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Pathways in Early Vision*

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Between the retinal ganglia and the higher centres of vision, visual information divides into several independent pathways each passing through physiological structures specialized for the analysis of different visual attributes. This paper first discusses the relative inputs of color and luminance information to these visual pathways and then examines the coding primitives available in each of the pathways. Finally, the capacities of the individual pathways are evaluated by examining which perceptual tasks—for example, shape from shading, relative depth from occlusion—can be performed on representations in each pathway.

There has been a great deal of interest in multiple visual representations recently, in both biological and artificial vision: the specialized regions in monkey prestriate cortex identified by Zeki and others (see Zeki, 1978, van Essen, 1985), the independent feature maps proposed in cognitive psychology (Treisman & Gelade, 1980; Treisman & Souther, 1985), and the intrinsic images used in computer vision (Barrow & Tenenbaum, 1978). The representations described in each of these fields varies but there is little disagreement concerning the potential importance of multiple representations to visual function. How can we examine these multiple representations in humans? Psychophysical techniques do not permit us to access individual visual areas directly but we may be able to restrict information to particular pathways through the visual areas by using stimuli defined by a single attribute. The stimulus information of a figure de-

fined by relative motion, for example, may pass preferentially through the prestriate region MT (van Essen, 1985) and so can probe its characteristics while a stimulus defined only by color may probe a different area (visual area V4, Zeki, 1978).

Physiological studies have produced a sketch of the pathways followed by various types of information in the visual system (see Maunsell & Newsome, 1987). At the level of the retina, only luminance and color appear to be coded and they follow separate neural channels through the lateral geniculate bodies and on to the cortex. The opponent-color information is transmitted by the parvocellular layers of the LGN and the luminance information by the magnocellular layers. More recent studies show that the actual situation is somewhat more complex with the red/green opponent-color information and the high spatial resolution luminance information being combined in the activity of R/G cells of the LGN and being decoded by cortical areas (Ingling & Martinez-Uriegas, 1985). In the first visual cortex V1, orientation, spatial frequency, motion, and binocular disparity emerge as new properties derived from the luminance and opponent-color information. The cells responsible for this derivation are often multidimensional, responding to preferred values of several attributes. There does appear to be some spatial clustering, however, of non-oriented, color-selective cells, surrounded by oriented luminance cells (Livingstone & Hubel, 1983). This initial, local specialization becomes progressively accentuated as color cells project to specific regions of V2 and then to V4, while oriented cells project to other areas. There is a similar segregation of directionally selective cells projecting from the lower layers of V1 to MT, an area specialized for motion, and from V1 to specific areas of V2 and then to MT. There is, in addition to this motion-specific pathway, a subcortical pathway through the superior colliculus and then to MT. Many aspects of these pathways remain to be determined and some may be organized according to response factors rather than stimulus factors. Several areas of the parietal cortex, for example, are known to be involved in eye movements (Andersen, Essick & Siegel, 1985). A simplified version of the various visual pathways is presented in Figure 1. (Of the attributes that we will examine here, only two, color and motion, have clearly defined physiological pathways. The others, luminance, binocular disparity, and texture may be involved in several pathways or none at all. Until further evidence is available, they can only be considered as reasonable candidates for pathways.) Following the multiple representations of the prestriate region in Figure 1, a combined representation of stimulus shape is proposed that then serves as input to high-level inference processes.
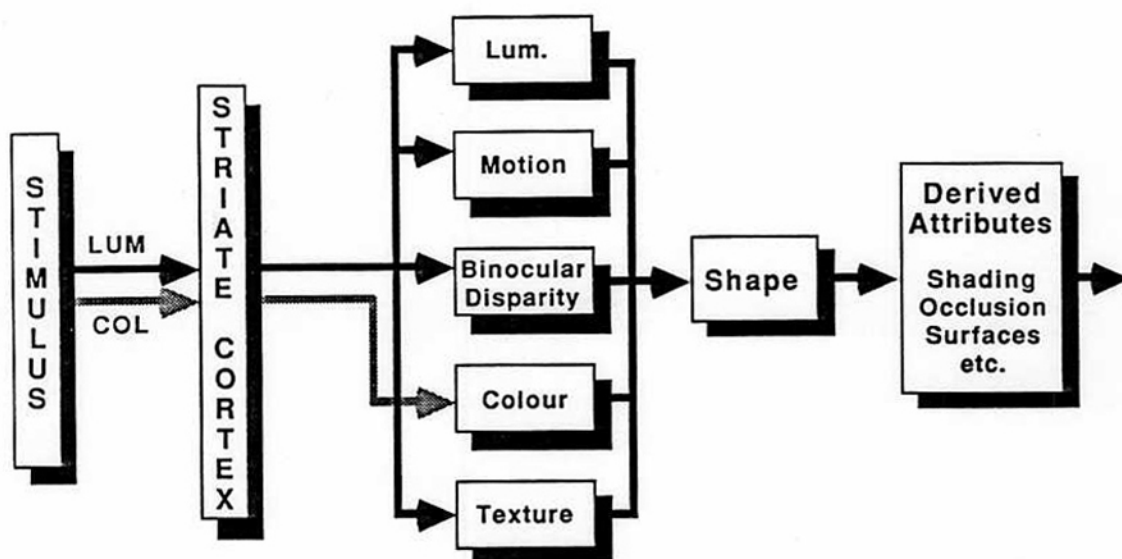
Figure 1.   Pathways in the visual system. Luminance (non-opponent) and color (opponent) pathways bring information from the retinal ganglia to the striate cortex where multifunction cells begin the analysis of orientation, motion and binocular disparity. Following the striate cortex, information is routed to areas performing specialized analyses of various attributes: color (area V4, Zeki, 1978) and motion (area MT, van Essen, 1985), for example. Luminance, binocular disparity, and texture are other stimulus attributes that may receive specialized analyses in separate areas of prestriate cortex. Each of these specialized areas generates a two-dimensional representation of the attribute being analyzed, contributing to an overall representation of stimulus shape—external and internal contours—from which higher level attributes such as shading, occlusion and surfaces can be derived.

The first issue that we have addressed is the relative inputs of the color and luminance pathways coming from the lateral geniculate to the various pathways that start out in area V1 and then diverge. Since there is an area specialized for the analysis of color (V4, Zeki, 1978), it is often thought that color information only contributes to the pathway leading to this area and not at all to other pathways that are involved in the analysis of motion or binocular disparity. However, we will see that color does contribute to motion (Cavanagh, Boeglin, & Favreau, 1985; Cavanagh, Tyler, & Favreau, 1984, Cavanagh & Favreau, 1985; Cavanagh & Anstis, 1986) and binocular disparity (de Weert & Sadza, 1983; Grinberg & Williams, 1985), although only weakly.

The next question we have examined is the coding primitives available in the different pathways. There have been many papers that have demonstrated orientation and size preferences for cells in area V1 and related these preferences to the spatial organization of

the cells' receptive fields. Receptive field shapes can therefore suggest likely dimensions of encoding for stimulus shape. We can examine coding dimensions in other pathways by determining receptive field shapes for cells that respond to stimuli defined by attributes such as relative motion or texture, for example. In addition to using receptive field shape as a physiological index of coding primitives, we can also use aftereffects to psychophysically probe the underlying dimensions of encoding. Tilt and size aftereffects have been used to support the notion of orientation and size coding and these tests can be extended to other stimulus representations such as random dot stereograms (Tyler, 1975), equiluminous colors (Favreau & Cavanagh, 1981) and kinematograms to evaluate whether size and orientation are encoded for these representations.

