

Subjective Contours at Line Terminations Depend on Scene Layout Analysis, Not Image Processing

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Subjective contours at abutting lines, commonly attributed to levels of the visual system where image properties are directly encoded, are shown to require an explanation at the level of visual surface understanding. By the use of stereoscopic displays, subjective contours could either be abolished where they were monocularly strong or be created where they were monocularly nonexistent. Furthermore, it was shown that subjective contours are determined by the boundaries of occluded rather than occluding regions. The results cannot be accounted for by adding a stereo component to existing image-based theories, such as those based on end-stopped cells. Instead, any plausible process must explicitly determine the position of bounding surface contours in the scene. Minimum requirements of such a process are given.

Subjective contours are of two major varieties: those that complete existing luminance contours across gaps (Schumann, 1900; Kanizsa, 1974; see Figure 1, top) and those that form along a set of line terminators (Ehrenstein, 1941/1987), especially along two sets of abutting line terminators (Kanizsa, 1974; see Figure 1, bottom left). In both cases, it is generally agreed that subjective contours serve the function of delineating the boundaries of occluding surfaces when luminance contours are camouflaged in the image by the luminance of the surrounding field. With respect to mechanism, there is considerable disagreement. Several physiological findings of great interest, discussed in detail, subsequently have encouraged the continuing widespread view that subjective contours are the product of low-level physiological mechanisms acting at early levels of the visual system that directly encode image properties. This marries function and mechanism in an unusually persuasive and satisfying manner.

It is the goal of this article to present a different view based on striking new findings. We used stereograms to manipulate the three-dimensional (3-D) placement of the contours of the abutting line effect. This is the simplest configuration giving rise to subjective contours and the one most readily explained by low-level theories (Treisman, Cavanagh, Fischer, Ramachandran, & von der Heydt, 1990). On the basis of our results, we argue that such subjective contours can be explained only at the level of scene analysis. We sketch out some of the complexities an adequate explanation must encompass. We also attempt to analyze in some detail why current image-based mechanisms cannot provide such an explanation.

The first critical underpinning of low-level theories of subjective contours is the finding by Hubel and Wiesel (1968) of cells that are end stopped, that is, whose response is influenced by the locus of the termination of a contour as well as its orientation, contrast, and other properties. A number of models (Finkel & Edelman, 1989; Grossberg & Mingolla, 1985; Heitger, Rosenthaler, von der Heydt, Peterhans, & Kübler, 1992; von der Heydt, Peterhans, & Baumgartner, 1984) have explained subjective contours by postulating integrative or summative processes applied to the activity of end-stopped cells at a set of collinear line terminators. Most of these models follow perceptual experience by requiring abutting contours (approaching from both sides) to support the presence of a subjective contour, although some require only a single set of terminators.

The second significant physiological finding, one that has given even stronger support to low-level mechanisms, was that many cells in visual cortical areas 17 and 18 of the cat and V1 and V2 of the monkey, which are sensitive to luminance contours (lines and edges) of a particular orientation, also respond to the orientation of a series of abutting collinear line terminations (Groszof, Shapley, & Hawken, 1993; Redies, Crook, & Creutzfeldt, 1986; Sheth, Sharma, Rao, & Sur, 1996; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984). These electrophysiological findings are further supported by optical imaging studies (Ramsden, Hung, & Roe, 2001). The discovery of cells responding to assemblies of line terminators is undoubtedly of great significance in extending our understanding of early contour processing. Previous to this, luminance contrast had been considered essential for eliciting a response from cells in early visual areas. Abutting lines of equal density, however, lack any luminance contrast along the abutment, and the fact that they nevertheless elicit a response does seem indicative of a new basis for contour detection in early visual areas.

It has been widely assumed that the responses of these cells directly mediate the perception of subjective contours. It has become common to read that such cells “signal illusory lines or

