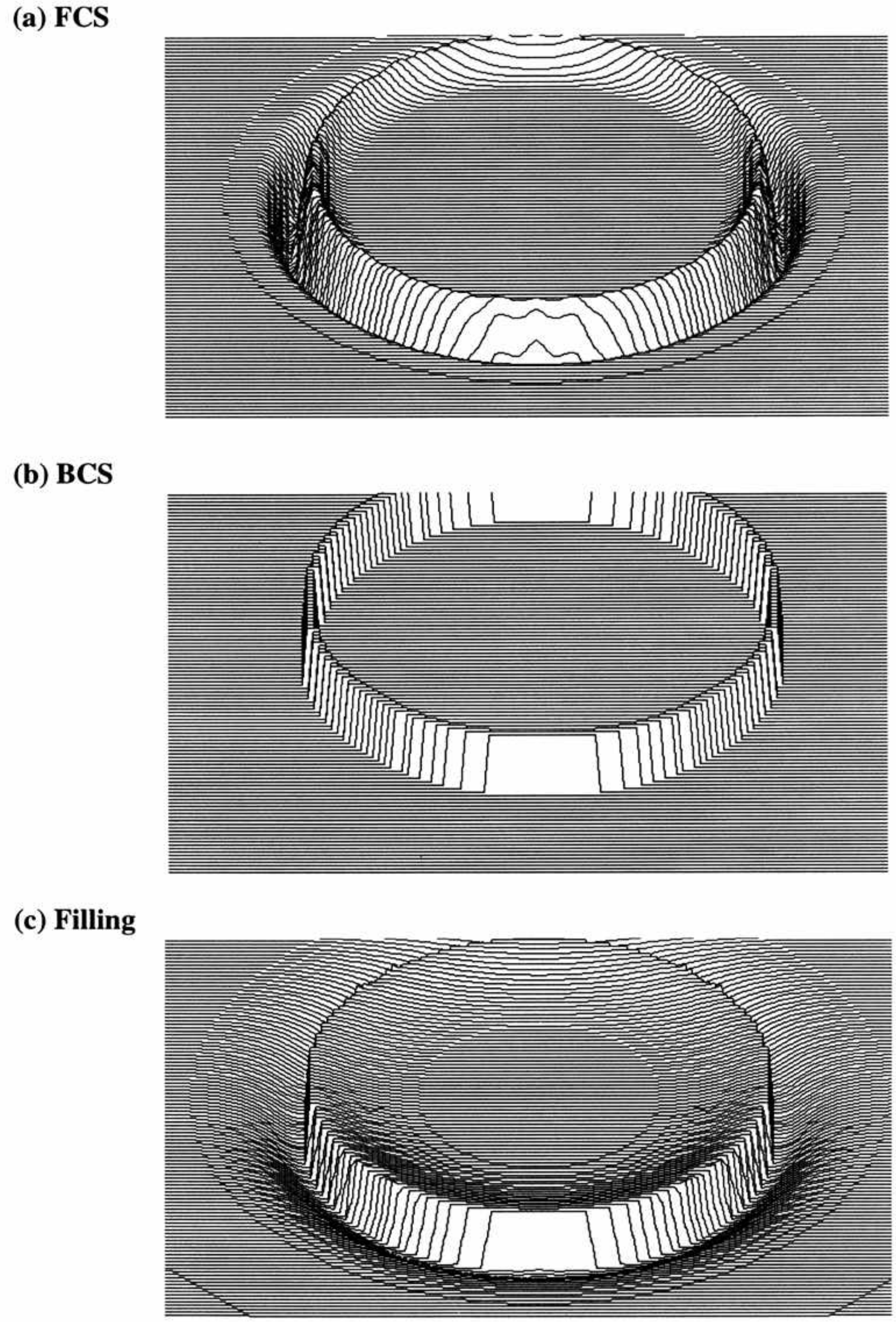


FIGURE 6. Epoch 1: neural response to target stimulus (disk). Surface plot of neural activations in (a) FCS, (b) BCS, and (c) filling-in layer. It can be seen that the disk brightness is beginning to fill-in to form a surface percept.

of the annulus. A cross-section through the center of the filling-in layer (at the level of the center of the target and through a segment of the mask stimuli) is shown in Fig. 9(a) for the four different gap sizes (columns) and at four different epochs (rows) in the stimulus sequence. For each gap size, the activation level at the center point is plotted as a function of time; this is shown in Fig. 9(b). The units of filling-in activation (brightness) are arbitrary, but positive values indicate brightness and negative values indicate darkness with respect to the Eigengrau that is zero.

