



Psychophysical Evidence for Boundary and Surface Systems in Human Vision

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Received 19 October 1995; in revised form 23 April 1997

Psychophysical evidence is given for the existence of two distinct systems in human vision: a fast, sign-invariant system concerned with extracting contours and a slower, sign-sensitive system concerned with assigning surface color. A class of stimuli we developed seems to selectively activate the fast, contour system. This stimulus is formed by adjacent fields of black and white spots, which flicker in counterphase at 15 Hz, on a uniform gray field. Although subjects can not discriminate the temporal phase relationship between the fields of spots, they can, nevertheless see a “Phantom Contour” separating the two indiscriminable fields. The surface characteristics (temporal phase relationship of the spots) can only be seen when the stimulus is significantly slower (flicker < 7 Hz). In addition, phantom contours disappear with equiluminant spots but can be seen with very low contrast spots (< 10% contrast), and are enhanced with peripheral viewing. Taken together, the results suggest that the fast contour-extracting system may be the magnocellular system or a magno-recipient area. Implications for a stimulus which could isolate a contour extracting system, or a magno-recipient area are discussed. © 1997 Elsevier Science Ltd

Human psychophysics Contour extraction Magnocellular system

INTRODUCTION

In this article, we examine a novel class of visual stimuli which we call “phantom contours” (Rogers-Ramachandran & Ramachandran, 1991). Experiments with these stimuli provide psychophysical evidence for the existence of two systems involved in object perception—a fast system dealing with contours and a slow one dealing with surfaces.

Figure 1 depicts the phantom contour stimulus. The two panels represent two frames of a movie generated on a Commodore Amiga computer. In the first frame (left panel), randomly positioned spots (37' arc each) are superimposed on a uniform gray field (13.4 deg × 15.4 deg, mean luminance = 93 cd/m²). Those on the top are white (144 cd/m²) while those on the bottom are black (9.1 cd/m²) producing a distinct texture border. In the second movie frame (shown in the right panel) we simply reversed the luminance of all the spots and then alternated between the two frames at a high rate—15 Hz (30 frames/sec). Thus, the stimulus is a field of spots all flickering in perfect synchrony except the two hemifields are phase shifted by 180 deg. That is, spots in the top half flicker black–white, black–white while those

in the bottom half flicker white–black, white–black. Spots in the two frames are perfectly correlated in space—i.e., their positions do not change.

At 15 Hz, flicker is perceived but it is impossible to discern whether any two spots are flickering in-phase or out-of-phase. That is, all the spots *look* identical. We were quite surprised, therefore, to observe a distinctly visible horizontal border separating the two fields, i.e., one sees a texture border defined by indistinguishable elements. We call this paradoxical percept a phantom contour.

We conducted a series of experiments using phantom contours to explore the critical factors underlying their perception and implications for understanding visual functions.

ORIENTATION DISCRIMINATION VS TEMPORAL PHASE DISCRIMINATION

We first tested orientation discrimination. Horizontal or vertical phantom contour stimuli were presented in 250 msec flashes and each of six naïve subjects was asked to judge the orientation on 20 trials. In each trial, a stimulus comprised three sequential 250 msec patterns: (1) noise mask; (2) test (example shown in Fig. 1); and (3) noise mask. The noise masks were identical in all respects to the test except their spots were positioned so that no contour existed. That is, in each frame of the movie half the spots were white and half were black, but they were randomly positioned in the field rather than being grouped into hemifields. The subjects correctly