Finally, we will examine the abilities of each pathway to support various perceptual tasks. The first research on the perceptual capacities of what I would call individual pathways was by Julesz (1971) on images defined only by binocular disparity. (Prestriate areas V3 and V3A may be involved in stereopsis, according to Zeki, 1979, but this is not well established.) Julesz not only asked what were the necessary conditions for depth to be visible in a random dot stereogram when no monocular cues were present, but more important, he asked what sorts of things could be seen with images defined this way. That is, the analysis of binocular disparity does not lead simply to the extraction of depth but also to the representation of the shapes of regions defined by their different depths. Julesz examined whether such shapes could produce classical visual illusions, identifiable letters and various other perceptual phenomena. We have extended Julesz's approach to an additional set of pathways and made comparisons across these pathways (Cavanagh & Leclerc, 1985; Cavanagh, 1985a, 1985b, 1987). Other laboratories have followed related programs examining vision for shapes defined solely by color (Gregory, 1977; as had Gestalt psychologists Lehmann, 1904, and Liebmann, 1927), texture (Nothdurft, 1985; Prazdny, 1986), and motion (Regan & Beverley, 1984; Prazdny, 1985, 1986).

COLOR INPUT TO VISUAL PATHWAYS

Motion

If motion and color are analyzed by different areas in the prestriate cortex, the perception of the motion of stimuli defined only by color should pose problems for the visual system. We found, first, that

motion could be seen, although somewhat degraded, for equi-luminous colored stimuli. We then asked whether this motion perception was mediated by a separate pathway specialized for colored stimuli or by a single motion pathway responding to both color and luminance information.

Ramachandran and Gregory (1978) had initially reported that motion could not be seen for equiluminous stimuli. Their stimuli were produced by alternating two fields of random dots, both containing a square region of identically organized dots whose position differed slightly in the two fields (Figure 2). The background regions were identical in the two fields. Rapid alternation between the two fields gives the impression of an oscillating square, floating above the background if black and white dots are used. Ramachandran and Gregory (1978) reported that when the black and white dots were replaced with red and green and adjusted to be of equal luminance, the oscillating central square was no longer visible. The reduced acuity of the color pathway did not seem to be a factor as, in all cases, the individual red and green dots were clearly seen. They suggested that there was a functional independence of color and motion analyses in the visual system and that the motion pathway responded only to luminance information.

Figure 2. A kinematogram is generated by alternating the left and right random dot fields shown here. They are superimposed spatially and exchanged at a rate of about 3 Hz. There is a background area of dots that remains fixed in the two fields and a central square area of dots that is displaced slightly from one field to the next. The kinematogram produces the impression of a sharply defined square that floats above the background.

It is not clear why the visual system would want to analyze motion only for luminance information and, certainly, physiological recordings do suggest some response of color-selective cells to motion (Michael, 1978, reports color-opponent, complex cells in V1)—although these findings are controversial (Lennie, Sclar & Krauskopf, 1985, report only nonoriented, color-opponent cells in V1). We therefore tried to replicate Ramachandran and Gregory's (1978) findings and found that motion was visible for equiluminous kinematograms although over a more restricted range of displacements and alternation rates (Cavanagh, Boeglin & Favreau, 1985). In fact, Ramachandran and Gregory had used a blank interval of 50 msec between the two random dot fields. The display during the interstimulus interval was black and the flicker that this produced when alternating with the random dot fields had masked the weaker motion signal from the colored stimuli. We were able to reproduce their findings for their condition and show that when the dark ISI was removed the perception of motion returned.

We also studied the perception of motion in simple stimuli: drifting equiluminous sinewave gratings (Cavanagh, Tyler, & Favreau, 1984). These appeared to be significantly slowed and occasionally stopped when compared to stimuli having luminance contrast. Relative speed judgements as a function of luminance contrast of a drifting, red/green or blue/yellow sinewave grating are shown in Figure 3. Observers were presented with a drifting color grating in the top half of the field and a comparison luminance grating in the bottom half. They adjusted the speed of the luminance grating until it appeared to match that of the color grating. When the relative luminance of the two colors approached equality, the apparent speed decreased to 40 to 60% of the actual speed. If we used stimuli that were moving quite slowly (less than 0.5° of visual angle per second), they could even appear to stop moving at equiluminance. The colored bars could be seen clearly and although it was apparent that the bars occasionally changed position this produced no subjective impression of motion. For any stimulus that could produce this stopped-motion phenomenon, the perception of motion could be reinstated by increasing the speed of the stimulus. We concluded that the input of color to motion was simply weaker, so that a particular stimulus could be above its pattern threshold and be seen clearly as colored bars, but below its motion threshold so that the bars did not appear to move (Figure 4).

Evidently, motion could be seen for colored stimuli, but it was not clear which pathway was involved in the response. Could there be cortical areas specialized for the motion of equiluminous, colored
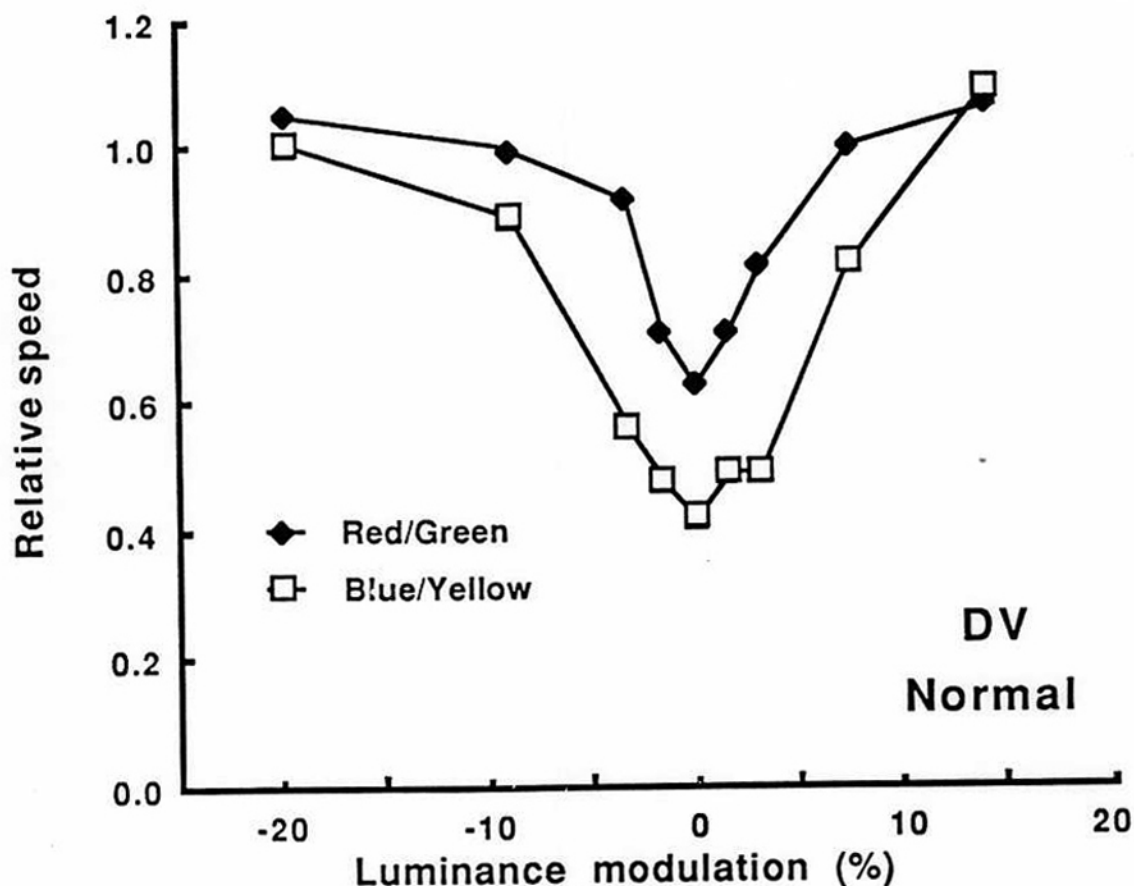
Figure 3.   The apparent speed of a drifting, colored grating decreases at equiluminance (luminance contrast 0%). The observer adjusted the speed of a 15% contrast, 0.5 cpd luminance grating to match the apparent speed of a 0.5 cpd, colored grating (red/green or blue/yellow) for several luminance contrasts between the two colors. This setting is then divided by the actual speed (1° of visual angle per second) to determine relative speed. The display subtended 8° of visual angle and the central 2° was masked in the case of the blue/yellow grating.