Because the target and mask stimuli are presented too rapidly to be perceived as distinct perceptual events, the brightness percepts reported in the psychophysical experiments would presumably correspond to the temporally integrated brightness values. It is apparent in Fig. 9(b) that the brightness percept at the center of the annulus increases as the gap size increases. The rate at

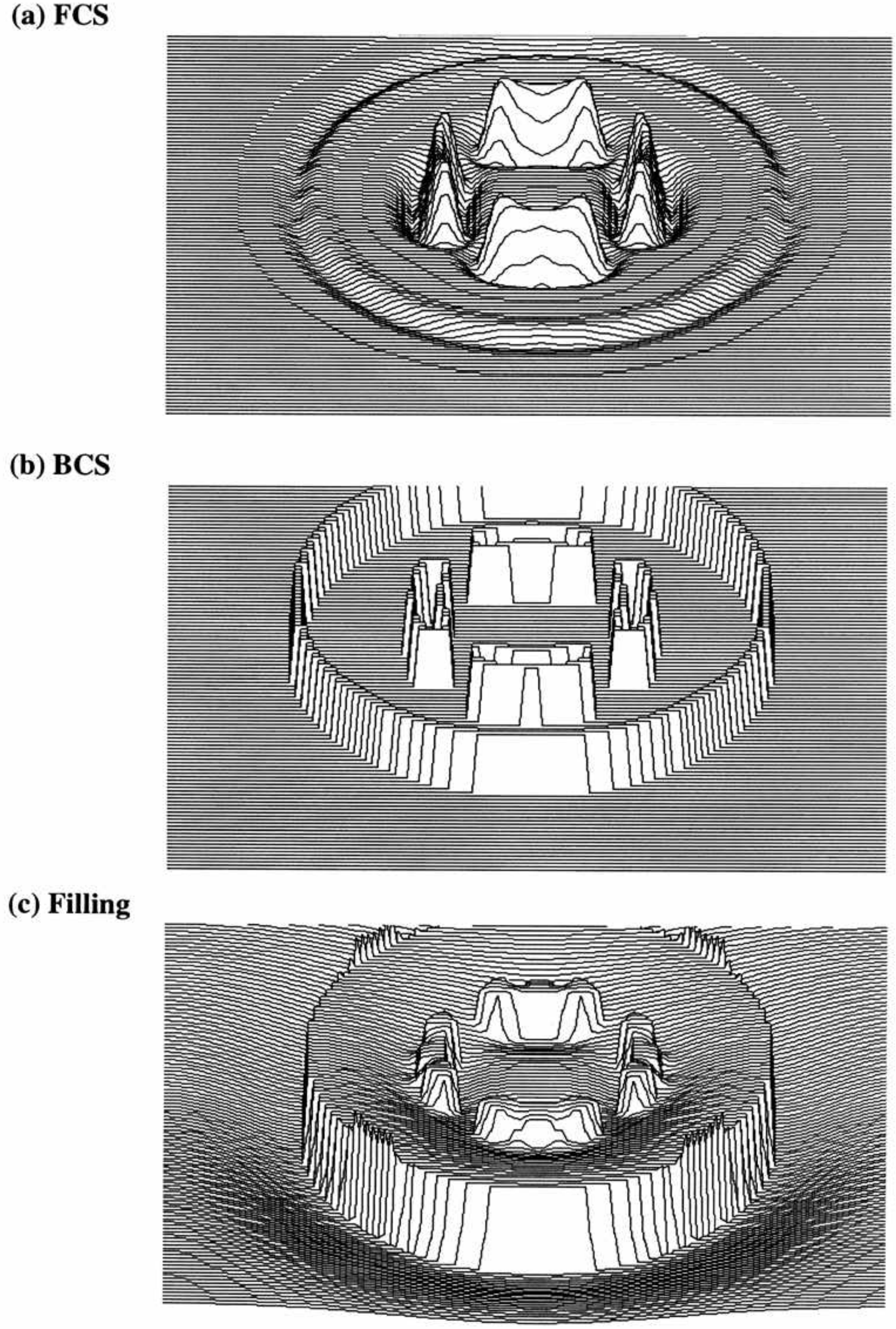


FIGURE 7. Epoch 2: neural response to masking stimulus (annulus). Surface plot of neural activations in (a) FCS, (b) BCS, and (c) filling-in layer. The FCS response to the disk is decaying away, but it can still maintain a boundary signal. The dome-shaped brightness percept is forming inside the mask.

which brightness increases as a function of gap size is plotted in Fig. 10. Each point in Fig. 10 is obtained by adding up (integrating) the six values that form a curve in Fig. 9(b). The brightness prediction as a function of annulus gap-size corresponds well to the curves published in Paradiso and Nakayama (1991).

The second criticism made by Paradiso and Nakayama (1991) has been refuted. The dome-like brightness percept inside the mask is shown in cross-section in Fig. 9 (row t4). Moreover, it varies monotonically with gap-size, just as in the psychophysical results. Again, this is because the FCS dark-edge response to the mask edges does not immediately cancel all central activity, rather some time is required for activity in the central areas to re-equilibrate. This re-equilibration is almost complete in Fig. 9 (row t5). Rapid re-equilibration to the Eigengrau percept is shown in Fig. 9 (row t6).