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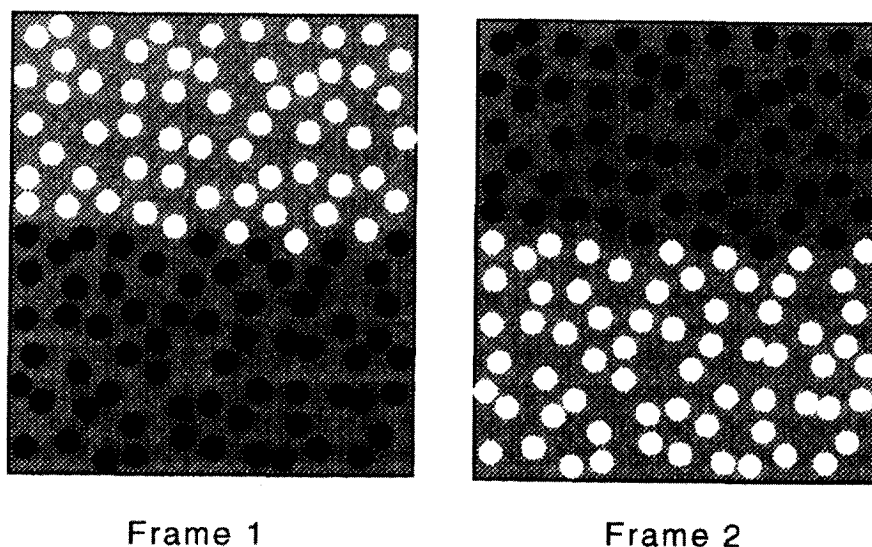


FIGURE 1. Phantom contour test stimulus. Black and white spots form a texture border in the first frame of a two-frame computer "movie". In the second frame, the contrast of all spots is reversed. When the movie runs at 30 frames/sec (15 Hz), the border is seen distinctly even though the spots defining the border are indistinguishable. We suggest this stimulus isolates a fast contour-extracting system which is unable to read surface sign (luminance or color).

judged orientation on virtually all trials (mean for all subjects was 99.4% correct).

Might this near-perfect performance reflect subjects' ability to judge the temporal phase relationship of the spots, rather than their ability to discriminate the contour itself? To rule this out, we ran a control experiment in which the contours were removed from the stimuli. As shown in Fig. 2, we used the same set of stimuli, but simply placed an occluding cross (0.75 deg wide) over the area where the horizontal or vertical contours were. We asked subjects to directly compare the spots and determine which two quadrants of flickering spots looked identical, the vertically, horizontally, or diagonally

aligned ones. Now performance was at chance level for all six naïve subjects (mean for all subjects, 20 trials each = 31% correct).

To further rule out the possibility that temporal phase discrimination contributes to perception of phantom contours, we presented the occluded contour stimuli again and asked subjects to adjust the flicker rate so that they could just discriminate which two quadrants were identical. To do so, they had to reduce the flicker speed from 15 to just under 7 Hz (mean for six subjects, five settings each = 6.97 Hz). Thus, surface characteristics can be perceived from a field of flickering dots but only when the flicker rate is much slower, about 7 Hz.

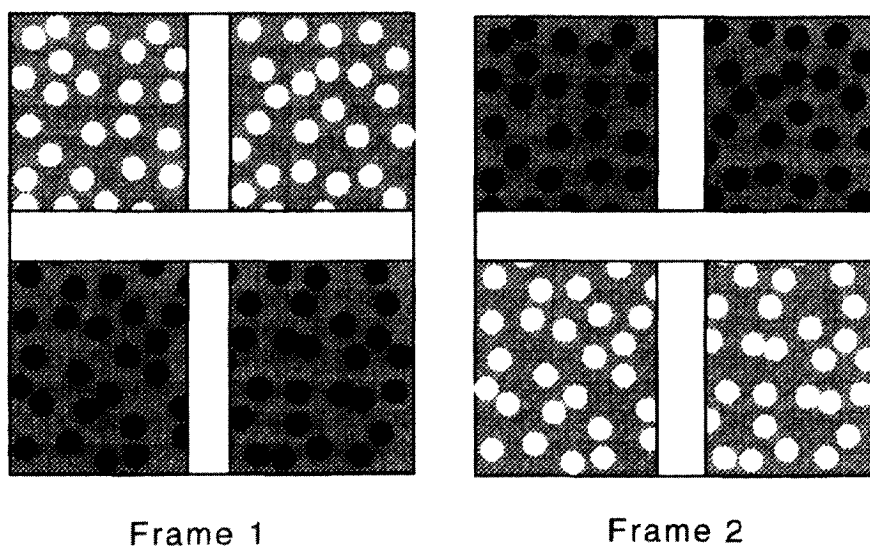


FIGURE 2. Stimulus used to test temporal phase discrimination. The "contours" of the phantom contour stimulus are occluded and subjects are asked to judge which two quadrants of spots are flickering in phase. The flicker threshold for this task is low, 7 Hz, and presumably relies on the slow, surface-processing mechanism.