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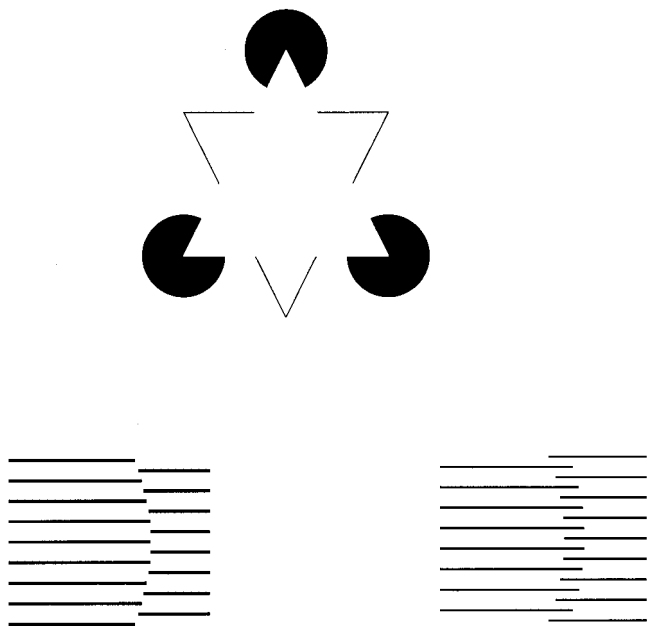


Figure 1. Top: Classical Kanizsa figure with subjective contours extending existing luminance edges. Bottom left: A subjective contour along abutting line terminations (see Kanizsa, 1974). Bottom right: Same figure as at bottom left, but with lines interleaved rather than abutting. The subjective contour disappears.

edges" (Spillmann & Dresch, 1995, p. 1360; Treisman et al., 1990, p. 289). The activity of these cells is nearly always assumed to arise from cooperation among end-stopped cells, as already described. In a similar vein, Soriano, Spillmann, and Bach (1996) assumed that the psychophysics of the abutting line illusion is directly informative about the properties of end-stopped cells in human vision.

There are, however, a number of observations that cannot be accommodated by theories pitched at the level of the encoding of local image properties. For example, in Kanizsa-type figures (Figure 1, top), the presence–location of subjective contours is not predicted well by image characteristics. The depth relations both within the indented circles themselves and between the circles and other components of the field are critical (Bradley & Petry, 1977; Harris & Gregory, 1973; Lawson, Cowan, Gibbs, & Whitmore, 1974; Nakayama, Shimojo, & Ramachandran, 1990; Rock & Anson, 1979). In Figure 2, reversing the stereo depth relationships between the circumferences of the circles and the vertical contours of the bites (compare fusion of the left and right pair) eliminates the subjective contour joining the contours of the bites and induces a contour completing the circles, which now appear as apertures through which the bites are visible. Depth relations entirely control what subjective contour is seen.

Yet, these and other observations that are not in line with image-based models of subjective contours, although acknowledged by the proponents of such models, have surprisingly not been regarded as a serious challenge to them. Such observations have tended until recently to be attributed to elaboration at a higher level of what is fundamentally a low-level image-based response.

In the present article, we show that subjective contours seen along line terminators derive from the processes that determine

scene properties and that they cannot be derived directly from the neural encoding of image properties.¹ To support this conclusion, we describe the appearance, disappearance, and position of subjective contours as the relative stereoscopic depth between lines is varied.

We argue that in determining whether a bounding contour of a surface exists at a particular locus, earlier stages provide data used by the visual system for such decisions. The key point is that this information is to be regarded only as data, to be interpreted by systems more competent to determine whether such bounding contours exist in the world. With these guiding ideas in mind, we outline a set of results that begin to reveal the operation of these systems in the genesis of subjective contours.

Observations

We began with two sets of lines (Figure 3A and Figure 3B). Stereoscopic depth was introduced pseudorandomly within one set (Figure 3A) to make the component lines vary in depth in a nonplanar arrangement, *the forest*. The other set, *the plane* (Figure 3B), was composed of lines all having the same stereoscopic depth. Lines were varied in length and orientation to avoid the wallpaper effect, in which false fusions occur between repetitive details in binocular images.

Fusion of Figure 3A and Figure 3B reveals that for neither the forest nor the plane alone, whether monocularly or stereoscopically viewed, is there a subjective contour along the horizontally aligned ends of the contours. When, however, the two sets are both presented, one abutting the other, the perceived situation alters (Figure 3C and Figure 3D). Monocularly, there is now a clearly visible subjective contour along the abutment. These observations generally support the view that abutting contours are required for subjective contours. Stereoscopically, however, abutment is shown to be insufficient. The presence of a subjective contour depends on which set appears nearer. When the forest appears farther than the plane (Figure 3C), the subjective contour is very strong (stronger than in the monocular view). When the forest appears nearer than the plane (Figure 3D), the subjective contour virtually disappears. This is remarkable in that the terminations and their abutment in the image were not altered by our manipulations. The same was true of the relative stereoscopic separation of the plane and the forest; the depth ordering of these two sets of lines, not their separation in depth, was the critical factor in eliciting a subjective contour. The much greater subjective contour strength obtained for the plane-nearer condition than for the forest-nearer condition is consistent with the fact that a coplanar set of lines can easily lie on a plausible surface, whereas a set of lines at random distances cannot. *A surface can occlude a set of objects; a set of objects cannot occlude a surface.*

Two additional phenomena that provide further insight into the processes underlying subjective contours were observed. First, the lines composing the nearer plane and the more distant forest were separated vertically (Figure 4B). Monocularly, this weakens the subjective contour seen when they abut (Soriano et al., 1996). Two

¹ It is possible that even at the level of V2 neurons in the monkey, some scene-related processing occurs (Gillam, Nakayama, & Gilbert, 2000).