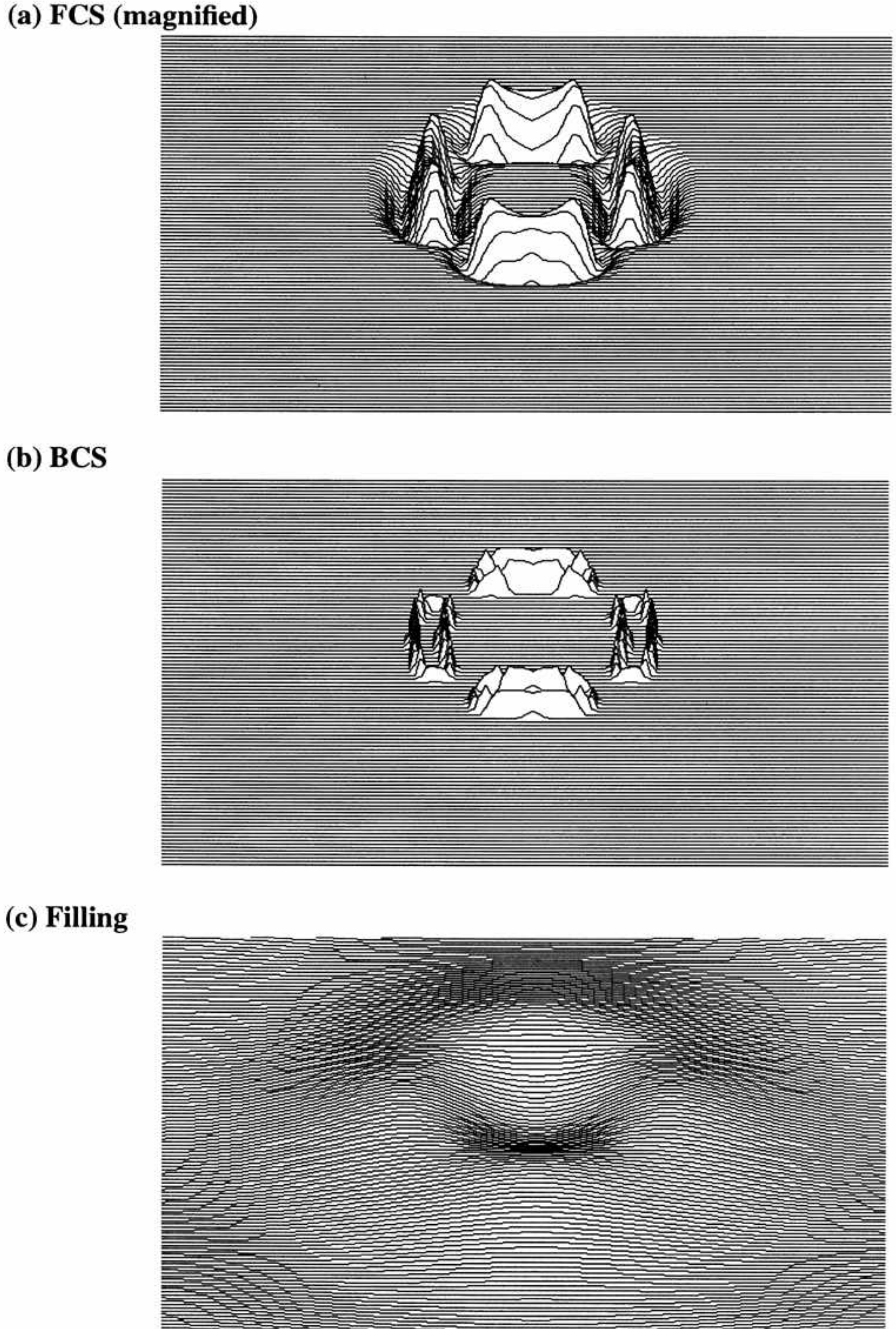


FIGURE 8. Epoch 3: decay phase. Surface plot of neural activations in (a) FCS (b) BCS, and (c) filling-in layer at the end of the target-mask sequence, after the mask has gone off. The ON- and OFF-activations quickly neutralize one another to reinstate the Eigengrau percept.

3.5. Experiment 5: U-shaped forward masking function

All of the previous simulations have looked only at backward masking effects. The last set of psychophysical experiments and results address the issue of forward masking. Under traditional contour-suppression stimulus conditions there is little or no forward masking effect; however Stoper and Mansfield (1978) have shown that under area-suppression stimulus conditions there is a U-shaped forward masking function of SOA that is approximately equal in magnitude to the backward masking function. These simulation experiments help verify that the BCS/FCS filling-in model is actually representing a distinct visual mechanism responsible for area-suppression.