We conclude, therefore, that orientation discrimination of phantom contours is based on perception of the contours, without perception of the temporal phase relationship of the spots or surfaces. In addition, these experiments indicate two distinct thresholds exist, 7 Hz for temporal phase discrimination and 15 Hz or higher for orientation discrimination. We suggest, and present further evidence below, that these two different thresholds represent two different systems involved in object perception—a fast contour-extracting system and a slower system which assigns surface color.

ADDITIONAL TESTS WITH PHANTOM CONTOURS

We tested phantom contour perception and temporal phase discrimination under four further conditions: equiluminance, low contrast, eccentric viewing, and with blurred stimuli.

Equiluminance

First, we repeated our experiments exactly except the spots were now made red and green instead of black and white. Provided a luminance difference exists between the two colors, phantom contours can be seen with colored spots. On the other hand, with equiluminance, i.e., when the brightnesses of the spots are made identical to each other (but not to the background), then at 15 Hz flicker the phantom contours are not visible; subjects simply see a homogeneous field of flickering spots and orientation discrimination is at chance level (mean for six naïve subjects = 52.5% correct). In other words, the system we have been calling the fast contour system is essentially color-blind. Only when subjects slowed the flicker rate to about 6 Hz could they make confident judgments of orientation (mean for six naïve subjects = 6.15 Hz, SE = 0.4).

Using equiluminant spots, we next determined the threshold for temporal phase discrimination by again occluding the region of horizontal and vertical contours and asking subjects to adjust flicker rate so that they could just judge which quadrant pairs were identically colored. As with luminance-defined spots, subjects all had to significantly reduce the flicker rate in order to perform this perceptual task (mean for six naïve subjects = 5.1 Hz; SE = 0.2).

Figure 3 contrasts the results for luminance-defined and equiluminant stimuli. For the former, we find two very different flicker thresholds; 15 Hz or higher for orientation discrimination (phantom contours), vs 7 Hz for temporal phase discrimination. For equiluminant stimuli on the other hand, the two thresholds are nearly identical and these are very close to the temporal phase discrimination threshold for the black and white stimuli. This pattern of results indicates that in the first condition (when phantom contours are perceived) only the fast contour system is activated, but for the other tasks, the flicker has been sufficiently reduced to allow the slow (surface) system to kick in so that surface perception (luminance and color) also occurs.

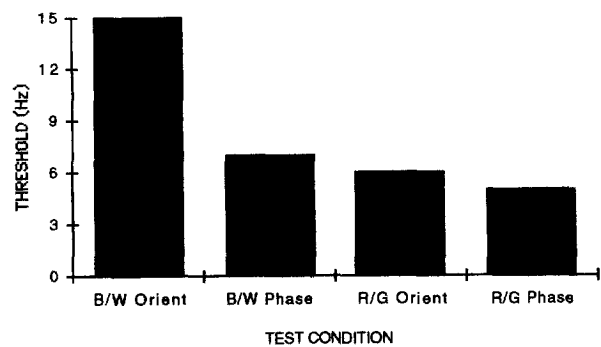


FIGURE 3. Flicker thresholds from four experiments (mean of six subjects): orientation discrimination with luminance-defined stimuli (1), and equiluminant stimuli (3); and temporal phase relationship discrimination with luminance-defined (2) and equiluminant stimuli (4). Only condition (1) has a high threshold (15 Hz or higher) and appears mediated by the fast contour system, while the other three conditions (2, 3, 4) produce low thresholds (7 Hz or less) and appear to depend on the slow surface system.

Reduced contrast

To rule out the possibility that phantom contours disappear at equiluminance simply because of low effective contrast, we repeated the experiments again but with contrast between the spots (as well as contrast between the spots and the background) reduced to less than 10%. We maintained the same mean luminance as in our initial conditions by using light and dark gray spots on an intermediate background. Once again, orientation discrimination was nearly perfect (Mean four subjects, 40 trials each = 98% correct), contrary to what we observed with the equiluminant colored spots.