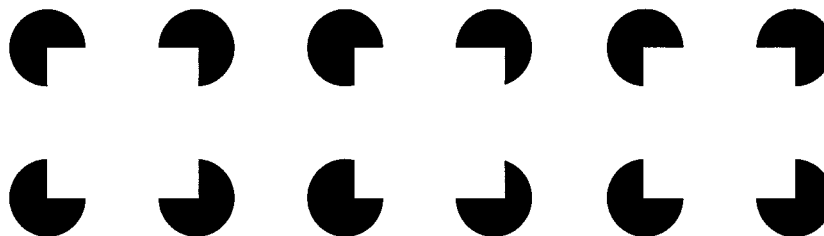


Figure 2. The left and right pairs should be fused in turn. The left pair, when cross-fused, gives rise to a perception of an occluding square completed by subjective contours in front of a set of amodally completed black circles. Cross-fusion of the right pair gives rise to the perception of four black holes through which an amodally completed black square is visible.

weak contours may appear along each collinear alignment.² Stereoscopically, however, there is still only one subjective contour, and it is more salient than the monocularly seen contours. It is seen as the occluding edge of the plane, and yet remarkably this apparent edge of the plane is no longer located along the ends of the planar contours but some distance above them, along the ends of the lines of the forest. Second, the lines composing the plane and the forest were moved together so that their component lines overlapped vertically and were thus interleaved (Figure 4C). Despite the fact that such interleaving ordinarily destroys subjective contours (Soriano et al., 1996; see also Figure 4C, monocularly, and recall Figure 1, bottom right), the subjective contour in the stereoscopic case is still strong and still located along the ends of the lines of the forest where the edge of the plane is again seen to occlude them. The lines of the plane are now seen to protrude beyond the edge of the planar surface into the forest region, like quills protruding from the sharp edge of a planar surface.³ The persistence of the subjective contour despite overlap of the lines may seem odd at first sight and in violation of what would be expected ecologically. Actually, it makes good ecological sense. Objects such as trees can be attached to an occluding surface such as a hill and extend beyond the occluding contour into the region of the visual field occupied by the occluded (far) objects. The reverse cannot be the case. Objects attached to a far occluded region would never extend into the region of the visual field occupied by the occluding surface.

These observations show for the first time that subjective contours are located at the terminations of apparently occluded objects, and although contours consistent with an occluding plane are also required (there was no subjective contour for the forest alone), these contours do not delineate the edge of the occluding surface and its subjective contour. We now describe in detail three experiments confirming and extending these observations.

Experiment 1

In Experiment 1, we presented subjects with a series of stereograms (shown, drawn to scale, in Figure 3). These stereograms represented (a) the forest alone, (b) the plane alone, (c) the forest far and the plane near, and (d) the forest near and the plane far. In addition, we presented subjects with the same stimuli (forest and plane) overlapped or separated, as shown in Figure 4. We used ratings to measure the strength of the subjective contour under each condition and a movable arrow probe to determine its appar-

ent location. In conditions in which both sets were present, the forest set was always placed above the plane set.

Method

Each set of lines (forest or plane) was made up of seven randomly oriented lines of different lengths, as shown in Figure 3. These lines were arranged so that their terminations along the leading edges of the forest and plane sets (their bottom and top edges, respectively) were aligned to form a horizontal edge.

The lines in the plane set were situated on the same depth plane (i.e., they were identical for both eyes), whereas the depths of individual lines in the forest set were varied over a disparity range of ± 4 minutes of arc (relative to the plane set) in a pseudorandom fashion. Three of the forest lines had crossed disparity, three had uncrossed disparity, and one had zero disparity. Positioning of the forest either in front of or behind the plane set was achieved by adding a standing disparity of either 6 minutes of arc (*forest near*) or -6 minutes of arc (*forest far*) to all lines in the forest set.