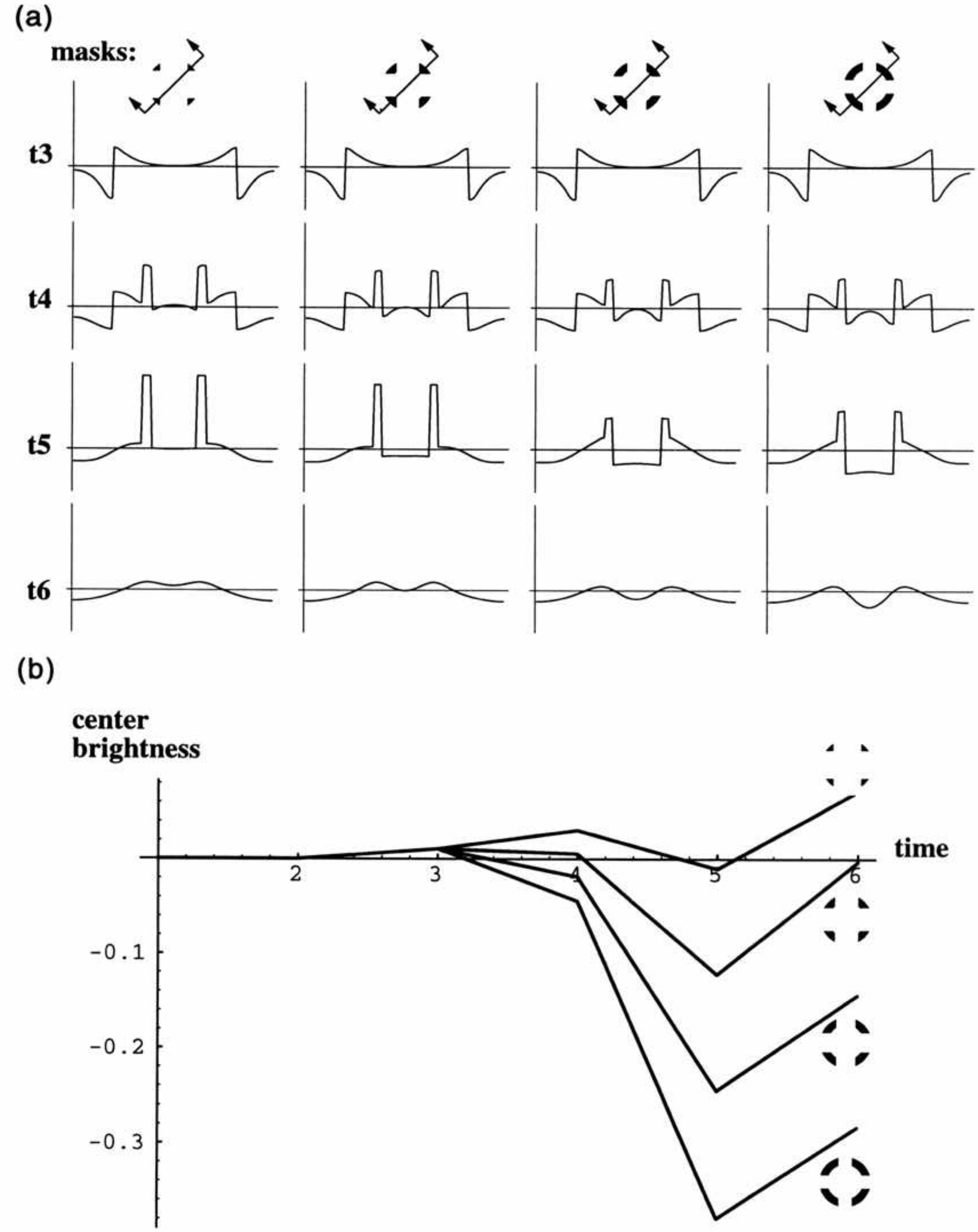


FIGURE 9. Flow slices varying masking annulus gaps. (a) Slices through the center of the two-dimensional surface plots of filling-in activation show the temporal sequence for four different annulus gap sizes (pictorially represented at the top of each column). (b) Plot of activation at the center as a function of time.

In this experiment the target was again a uniform white disk and the mask was a pair of white squares, each 1 deg wide and separated by 1 deg, centered with respect to the disk. In the simulations the mask size was correctly proportioned with respect to disk diameter.

Figure 11(a) shows the filling-in layer activation just after the disk was presented in a forward masking experiment; Fig. 11(b) shows the binary threshold of the filling-in layer activation, which corresponds very well to the figure published by Stoper and Mansfield (1978). Though the authors used this type of illustration to represent the psychophysical percept, in the text they make it clear that "the sharp discontinuity between the black center and the bright edges shown in Fig. 12(b) was in fact not visible; instead there was a gradual, difficult to localize transition" (Stoper & Mansfield, 1978, p. 1671). The same type of brightness surface curvature as was observed under backward masking can be seen here under forward masking conditions.