Eccentric viewing and blurred stimuli.

In a third condition, we asked whether phantom contour visibility might increase with eccentricity, given that the proportion of M cells is greater in the periphery. Recall that with central viewing, as in the first experiment, performance is nearly perfect. So, to make the task more difficult, we modified the stimuli by removing some of the spots thereby degrading the texture border (see Fig. 4). In the set of four stimuli shown, we arbitrarily label the most dense one “100% Spot Density”. The next one, which has half the spots removed, is labeled “50% Spot Density”, and so on for 25% and 12.5%.

For each spot density condition, 25 trials were run in which six subjects each judged whether phantom contours were horizontal or vertical. As shown in Fig. 5, the task is increasingly difficult with the sparser textures. At 25% spot density, performance drops to chance ($X = 55\%$). We repeated the experiment, but now had subjects fixate 5 deg eccentrically. As shown by the dashed line, performance improves. At 25% density subjects attain 80% correct and performance drops to chance only with the sparsest pattern. The third line on this graph is nearly identical to that for peripheral viewing and was obtained when the stimulus was blurred (by placing a sheet of velum directly over the computer

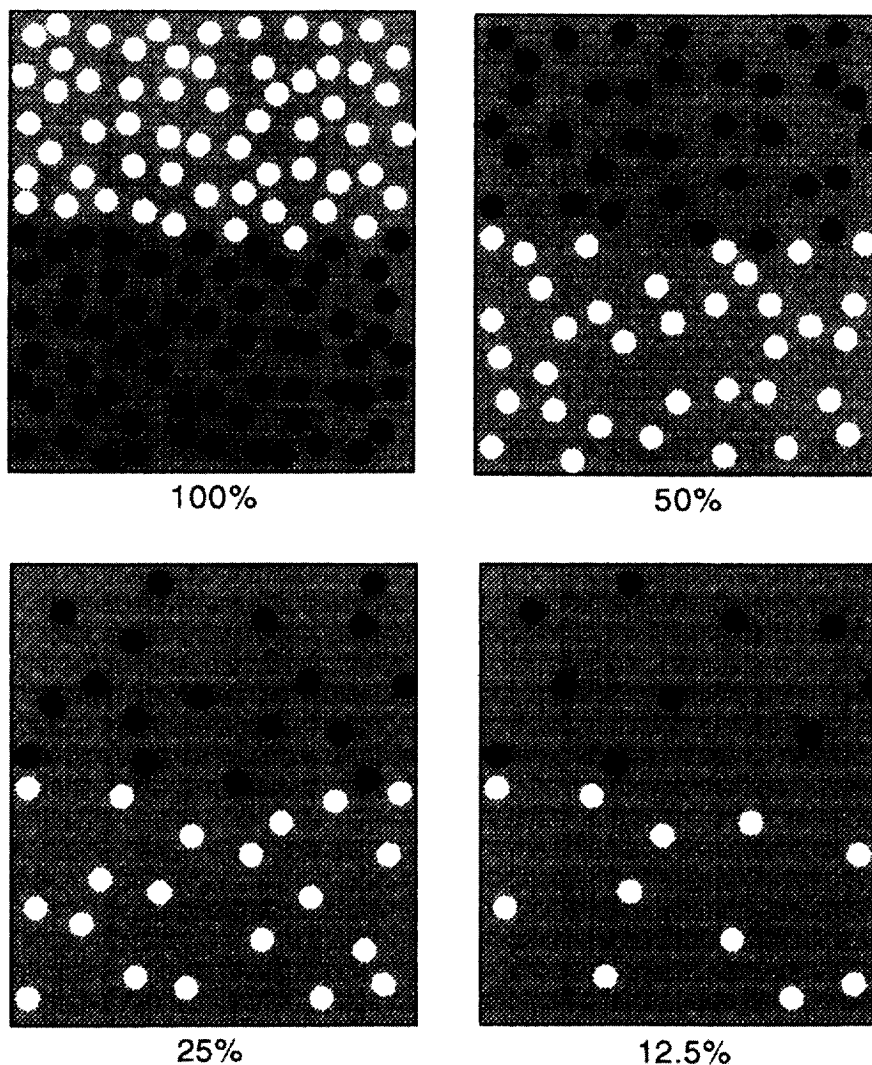


FIGURE 4. Spot density stimuli. Four sets of phantom contour stimuli with progressively degraded contours.