When both forest and plane were present, they were either arranged so that their horizontal edges abutted or so that the vertical locations of the forest and plane sets were offset, by varying amounts, symmetrically about the center of the display, to produce different degrees of overlap or separation between them (as shown in Figure 4). The total magnitude of the vertical offset was ± 2 , ± 4 , ± 6 , ± 10 , or ± 14 minutes of arc. Positive offsets produced a vertical gap between the sets, whereas negative offsets produced overlap. The conditions thus consisted of (a) the forest alone, (b) the plane alone, (c) the forest near with forest and plane abutting, (d) the forest near with forest and plane separated by 2, 4, 6, 10, and 14 min of arc, (e) the forest far with forest and plane abutting, and (f) the forest far with forest and plane separated by 2, 4, 6, 10, and 14 min of arc. Each subject completed four trials per condition.

Apparatus and subjects. The stereograms were generated and presented with a Power Macintosh 7600/120 computer and displayed on a Samtron 17-in. (43-cm) multisync monitor (SC-728SXL). Stereoscopic presentation was achieved through mirrors configured to form a Wheatstone stereoscope. The viewing distance was 100 cm. At this distance, the

² In Soriano et al.'s (1996) experiment, the lines were orthogonal to the collinear implicit edge. Gillam (1987) showed that subjective contours can be seen along two separated collinear edges when the lines are random in orientation length and separation, as was the case in our experiments.

³ In their study, von der Heydt and Peterhans (1989) found that the responses of cells in the monkey visual cortex to abutting gratings were not destroyed when overlap was introduced (presumably because luminance contours were then created), although no subjective contour was visible under these conditions.