stimuli (Figure 5)? Using a motion aftereffect paradigm, we (Cavanagh & Favreau, 1985) showed that this was not the case. Following adaptation to drifting luminance gratings, motion after-effects could be seen on equiluminous colored tests, and vice versa, implying a single, common site for motion adaptation. In addition, following adaptation to a luminance grating, the motion aftereffect seen on a colored test could be nulled by moving the colored test in the opposite direction, an interaction that required a motion pathway accessed by both color and luminance information.

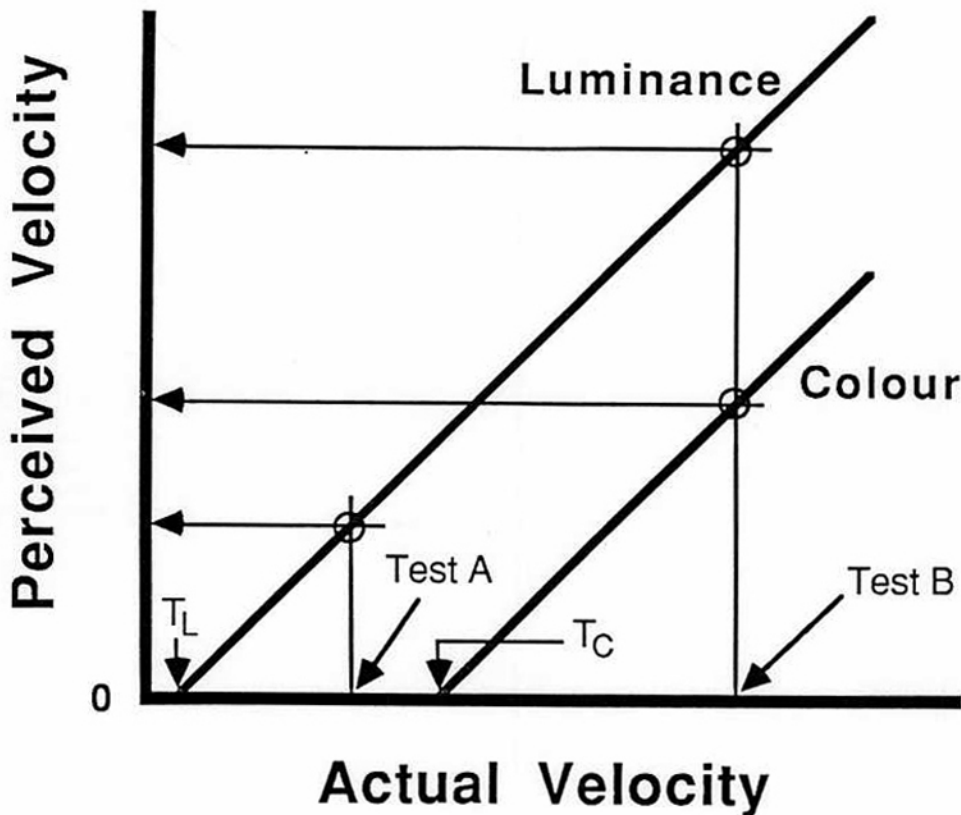We next measured the strength of input of colored stimuli to this

Figure 4. Perceived velocity as a function of actual velocity. If a colored grating is above its threshold for form perception but below that for motion perception (T_C), its bars can be seen but its motion is not visible (*Test A*). If the grating's velocity is then increased above its threshold, its motion becomes visible but it appears to move more slowly than a luminance grating drifting at the same speed (*Test B*). This independence between form (defined by color) and motion perception implies separate analyses of form and motion. T_L and T_C are the threshold velocities for luminance and color stimuli, respectively.
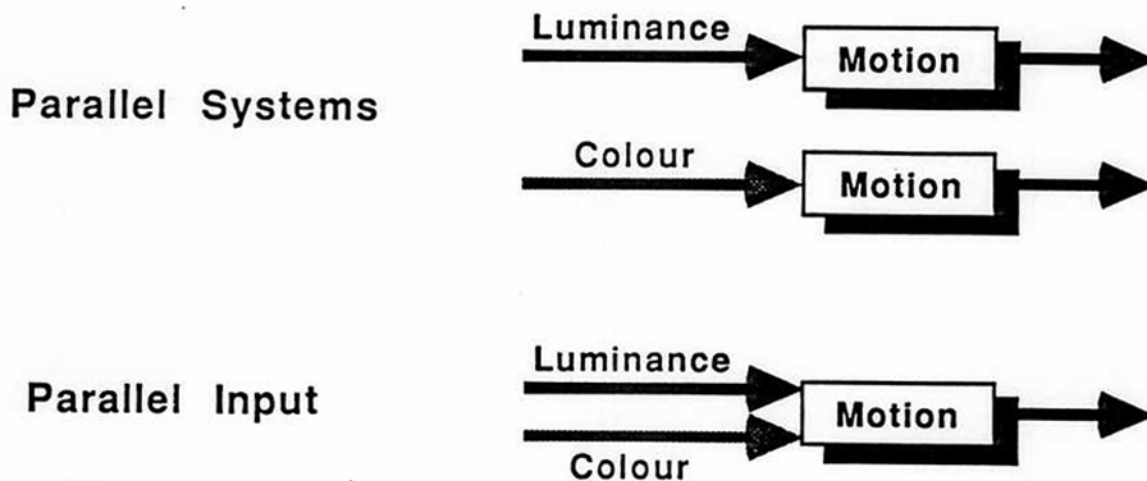

Figure 5. Parallel systems: one specialized for the motion of luminance-defined stimuli and the other for color-defined stimuli. Parallel input: a single motion system responding to both luminance and color.