monitor) and viewed centrally. We are not sure why performance improves so much in this case. Removal of high spatial frequencies may provide a more optimal stimulus for the fast contour system (if, for example, its receptive fields are large) or perhaps high spatial frequencies somehow mask or inhibit perception of the phantom contour.

SUMMARY: EVIDENCE FOR TWO SYSTEMS

To summarize, the ability to discriminate phantom contours is seen at high temporal rates (15 Hz or higher) or with low contrast (<10%), is enhanced by peripheral vision or with blur, but disappears at equiluminance. On the other hand, the ability to judge temporal phase relationships for these patterns is only seen for lower temporal rates (7 Hz or less), but is equally good for luminance or equiluminant stimuli. Taken collectively, these findings indicate two different systems exist in human vision. One of these is a fast contour-extracting system that can signal contours but not their polarity and the other is a slow system that signals surface qualities.

The contour system signals the presence of a border but cannot tell which side of the border is black and which side is white. That is, it can detect that there is a difference between the two sides and also follow high flicker rates, but it cannot signal the direction or the "sign" of the difference. The surface system, on the other hand, can potentially signal the surface characteristics (color and luminance) but at 15 Hz, the speed of flicker is too high for it to follow. Thus, the phantom contour stimulus seems to isolate or selectively activate the fast boundary extracting system. So what is perceived is the output of the contour system alone, a contour defined by two surfaces which look identical.

If indeed the phantom contour stimulus isolates the boundary system, phenomena thought to depend upon the perception of contours should be seen whether contours are real or are defined by phantom contours. We therefore constructed a variety of visual stimuli using phantom contours (i.e., contours defined by spots phase reversing at 15 Hz) and compared visibility of these to that of comparable stimuli defined by real contours. For example, complex shapes such as letters or numbers are

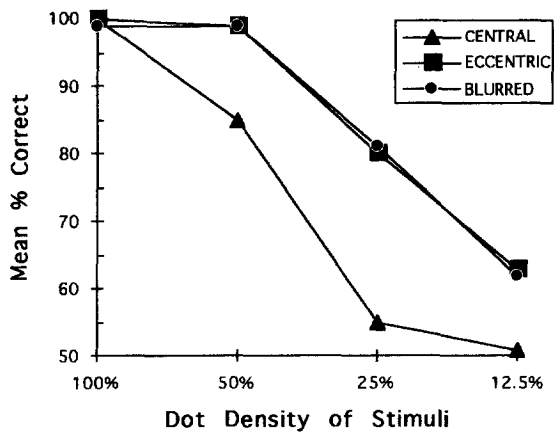


FIGURE 5. Results of testing with the spot-density stimuli shown in Fig. 4. As the texture becomes sparser, phantom contour visibility (measured by forced choice orientation discrimination) decreases. All functions have a similar shape but performance is worst for central viewing, while performance for peripheral viewing or for a blurred stimulus is better.

readily seen, and the tilt illusion and spatial frequency aftereffect appear normal when conveyed by phantom contours (see Fig. 6 for details). Apparent motion can also be conveyed by phantom contours. Using a movie where, in successive frames, the phantom contour edge is shifted along horizontally or vertically (but the positions of the dots are completely uncorrelated in each frame), subjects are able to see smooth continuous motion when the dots are flickering at 15 Hz. In fact, we have identified only one phenomenon which appears abnormal when defined by phantom contours, namely, binocular rivalry.