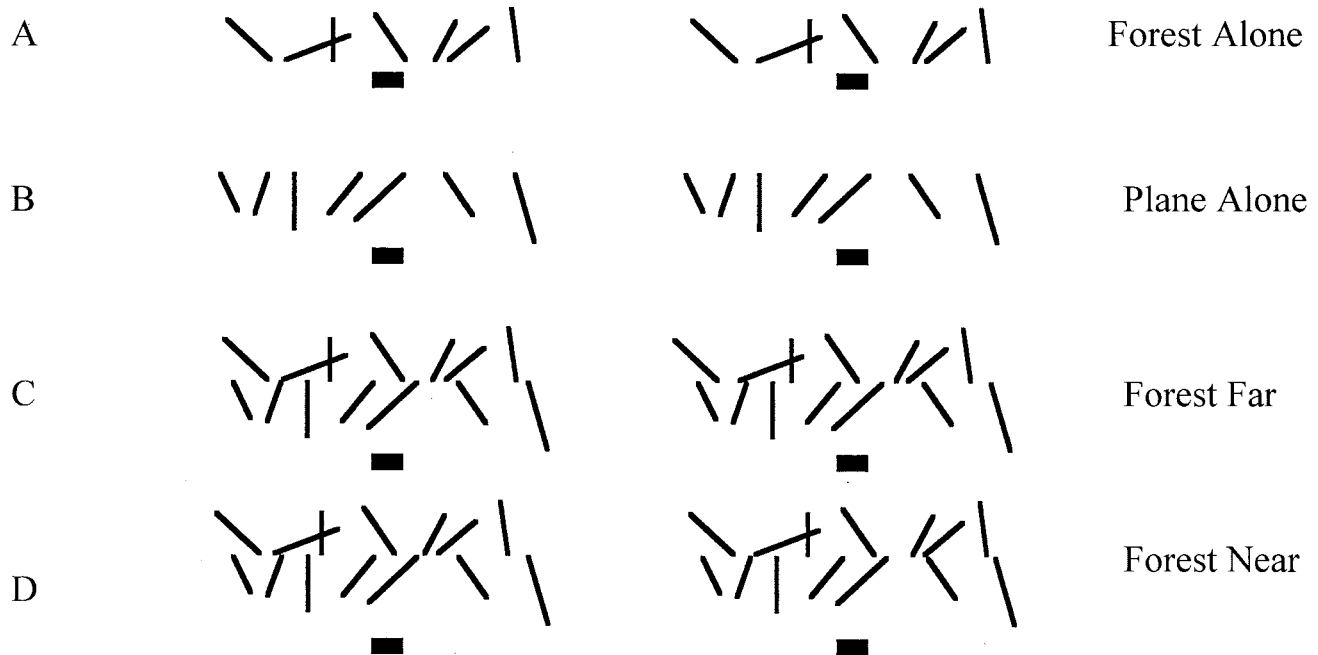


Figure 3. The stereo image pairs should be cross-fused. A: Forest alone. Lines are stereoscopically placed at random depths. B: Plane alone. The lines are coplanar. In neither condition does one see a subjective contour along the horizontally aligned line terminators. C: Forest far. The forest is stereoscopically more distant than the plane, and the line ends of the forest and the plane are abutting. A subjective contour is now evident in the monocular image, which becomes stronger with stereoscopic viewing. D: Forest near. The subjective contour is significantly weaker than in the forest far case and even weaker than in the monocular case. For an explanation, see the text. (Note that if the stereograms are fused through a handheld device, with the left image going to the left eye and the right image going to the right eye, forest far and forest near should be interchanged.)

overall area of the forest set subtended a visual angle of 172 min of arc wide by 35 min of arc high, and the plane set subtended a visual angle of 186 min of arc wide by 42 min of arc high.

Two women and 2 men participated. All were experienced psychophysical observers with normal or corrected-to-normal vision. Two (J.F.K. and T.A.N.) were naive with respect to the stimuli and experimental aims.

Procedure. In each trial, the observer first rated the strength of any subjective contour (in terms of clarity and crispness) on an 8-point scale. On this scale, a rating of 1 indicated a weak, fuzzy contour, and a rating of 7 indicated a sharp, clearly delineated contour. A rating of 0 indicated no perceived contour. If the observer saw more than one subjective contour, he or she was instructed to rate the stronger one.

A rating scale was drawn binocularly, 148 minutes of arc below the display center. Subjects indicated their judgment on this scale with a mouse-controlled arrow that was presented monocularly. If they did not see a contour (rating of 0), the trial ended, and the next trial followed. Otherwise, they moved an arrow up or down until its tip appeared on the subjective edge they had just rated. Between trials, a message was displayed, and the trial began once the mouse button was clicked.

Ratings and localization settings were averaged for each condition and each subject. Localization data were not included in the analysis for any condition in which the subjective contour strength was extremely weak (i.e., was defined as having a rating of 2 or less on more than half of the trials).

Results

Figure 5 shows ratings for each of the 4 subjects individually for the forest alone, plane alone, abutting-forest near, and abutting-

forest far conditions. It can be seen that, in the case of all subjects, there was little sign of a subjective contour for either forest or plane alone. When the plane was placed nearer than the forest, the strength of the subjective contour markedly increased. When the forest was placed nearer, the subjective contour was very weak, despite an equivalent image abutment.

Figure 6 shows mean rated contour strength averaged across the 4 subjects as a function of degree of separation or interleaving. Positive values represent separations of the sets of lines. Negative values represent overlap. Considering the perfect abutment case as allowing the maximum subjective contour strength, there was a surprising degree of tolerance to spatial offset in the two directions. Figure 7 shows the mean probe setting indicating subjective contour location for each subject. On these plots, settings along the edge of the plane would fall along the negatively sloped 45-degree line. Settings along the edge of the forest would fall on the positively sloped 45-degree line. The strong conformity of all subjects to the positively sloping 45-degree line confirmed that the contour always followed the edge of the forest and not the edge of the plane.

Discussion

That the boundaries of the forest and not the plane delineate the subjective contour is in strong opposition to the notion that end-stopped cells cooperate to form subjective contours. Models of