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common motion pathway using a motion nulling paradigm (Cavanagh & Anstis, 1986). We can measure the contrast of an unknown grating by varying the contrast of an otherwise identical grating moving in the opposite direction (Figure 6). The direction of perceived motion of the combined gratings is determined by the grating with the higher contrast. When the two gratings have equal contrast, a motion null—counterphase flicker—is obtained. We asked observers to adjust the contrast of a luminance grating until it just nulled the motion of a color grating moving in the opposite direction. This contrast setting was taken as the "equivalent luminance contrast" of the color grating. The equivalent contrast for color stimuli was, at best, about 10%, one tenth the maximum contrast possible for luminance stimuli. When these strengths were expressed as multiples of the respective color and luminance thresholds, however, the two types of stimuli had approximately equal influence on the perception of motion.

Although we had shown that color stimuli influenced the motion system, we had not proven that they did so through the opponent-color pathways. The luminance pathway responds to the relative luminance difference between two colors so it should be possible to adjust the luminance of one of the colors relative to the other until there is no response in the luminance pathway. However, if the cells in the luminance pathway have a variety of equiluminance points (Derrington, Krauskopf & Lennie, 1984) then no color pair can be simultaneously equiluminous for all cells. The motion seen for an equiluminous stimulus may therefore be due either to the contribution of the opponent-color input to a motion pathway or to this residual noise response in the luminance pathway. To test the possibility of opponent-color input, we presented a green/purple stimulus that fell along the tritan confusion line, differentially stimulating only the blue-sensitive cones (these cones have no input to the luminance pathway, Eisner & MacLeod, 1980; Cavanagh, Anstis & McLeod, 1987). We found an equivalent luminance contrast of about 4%. Moreover, following bleaching of the blue-sensitive cones, this stimulus had zero equivalent contrast. Since bleaching the cones eliminates their response to the stimulus, and eliminated the motion as well, we concluded that the input had passed through the blue-sensitive cones and, therefore, through the opponent-color pathway.

Overall, these studies indicate that there is a common motion pathway for opponent-color and luminance information and that the color input to the motion system is as effective, when considered in terms of threshold contrast multiples, as luminance input. On the other hand, the speed of equiluminous color stimuli is seriously misjudged. An understanding of this misperception of color velocity may
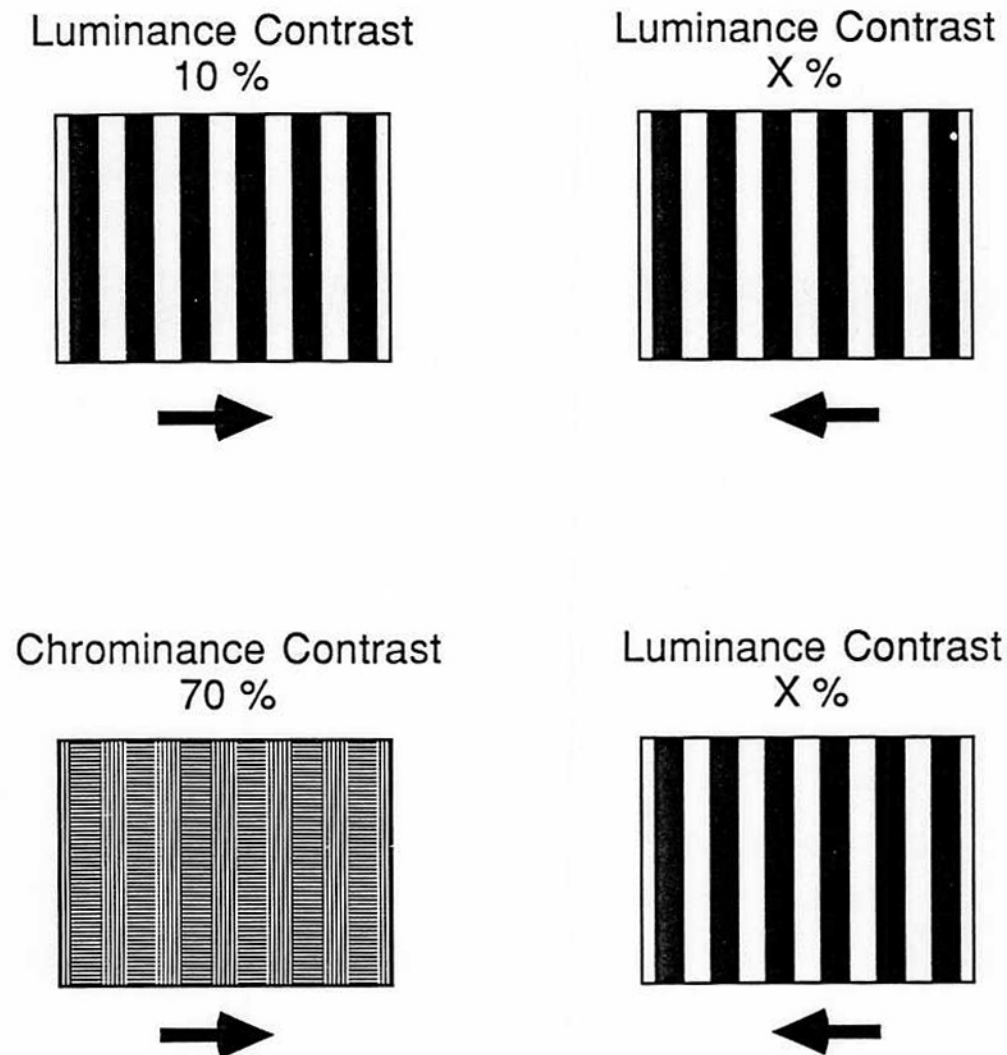
Luminance Contrast
10 %

Luminance Contrast
X %

Chrominance Contrast
70 %

Luminance Contrast
X %

Figure 6. Opposing motion paradigm. On top: if two luminance gratings with the same spatial and temporal frequencies are superimposed and drifted in opposite directions, motion is seen in the direction of the grating having the higher contrast. If both gratings have the same contrast, no motion is seen, only counterphase flicker. The contrast of the rightward moving grating can therefore be measured by adjusting the contrast of the leftward moving grating until no motion is seen: the contrast setting to obtain the motion null would be 10%. Similarly, on the bottom, a chromatic grating drifting to the right is superimposed on a luminance grating drifting to the left and the contrast of the luminance grating is adjusted until a motion null is obtained. The resulting contrast is the "equivalent luminance contrast" of the chromatic grating.

provide an important test of the several models of velocity judgement (Watson & Ahumada, 1985; Adelson & Bergen, 1985; van Santen & Sperling, 1985).

Stereopsis

Initial studies by Lu and Fender (1972), Gregory (1977), and others demonstrated that depth in random stereograms was lost at equiluminance even though depth was not lost for figural stereograms. However, de Weert and Sadza (1983) showed that observers actually could judge depth in equiluminous random dot stereograms even though the subjective impression was very weak. De Weert and I have made some preliminary measurements showing, in addition, that the difference between random dot stereograms and figural stereograms may be due only to a difference in spatial frequency content and not to any qualitative difference. Our measurements showed that the depth perceived in a stereogram decreased as the colors approached equiluminance in much the same way that the apparent speed of drifting colored gratings decreased at equiluminance. Grinberg and Williams (1985) showed that depth could be seen in random dot stereograms that only stimulated the blue-sensitive cones. Since these stimuli are restricted to the opponent-color pathway, they concluded that color information did contribute to stereopsis.