Orthogonal gratings were presented to the two eyes and these were counterphase flickered at 15 Hz. To our surprise, instead of rivalry, we saw a plaid. Only when the flicker rate was reduced to 6–7 Hz was rivalry restored, suggesting, perhaps, that rivalry may require the involvement of the slow surface system. It is possible of course, that rivalry is knocked out at 15 Hz simply because, as Helmholtz first observed, it does not occur with briefly flashed stimuli. This remains to be determined, but it is noteworthy that rivalry is restored at 7 Hz, the same speed that our slow surface system is activated.

Finally, we note the intriguing phenomenon of metacontrast, which has been attributed to a fast system masking the output of a slower system (Breitmeyer & Ganz, 1976). In this illusion, when a square is flashed on for 250 msec and then followed by flanking rectangles, flashed for 250 msec, the square is not seen, i.e., it is masked by the rectangles. The illusion does not occur if the flanking rectangles are presented at the same time as the square. The masking only occurs when the flanks follow the square, hence its also called backwards masking. Whether or not the fast and slow system of metacontrast correspond to our contour and surface system remains to be seen. However, both illusions exemplify that object perception is not a unitary phenomena but consists of interactions of multiple systems, each with different characteristics.

DISCUSSION AND SUMMARY

We have tested the visibility of phantom contours under a variety of conditions and note that striking parallels exist between properties of magnocellular

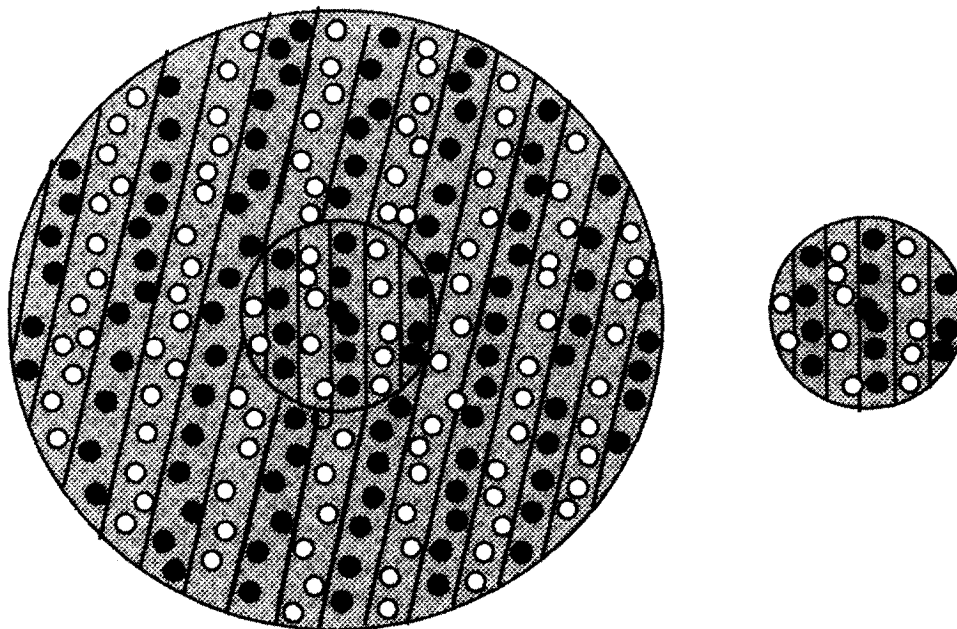


FIGURE 6. Schematic of tilt illusion stimulus conveyed by phantom contours (spatial frequency of 3 c/deg). A perceived counterclockwise tilt in the left central disc is induced by the surrounding pattern (tilted 12 deg clockwise). The magnitude of this is measured by matching the right pattern to appear parallel to the pattern on the left. The mean tilt illusion measured for six subjects was 5.0 deg with phantom contours (i.e., spots were counterphase flickered at 15 Hz) vs 2.5 deg when the spots were not flickered. Thus, flicker actually appears to produce a two-fold enhancement of the tilt illusion.

receptive fields and phantom contour visibility, e.g., high temporal resolution, lack of sensitivity to equiluminous colored stimuli and sensitivity to low contrast or peripheral stimulation. It is tempting to speculate, therefore, that the contour and surface systems we have identified may correspond to the M and P streams.