For the current simulations each integration time step was calibrated to be 0.2 msec, for example the 20 msec target and mask stimuli are each presented for 100 time

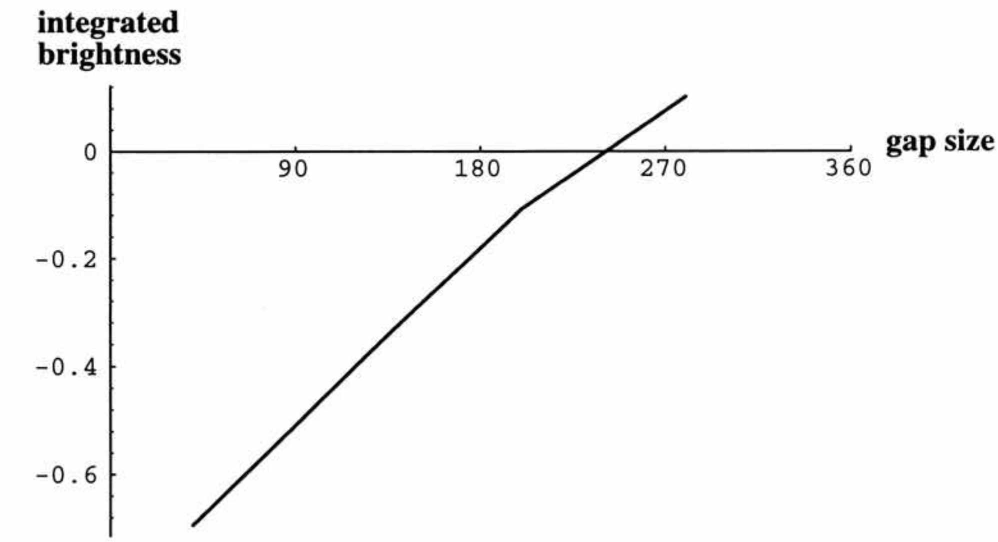
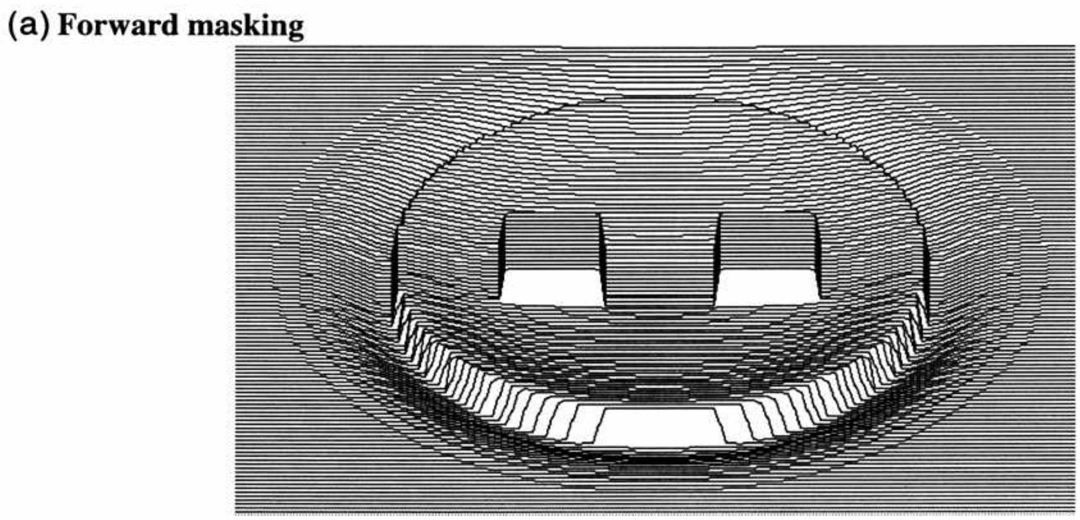


FIGURE 10. Brightness vs annulus gap-size. Temporally integrated activation at center point for four annulus (mask-stimulus) gap-sizes. Abscissa gap-size is in terms of the total amount of perforation of the annulus in degrees; a total gap-size of 360 would result in no annulus segments left at all. Results compare favorably to Fig. 7 of Paradiso and Nakayama (1991).



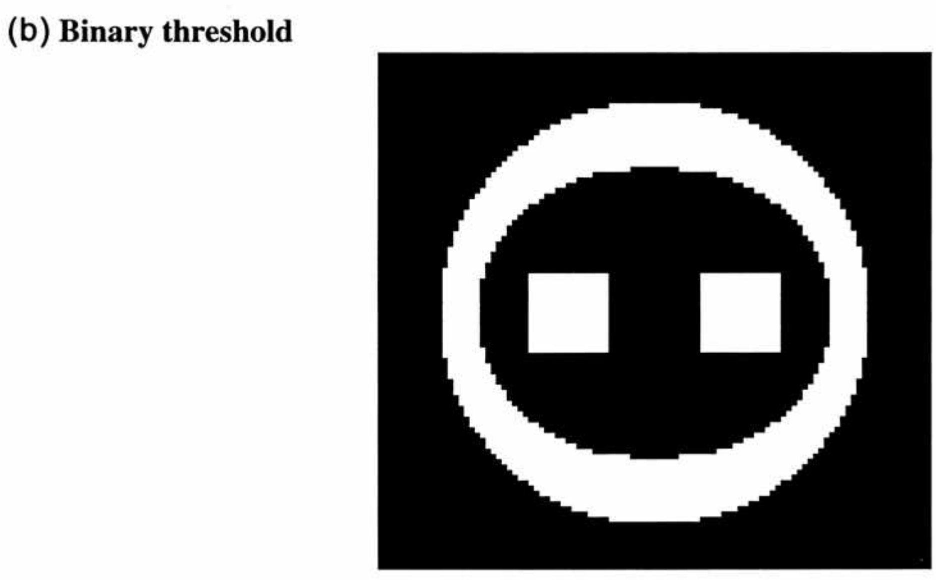


FIGURE 11. Simulated forward masking perception. The filling-in layer activation during a forward masking simulation experiment. (a) A surface plot, (b) a binary threshold of the surface activity, which compares very favorably to the percept illustrated in Fig. 3 of Stoper and Mansfield (1978).