Overall, evidence points to a color contribution to at least color, motion, and binocular disparity pathways. Whether or not color influences all pathways, it is certain that its influence on motion, stereo, and texture is less than that of luminance information. This may be simply a function of the higher thresholds for color. As was seen for motion, the contribution of color was equivalent to that of luminance in terms of threshold multiples but since the maximum obtainable color saturation was only about 40 times the threshold value while the maximum luminance contrast was approximately 400 times its threshold, the effect of color is typically much less than that of luminance.

CODING PRIMITIVES

How is image information coded in each representation? The visual areas that we have discussed, V1, V2, V3, and V4 and MT, are retinotopically organized, preserving adjacency. Image information could be coded simply in terms of local value, such as a point by

point color value (perhaps both hue and saturation). This type of coding requires sampling the retinal array for only small, local areas and suggests that physiological studies would find only circular receptive fields of a fixed size. Studies have shown circular receptive fields for retinal and LGN cells but most cortical cells show quite a different structure. Hubel and Wiesel (1968) described oriented fields (Figure 7) that prefer a particular orientation and width of a line as the optimal stimulus. Moreover, many cortical cells respond to stimuli within the same retinal region, with different cells responding to different orientations and sizes. Thus, at each retinal location, the stimulus information is represented by the pattern of activity across a set of cells that code, among other things, orientation and size.

Others have tried to identify the receptive field structure, and thus coding primitives, for stimuli defined by color and by binocular disparity. The evidence concerning color is contradictory. Michael (1978) has reported that many cortical cells with oriented receptive fields that respond best to color contrast in the absence of luminance contrast. Lennie, Sclar, and Krauskopf (1985), however, have not been able to find any oriented cells responding principally to color and not luminance. Poggio, Motter, Squatrito & Trotter (1985) have studied neurons that respond to bars defined by random-dot ster-
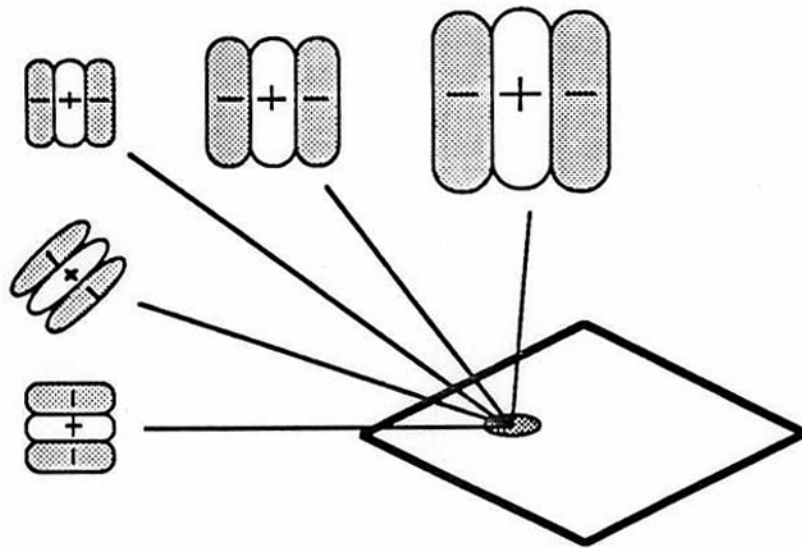

Figure 7.   Coding primitives can be established physiologically by demonstrating that there are many cells responding along different stimulus dimensions for each retinal area. Recordings in the striate cortex show that for each retinal area there are cells tuned to several different sizes and orientations.

Adapt   Test   Percept
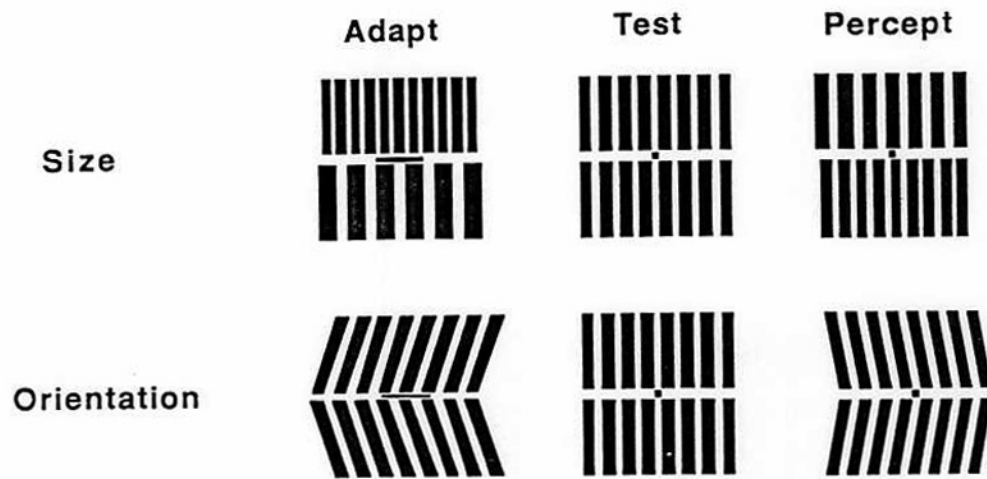
Size

Orientation

Figure 8.   Coding primitives can be established by psychophysical techniques demonstrating size- and orientation-specific aftereffects.

eograms and claim much reduced or absent orientation sensitivity for these cells.

Psychophysical techniques have also been used to identify the underlying coding primitives. Blakemore and Sutton (1969) and Campbell and Maffei (1971) as well as many others have demonstrated size and orientation specific aftereffects that demonstrate encoding of size and orientation for stimuli defined by luminance. In general, if an observer is exposed to a stimulus having a specific size or orientation for several minutes, subsequently viewed stimuli of slightly different values will change their perceived size and orientation (Figure 8).

Olga Favreau and I (Favreau & Cavanagh, 1981) were able to show that luminance and color stimuli could induce simultaneous size aftereffects in opposite directions. This demonstrates that there must be parallel encoding of size information for both color and luminance. Eisner (1978) also showed that a tilt aftereffect could be induced for equiluminous stimuli, implying orientation coding for color. Since the evidence concerning oriented color-selective cells in V1 is contradictory, the site of the adaptation producing these size and orientation-specific aftereffects may be further along the color pathway. Zeki (1978) has shown that many cells in area V4 that are selective for color also show orientation preferences.

Tyler (1975) has tested the possibility that binocular disparity may be coded according to size and orientation. He claimed to find tilt and spatial frequency aftereffects for gratings defined by random-dot stereograms. These effects are not dependent on the size and

orientation tuning of the binocular cells responding to retinal disparity. In a random dot stereogram, many cells will respond to the texture elements having various disparities between the two retinal images. These texture elements may have random orientations and sizes. Tyler's effects, however, were specific to the bars defined by disparity over a large spatial extent. Any cells responding to these areas must integrate over many first-order cells responding to retinal disparity. Although Tyler's data are suggestive, Wolfe and Held (1982) found only small tilt aftereffects when attempting the same experiment. No published reports have appeared for stimuli defined by texture or motion but our initial tests indicate that, if these aftereffects exist, they may be very weak.