The possibility of using phase-reversing edges to isolate the magnocellular pathway has previously been suggested by Livingstone & Hubel (1987). The main difference between their stimulus and the present one is that we have used a texture border composed of spots instead of a real luminance edge and this has the advantage of getting rid of potential edge artifacts that could arise from spatial non-linearities. Such artifacts are impossible to avoid if real luminance edges are used. Also, since the spots that define the texture are themselves indiscriminable (when flickering at 15 Hz), our stimulus may be the only known example of a "texture border" defined by elements that look completely identical.

Before considering this possible basis of phantom contours further, however, we must add some cautionary notes. First, as Schiller has emphasized, these two systems, M and P, are not quite as segregated in their properties as originally believed. For example, many magnocellular neurons do show some color selectivity in that their surround is tonically suppressed by long-wavelength light (e.g., Wiesel & Hubel, 1966; Schiller & Malpeli, 1978). Second, we have argued that the fast contour system we have identified is insensitive to the sign of the contour. Unfortunately, with the notable exception of a study by Gouras & Kruger (1979) of interblob neurons, the sign-sensitivity of cells has not been studied very carefully at different points along the M and P streams and indeed, we do not know at what stage the sensitivity is lost. Third, some P cells can respond to very high rates of flicker, up to 30 Hz (Merigan & Eskin, 1986), whereas the surface system we have been talking about is essentially non-functional at speeds beyond about 7 Hz.

At this point then, there is insufficient evidence to conclude that phantom contours are selectively activating the M stream. We should bear in mind the lesson of equiluminous stimuli. These are clearly a powerful tool (e.g., Ramachandran & Gregory, 1978; Cavanagh, Boeglin, & Favreau, 1985) but appear more like a partial sieve than a scalpel for dissecting out the P stream. Physiologists and psychophysicists have found considerable "leakage" of color into the M system (e.g., Livingstone & Hubel, 1988; Schiller, Logothetis, & Charles, 1990).

These objections are not insurmountable, however, because the M and P pathways may project to areas in the brain whose properties are even more clearly segregated than those of the pathways themselves. In other words, the two systems we have identified may correspond to an M-recipient and a P-recipient area in the brain, rather than to M and P pathways.

Finally, we emphasize that the importance of our

findings does not depend solely on the presumed correspondence with the physiology. Even if there is no such correspondence, our results are interesting in themselves because they demonstrate the existence of two systems—(1) a fast sign-invariant system concerned with extracting contours and indifferent to surface color; and (2) a slow sign-sensitive mechanism that is concerned with assigning surface color.

If phantom contours do indeed isolate the fast contour-extracting system as we have suggested, they could be used by both psychophysicists and physiologists. First, they could be used to determine the contribution made by the fast contour system to a variety of perceptual illusions. For example, one could determine whether any given visual illusion such as motion, the tilt illusion or binocular rivalry is driven primarily by the contour system, the surface system or by both. Secondly, it might be interesting to present phantom contours to lesioned monkeys and to cells at various points in the visual path to determine whether they do indeed selectively stimulate M cells. If they do, then one could use them in a variety of perceptual and physiological experiments to determine M cell contribution to any given visual function. In fact, phantom contours would provide a means to study the Magno pathway without physically lesioning Parvocellular pathways, i.e., one could simulate Parvo lesions in humans and study M functions in isolation.

Finally, phantom contour stimuli may have clinical utility. In certain patient populations, such as patients with glaucoma (Quigley, Dunkelberger, & Green, 1988) and perhaps Alzheimer's (Sadun, 1990) and dyslexia (Livingstone, Rosen, Drislane, & Galaburda, 1991) there is a selective loss of retinal magno cells. Thus, decreased sensitivity to phantom contours might provide an index for the integrity of the magno system. The results from initial studies with glaucoma patients using our stimuli are promising (Simpson & Flanagan, 1992).

Experiments with phantom contours, as well as metacontrast, point to the existence of separate systems concerned with contours and surfaces. By studying these phenomena we may eventually begin to understand how the brain uses the output of these two systems to construct a 3-D representation of the world.

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Acknowledgement—Supported by AFOSR 89-0414 and ONR N00014-91-J-1735