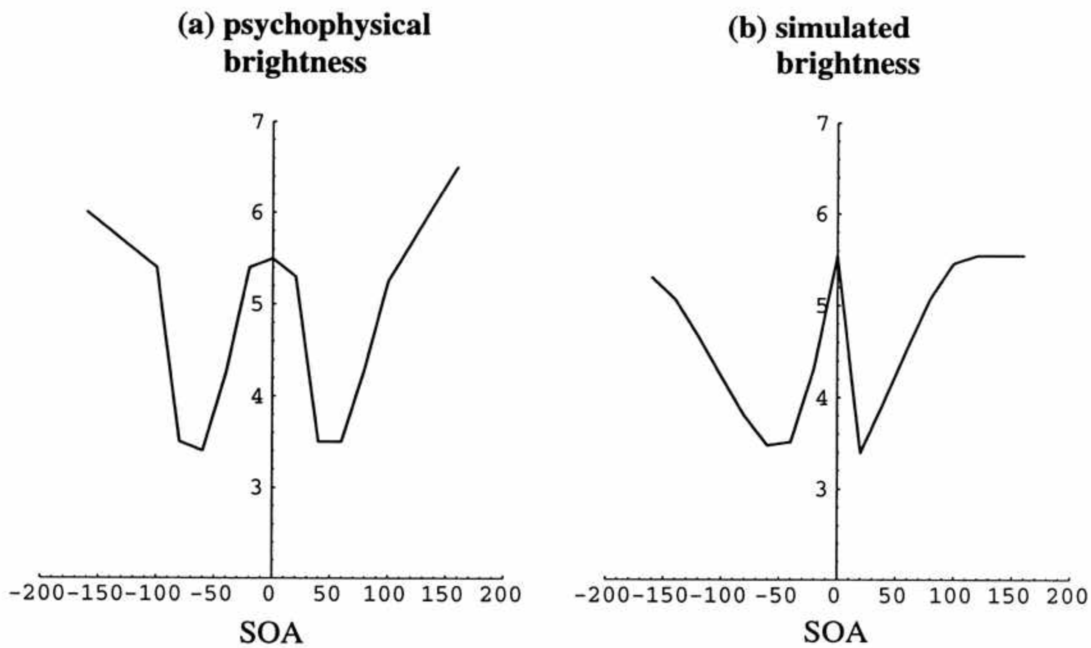


FIGURE 12. Brightness vs SOA. Brightness at the center point of the target as a function of stimulus onset asynchrony. Forward masking SOA times are plotted as negative values, backward masking times are plotted as positive values. Psychophysical results (a) are adapted from the central 400 msec interval of the psychophysical data published by Stoper and Mansfield (1978). Simulation results (b) are obtained from an average of the filling-in activation just after onset of the target, as explained in the text.

steps. When calculating a brightness function of SOA, each trial is different by what correspond to 20 msec SOA increments.

In the psychophysical experiments the subject was asked to rate brightness "at the moment the disk flashed"; magnitude of brightness estimates were with respect to the adaptation field. The brightness level was calculated from the simulations by integrating the filling-in layer activation over a temporal epoch that corresponded to a 100 msec interval, starting at 20 msec after the target was presented.*

Figure 12 shows a comparison of the psychophysical results of Stoper and Mansfield (1978) with the BCS/FCS model simulation results. The backward masking function (positive values) reaches a higher brightness than the forward masking function (negative values) in both the psychophysical data [Fig. 12(a)]and in the simulation data [Fig. 12(b)].

The U-shaped forward masking function is an emergent property to the model and arises without additional design considerations.† Backward masking non-monotonicity was not the issue here and no attempt was made to obtain a U-shaped backward-masking function. Note however that the squares that form the mask in this area-suppression experiment are themselves incidentally affected by a luminance-suppression (masking by light from the disk) that is a monotonic function of SOA. Consequently the squares would have less dark edge effect at short SOAs, which could produce a U-shaped backward masking function if the luminance suppression were implemented in the model.