To summarize, size and orientation coding may be present for motion, binocular disparity, and texture representations but this is not as firmly established as it is for color and luminance.

IMAGING CAPABILITIES

In order to study the capacities of each pathway for shape analysis, our computer graphics system constructs images defined by a single attribute: color, relative motion, binocular disparity, texture, or luminance. Starting from a video image of a black and white stimulus, the black areas are replaced with, for example, a random texture moving in one direction, and the white areas with a similar texture moving in the opposite direction. Figure 9 demonstrates this attribute replacement for texture and binocular disparity.

The areas of the prestriate cortex may restrict their input information in order to perform a highly specialized analysis of one particular attribute, such as, for example, color constancy in the case of area V4 (Zeki, 1978). However, these areas, in addition to performing specialized analyses, are also capable of representing shape: a two-dimensional map of regions differentiated by the attribute in ques-
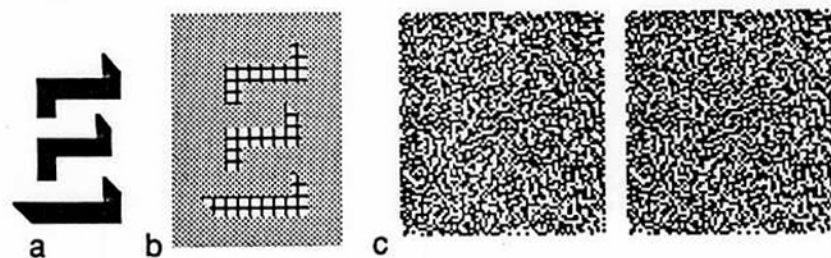

a   b   c

Figure 9.   Attribute replacement generates figures defined by texture (b) or binocular disparity (c) from an original figure (a) defined by luminance.

tion. Gregory (1977, 1979) has suggested that each attribute may provide a rough map of the visual stimulus and that these maps may be aligned to the luminance representation which he considers the master map.

We were interested in examining what perceptual abilities were supported by the shape information in a single representation in the absence of any luminance "master map." In particular we found that information signalled by stimuli having explicit contours, for example, T-junctions indicating occlusion (Figure 10), was effective no
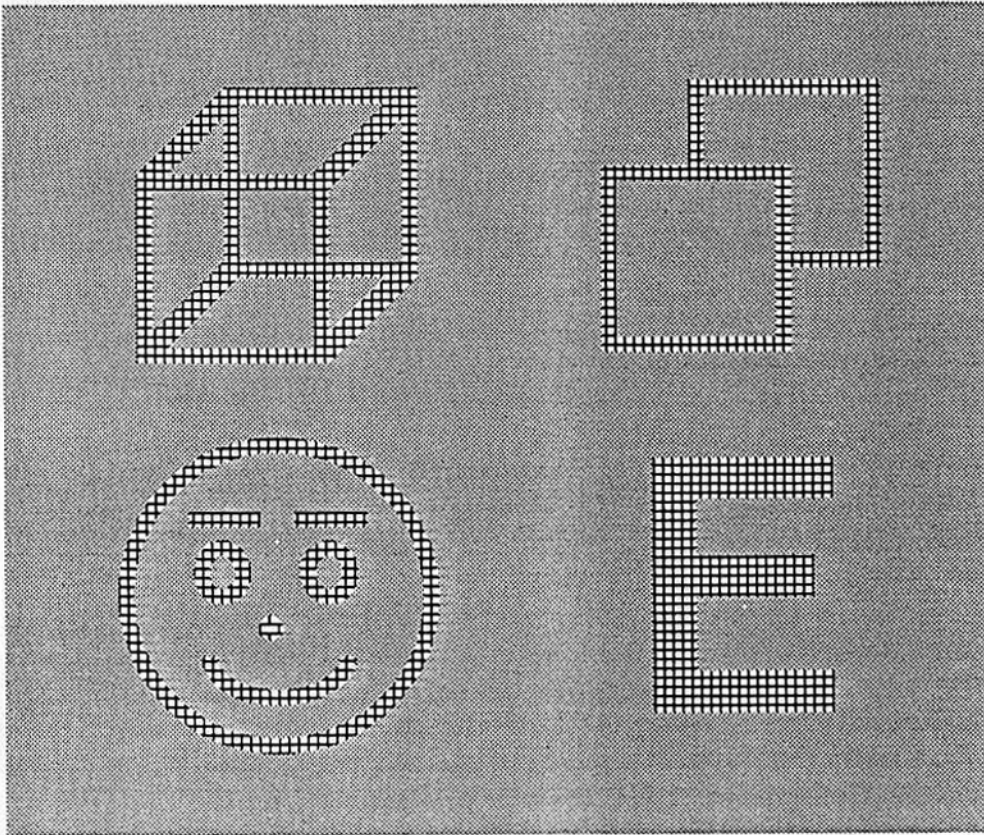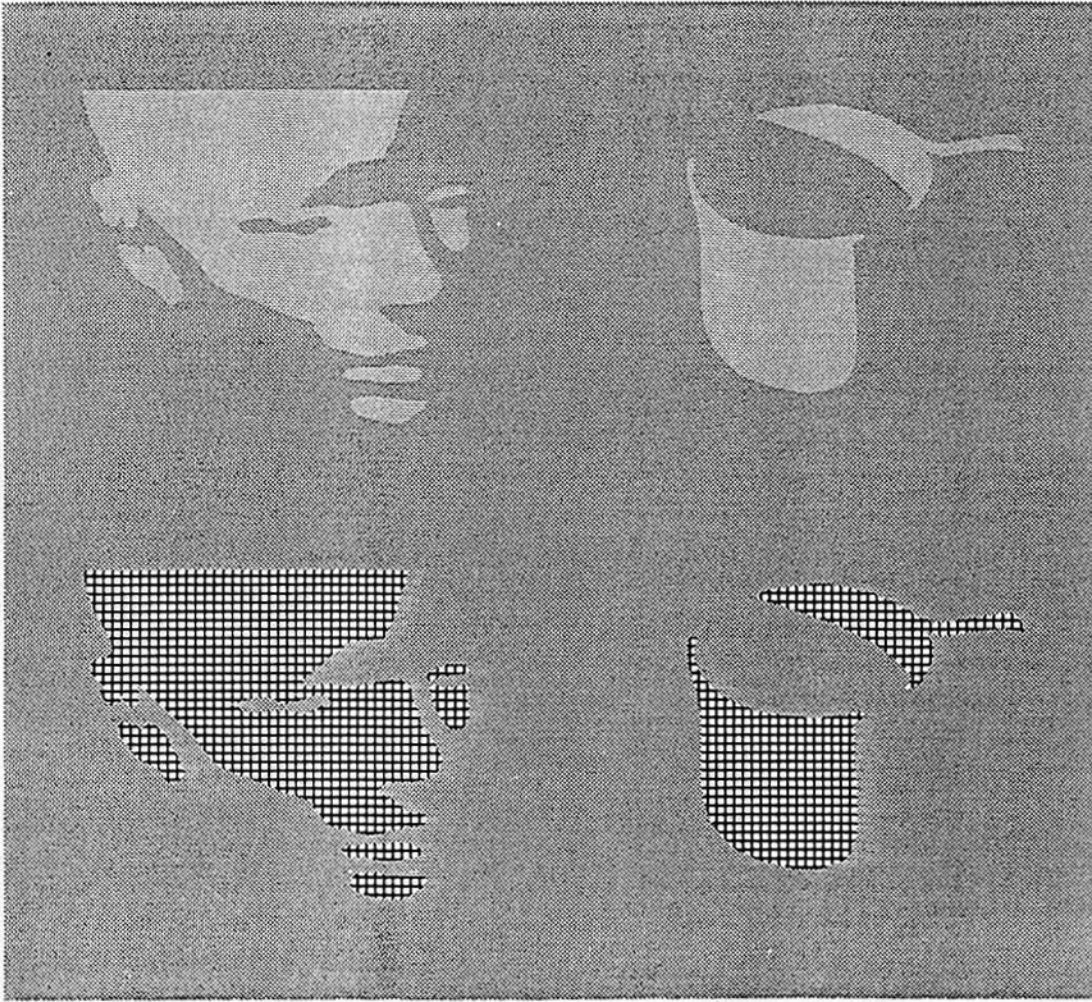