A comparison between the forward masking curves of Stoper and Mansfield (1978) to those of Paradiso and Nakayama (1991) is not easy because very different masking stimuli and very different brightness estimates were used. When Stoper and Mansfield used a continuously repeated masking sequence they also obtained a considerably stronger masking effect and monotonic forward and backward masking functions comparable to the monotonic forward and backward masking functions obtained in the dichoptic experiments of Paradiso and Nakayama. Stoper and Mansfield deliberately used a discontinuous mask that was not too strong; consequently the masking effect was in a range where it could be parametrically varied with SOA. The continuous circular mask used by Paradiso and Nakayama in their SOA experiments had "a powerful effect on the brightness in the center of the target" (p. 1225) and so

*The U-shaped forward masking curve is robust with respect to changes in the integration duration and starting time. These particular times were chosen to produce a set of curves that have approximately equal forward and backward masking effects that compare well to the psychophysical data. These values seem reasonable, if not too conservative. In the psychophysical results the apparent brightness remains constant over time when the target and mask are presented in a sequence with a repetition rate of 250 msec (Stoper & Mansfield, 1978). Werner (1935) argued that the disk percept would have just begun forming at 132 to 265 msec after its presentation (Kolers & Rosner, 1960, p. 3). In the simulations the disk edge response in the filling-in layer reached approximately 50% of its peak masking experiment value, at what corresponded to 20 msec after target presentation.

†This is different from the type of mechanisms described by Weisstein (1968) and Breitmeyer and Ganz (1976) for obtaining U-shaped functions.

completely blocks brightness that the area inside the annulus appears dark with respect to the bright disk. Presumably if a different mask had been used here, such as an annulus with large gaps, which produced the gray dome in the center, then forward masking would have been observed by Paradiso and Nakayama in their monoptic displays. Nevertheless, in the dichoptic stimulus condition, forward masking was observed and was roughly the same monotonic function as was shown by Stoper and Mansfield (1978) when they used sequential presentation.

4. GENERAL DISCUSSION

Over 100 years ago Hering (1878) made the distinction between (i) area-contrast, also called brightness contrast, and (ii) boundary-contrast, also called edge contrast. Both were considered to be due to reciprocal interaction, but they have very different spatial extents.* At present, boundary-contrast is fairly well understood in terms of single neuron data; however the way in which boundary-contrast produces area-contrast and determines the extent of surfaces is still largely unknown. Neurophysiological correlates of area-contrast have never been found in boundary-contrast sensitive cells (Baumgartner, 1986) and our knowledge of the neurophysiological basis of area-contrast has improved little since the time of Hering (Fiorentini *et al.*, 1990, pp. 137–138).

Most of the contour-suppression masking data is accounted for by various edge contrast mechanisms (see, e.g. Weisstein, 1968; Breitmeyer & Ganz, 1976); however these mechanisms are not sufficient to account for area-suppression (see Stoper & Mansfield, 1978, pp. 1672–1773 for a discussion of this). Stoper and Mansfield (1978) suggest that a combination of filling-in theory and contour mechanisms (specifically the sustained-transient theory) may be desirable. The filling-in theory provides an area-suppression mechanism while the contour mechanism provides an edge signal suppression mechanism. The simulations shown here indicate that their reasoning is correct. The results clarify how the brightness percept arises from two mechanisms: (i) the interaction of ON- and OFF-responses to contrast stimuli, and (ii) the transients in the diffusion gradient as these signals flow during the filling-in process. Stoper and Mansfield (1978) hypothesize that the low-level brightness system has a shorter time constant than the higher level system, i.e. the low-level system is capable of greater temporal resolution. Under area-suppression conditions the mask edge correctly indicates a black background while the target edge correctly indicates the same area to be white. The sluggish high level system would not resolve the two edge signals in time and the same area "appears as black and white at the same time" (p. 1673).

It can be seen that the BCS/FCS model contains both the mechanism for contour-suppression and area-suppression and that they operate with different time constants as conjectured by Stoper and Mansfield (1978). The opposite direction of contrast contour annihilation that would occur in the FCS under traditional contour-suppression masking conditions corresponds to the fast contour system, while area-suppression effects that occur in the filling-in layer correspond to the slow system.

4.1. Shading effect

Werner assumed that formation of a figure has a time–course and a spatial gradient, and that the latter is highest at the border of the figure. Then he argued that the target disk would have just begun forming at its border when the masking ring appeared (Kolers & Rosner, 1960, p. 3). The shading effect is reported in classical metacontrast displays where the target is only partially bounded by the mask (Stigler, 1910; Werner, 1935). Shading effects also occur in stabilized image experiments where one bounding contour of a figure is stabilized (Gerrits & Vendrik, 1970) as well as in stimulus conditions where the non-stabilized background of a stabilized image is not homogeneous, but rather two different colors (half red and half yellow), "the subject observes one half of the [stabilized] object becoming red, the other half yellow, the transition of red to yellow being gradual" (Gerrits *et al.*, 1966, p. 430).

Paradiso and Nakayama (1991) put forth an explanation of this shading effect in terms of an elastic fabric that is tacked down by darkness and pulled up by brightness. They conjecture that two mechanisms are necessary to account for their data: (i) a filling-in mechanism and (ii) a smoothing mechanism. In fact the BCS/FCS model has all of the desired properties. The smoothing is a natural consequence of a Laplacian diffusion process used in the model. The diffusion gradient is created with respect to the Eigengrau by brightness sources and darkness sources (that are relative brightness sinks). No additional smoothing mechanism is required. Their metaphor of elasticity that would pull the system back down to equilibrium is instantiated in the model at the filling-in layer by the two processes that bring the activation back to Eigengrau: the passive diffusion and more importantly the rapid neutralization due to mixing of brightness and darkness.† The main theoretical difference between Paradiso and Nakayama (1991) and Grossberg seems to relate to how darkness is handled.

4.2. Darkness filling-in

One question that is often raised is whether darkness filling-in occurs in the same way that brightness filling-in does. It is clear that in traditional metacontrast stimulus conditions the contour-masking effect occurs with either white figures on dark background or black figures on white background (Werner, 1935; Kolers & Rosner,

*von Békésy (1968) coined the term "Hering-type lateral inhibition" in honor of this distinction.

†The theory of the BCS/FCS also includes opponent mechanisms that would rapidly bring the system back to equilibrium.

1960, p. 3; Raab, 1963, p. 122), and a symmetrical Hering–Hurvich–Jameson type of opponent-process is usually supposed. The BCS/FCS model would predict that darkness fills-in the same way that brightness does, because of the symmetry of the ON- and OFF-channels in the FCS and the symmetry of the ON- and OFF-filling-in activations. Rather than supposing a floor of darkness from which brightness is lifted up or tacked down as Paradiso and Nakayama (1991) suggest, it seems more likely that darkness summation occurs away from the Eigengrau just as brightness summation does. Consistent with the Hering–Hurvich–Jameson theory of opponent processes is the findings by Werner, Cicerone, Kliegl and Della-Rosa (1984) suggesting that darkness (blackness) of a color is inversely related to its luminance (Fiorentini *et al.*, 1990). It is reported in stabilization experiments that "a spreading of blackness can be seen" (Gerrits *et al.*, 1966, p. 432) and that the "deep black is much more homogeneous and much darker than the Eigengrau" (Gerrits *et al.*, 1966, p. 431). Nevertheless, darkness filling-in is an open issue.

4.3. Modeling issues

The simulations use only a single spatial scale implementation of the BCS/FCS model. Consequently larger areas cannot recruit larger spatial scale receptive fields, that could pour larger amounts of brightness signal into the filling-in area farther from the edges. This causes some unnatural temporal distortions because it takes longer for the small spatial frequency signal to reach a spatial location away from its generating contour.

The simulation results of the Paradiso and Nakayama (1991) stimuli are very robust with respect to parameter variation and the qualitative results presented here can be produced over a large range of time calibrations. The Stoper and Mansfield (1978) simulations were less forgiving and required that time be calibrated so that less brightness integration occurred. Simulations not shown here verified that the Paradiso and Nakayama (1991) experiments produce the same qualitative results and brightness functions of gap-completion when using the time calibration that better suited the emergence of the U-shaped SOA function. The flexibility with respect to time calibration results because the model produces a surface percept that scales with stimulus presentation time and SOA in such a robust way that there is little difference except for an overall gain change. This degree of freedom comes from the filling-in equation; the steady state brightness level is kept from increasing forever only because of the passive decay term. Given constant contour signal input to the filling-in layer (as in an unrealistic situation where the image is stabilized but there is no contour signal decay), the steady state level of brightness is very much higher than the brightness values that result from these masking experiments. It may be desirable to use transients that quickly introduce a bolus of energy into the filling-in layer; this has been shown to result in much faster convergence rates in the BCS/FCS model when the system is integrated in time rather than solved at steady state [see Arrington (1993a), Appendix C: Filling-in with Transients]. It is reasonable to expect that there will be an intersection of parameter constraints that arise from the prediction of more and more psychophysical data, but until these constraints are manifest, the existing degrees of freedom should be maintained. With the inclusion of multiple spatial scales and transient and sustained signals the model may accurately provide quantitative results under both masking conditions and normal viewing conditions. As Stoper and Mansfield (1978) suggested, what may be needed is a true integration of sustained-transient theory with filling-in theory. This is the subject of ongoing research.

5. CONCLUSION

The scope of brightness predictions made by the BCS/FCS model has been increased to include the transient temporal dynamics under masking conditions. The simulations support the psychophysical research of Paradiso and Nakayama (1991) and Stoper and Mansfield (1978); however the former were wrong in asserting that the BCS/FCS model cannot account for their data. It has been shown that the findings of Paradiso and Nakayama (1991) which they regarded as being against the BCS/FCS model actually support it. It can be concluded from the proceeding simulation experiments that the dynamic BCS/FCS is very good at predicting the relative brightness percepts in a wide variety of brightness masking experiments. The simulation results also further support the filling-in hypothesis of brightness perception.

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Acknowledgements—The work described in this paper was supported by a grant from the Office of Naval Research, ONR N00014-91-J-4100, while in the Cognitive and Neural Systems Department Ph.D. program at Boston University (Arrington, 1993a), and through a fellowship from the McDonnell–Pew Center for Cognitive Neuroscience at MIT (Arrington, 1993b).