Figure 10. Stimuli with explicit contours. These stimuli are defined by a difference in texture and should be invisible if you squint your eyes. The stimuli: a Necker cube seen as a wire frame—the background can be seen through the areas between the cube contours; an occlusion figure with one square, opaque sheet covering one corner of a similar sheet—the areas between the contours hide the background; a smiling face; the letter E. In general, the same interpretations are reported for these stimuli whether defined by luminance, texture, color, relative motion or binocular disparity. However, large individual differences are found in the latter two cases when there are conflicts between depth implied by the picture and depth indicated by relative motion or binocular disparity.

matter which visual pathway was used (Cavanagh, 1985a), Simple, two-dimensional letter shapes could be easily identified. Three-dimensional objects defined by complete contours in line drawings involving occlusion and perspective were interpreted in the same fashion whether represented by luminance, color, or texture. When relative motion or random dot stereograms were used to present these same drawings, the depth suggested by stimulus shape (due to occlusion and perspective, for example) sometimes conflicted with the depth indicated by the relative motion or binocular disparity used to present the figure. Many observers could see the depth implied by the drawing despite the conflict, although others could not. In cases where there was no conflict between the depth inferences in the picture and the depth used to present the picture (based on either relative motion or binocular disparity), the pictures were interpreted in the same manner as for luminance, color, or texture presentations. Shape information involving explicit object contours therefore appears to be represented equally well in any of the pathways. The depth and surface inferences based on these shape representations probably occur after this level of separate pathways and accept shape descriptions from any pathway. There was no indication that luminance information had any priviledged role to play in these images.

The results for stimuli involving implicit contours were strikingly different. We studied two stimuli of this type: shadows (Cavanagh & Leclerc, 1985) and subjective contours (Cavanagh, 1985b). In both cases, a luminance difference was necessary between the two image areas (e.g., the open grid and the fine dot areas of the E in Fig. 9b). If the parts of the stimuli were presented without a luminance difference, they were interpreted as separate, unconnected islands of color or texture (see Figure 11). If a luminance difference was then introduced, the overall global organization of the stimulus would become visible. Moreover, it was not sufficient for the mean luminance of the two image areas to be different; this luminance difference also had to be in the same direction all along the edge between the regions. Studies of filtered images showed that any frequency band signaling inappropriate or inconsistent edge polarity could veto the edge as a potential shadow border or suppress a subjective contour. Thus the luminance pathway is essential for shadows and subjective contours but it appears that it is the edges that are signaled at this low level and not the entire shadow region or subjective surface. We verified that the reduced resolution and contrast inherent in texture or color representations were not the cause of the failure to see shadows and subjective contours.

Figure 11. Stimuli with implicit contours: shadows. Many of the contours of these figures are shadow contours, not object contours and many of the object contours, both external and internal self-occlusions, are implicit. The interpretation of these figures changes when an appropriate luminance difference is present between the shadowed and non-shadowed areas (top row) compared to when no luminance difference is present (bottom row). The interpretation of surface relief due to shadows occurs for stimuli defined by luminance and but not for stimuli defined by texture (shown here), color, relative motion or binocular disparity.

It might seem self-evident that shadows would require luminance information to be properly interpreted: a real shadow is always darker than the adjacent nonshaded region. Shadow analysis may therefore be part of the specialized luminance analysis just as seeing colors is part of the specialized colour analysis. This is not a convincing argument, however, since the inference of depth from

shadows must be based on their shape (necessarily in our stimuli which did not have any luminance gradients), not on their darkness. Rainbows can be identified in black and white images because of their shape but depth from shadows is not perceived in images defined only by color even though all the essential shape information is there. Moreover, it seems unlikely that an early level of the visual system such as the luminance pathway would be independently capable of the depth and surface inferences involved in interpreting shadows. It is reasonable to assume that higher level analyses are participating in these inferences but perhaps these analyses access only luminance information and, in particular, the location of appropriate luminance borders having consistent polarity. By ignoring shape information in other pathways, the visual system would give up opportunities to reject areas as shadows because of impossible colors or inappropriate depths, motions or textures. This is what our data showed as observers saw depth in shadow images having appropriate luminance patterns even when they violated the color, depth, motion, and texture contraints of natural shadows (Cavanagh & Leclerc, 1985).

Luminance may be a natural aspect of shadows, but this is not the case with figures producing subjective contours. Theories of subjective contours are generally based on high-level inferences of occluding surfaces. Gregory (1972), Rock and Anson (1979) and Kanizsa (1979) all suggest that the occluding surface is hypothesized to simplify the interpretation of the image. Thus, in Figure 12 (top left), it is easier to see eight circular disks covered by two square, opaque sheets (one disk completely covered) than seven, irregular, three-quarter pie shapes. These cognitive explanations are based entirely on stimulus shape and therefore should be unaffected by the manner in which the shapes are presented. On the contrary, subjective contours were only visible when there was a luminance difference between the regions defining the shapes (Cavanagh, 1985b; Pradzny, 1985; Brussell, Stober, & Bodinger, 1977). In this case, the lack of equivalence between the different pathways when presenting the same stimulus shapes contrasts with the equivalence of the pathways for explicit shapes presented as line drawings (Figure 10). It is evident that the perception of subjective contours cannot be a shape-based phenomenon. This conclusion is also supported by the physiological studies of von der Heydt, Peterhans and Baumgartner (1984) who report cells in area V2 that respond to subjective contours. It may be that low level analyses (based on these area V2 cells that, according to our findings, should respond only to luminance) signal contours in areas of the figures where there are no physical contours.
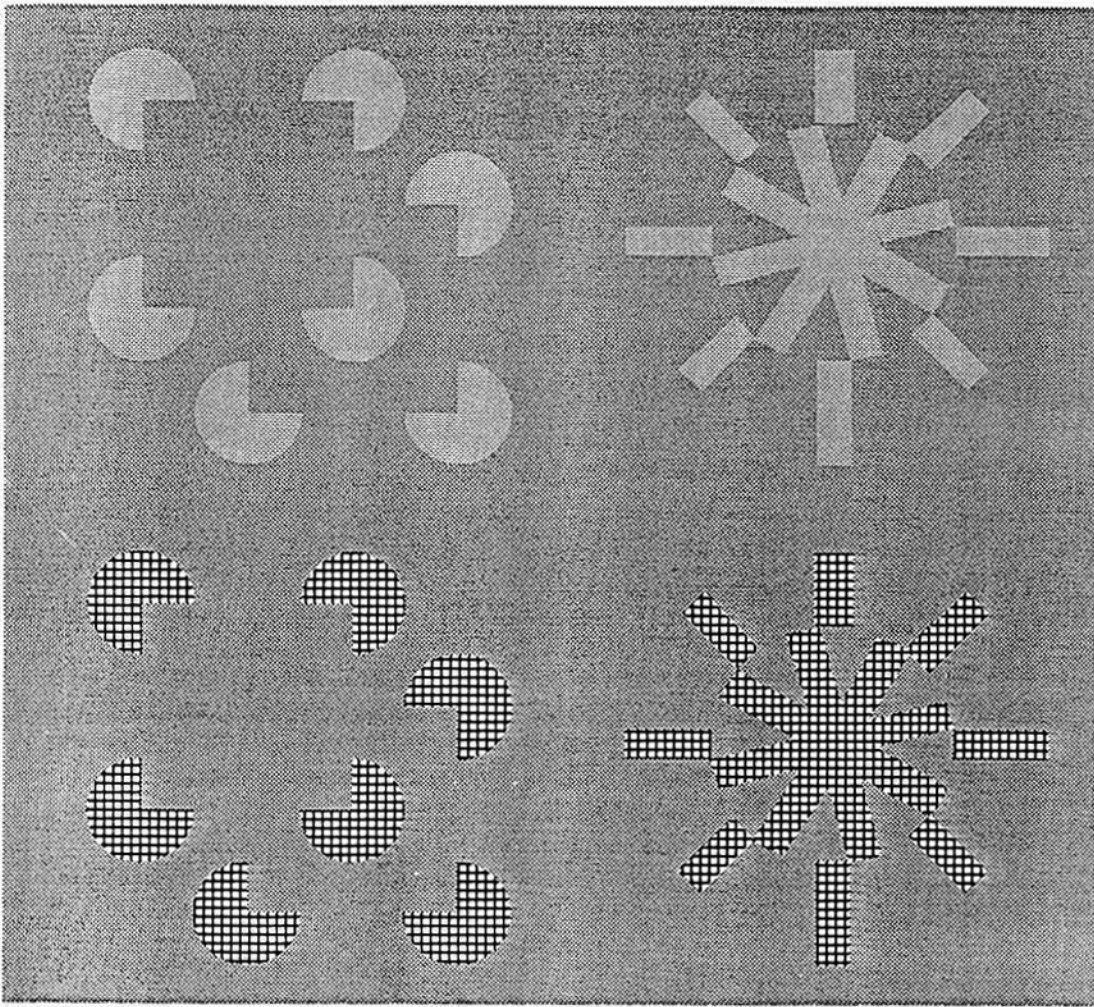
Figure 12.   Stimuli with implicit contours: subjective contours. When there is a luminance difference between the inducing elements and the background, subjective contours can be seen in these figures (top row). When these same figures are presented without a luminance difference (bottom row), subjective contours are weak or absent.

Higher level analyses may then use these contours to assert appropriate subjective occluding surfaces.

CONCLUSIONS

The results of the work that I have described here are summarized in Figure 13. Color information appears to contribute to motion and binocular disparity analyses. This can only improve the adap-
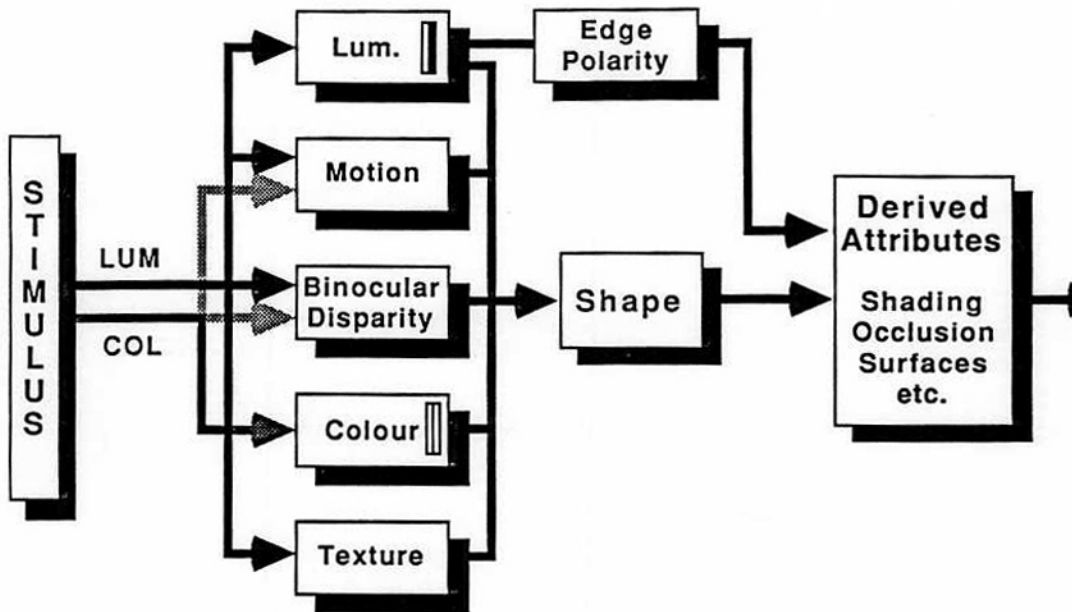
Figure 13. Pathways in early vision. Color information contributes to motion and binocular disparity analyses in addition to color analysis. Both color and luminance analyses make use of size and orientation coding primitives. Shape defined by explicit contours is signaled by all pathways but shape defined by implicit contours is only signaled by the luminance pathway, most likely in terms of assertions of constant polarity edges in the stimulus.

tiveness of the visual system by allowing some motion and depth responses to stimuli defined only by color or only by binocular disparity. The responses are, however, rather weak so that reducing luminance differences between a stimulus and its background remains a very effective camouflage technique. Coding primitives involving size and orientation are used in the color and luminance pathways and perhaps in the other pathways as well, although this remains to be demonstrated convincingly.

Shape information was equally well signaled by all the pathways but shadows and subjective contours appeared to depend on a special purpose process in the luminance pathway. It is possible that this process involves signaling appropriate luminance borders that maintain a consistent contrast polarity all along their length.

The ability to probe individual pathways in the visual system opens many new possibilities for understanding vision. Each pathway may be thought of as a pared down visual system, less complex than the whole and easier to understand. On one level, much of the visual research done using luminance-defined stimuli needs to be

repeated on the remaining pathways to determine their capabilities and this work is underway in several laboratories. On another level, new experiments testing how information is integrated across the individual representations will identify important principles in image understanding.

In the research that I have reported, I have assumed that the stimuli used were able to isolate visual pathways. A basic goal of this research is to examine to what extent this isolation is actually achieved. Possible techniques include identifying cortical magnification factors for these stimuli and comparing them to physiological data (Gattass, Sousa & Covey, 1985) for the visual areas involved.

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