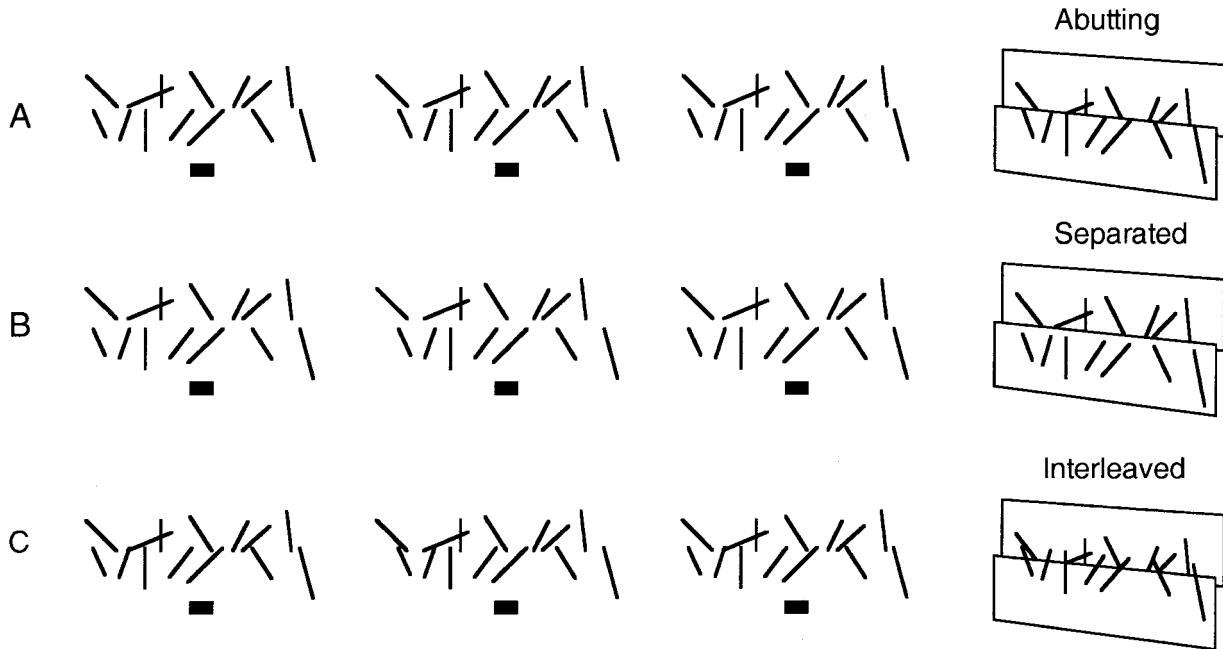


Figure 4. In each row, the left pair when cross-fused produces the forest far condition, and the right pair when cross-fused produces the forest near condition. If a stereoscopic device is used, these conditions will be reversed. Stereograms in the forest far condition. A: Line terminators from both forest and plane abut along a common horizontal line. B: Line terminators are separated. C: Some of the lines from the plane extend beyond and are thus interleaved within the lines of the forest. When either the left or right eye views of the stereograms in Panels B and C are viewed without fusion, there is a marked reduction in subjective contour strength relative to the equivalent views in Panel A. In the stereoscopically fused image, however, when the forest is far, these offset conditions produce very strong subjective contours. These contours appear along the edge of the forest and not along the edge of the plane. Diagrams in the right column illustrate the positions of the subjective contours seen.

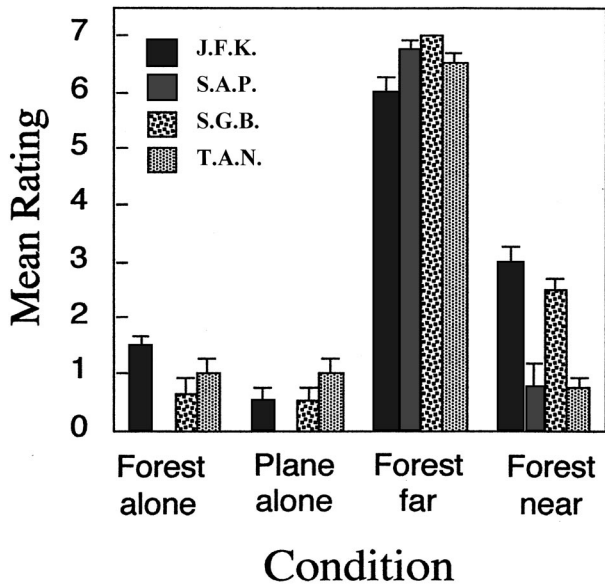


Figure 5. Experiment 1: Mean ratings of subjective contour strength for all of the configurations shown in Figure 3, for subjects J.F.K., S.A.P., S.G.B., and T.A.N.

stereopsis concerned with surfaces (Marr & Poggio, 1976; Nelson, 1975; Sperling, 1970) all postulate cooperative interactions among cells tuned to like disparities. On this basis, greater cooperation would be expected among cells tuned to the same disparity (consistent with the plane) than among cells tuned to different disparities (consistent with the forest), and subjective contours should be stronger along the terminations of the lines of the plane.⁴ In fact, we obtained just the opposite pattern of results. Subjective contours were found to occur much more strongly along the lines of the forest.

In summary, our findings show that in perceiving subjective contours and their associated surfaces, we cannot appeal to the known properties of end-stopped visual neurons or models incorporating their properties. Such models predict the presence of subjective contours when they are absent (forest in front case; Figure 3D) and predict their absence when they are present (interleaved case; Figure 4C). What provides a more satisfactory

⁴ It seems likely that the planar surface would not need to be in the frontal plane to have the effect of eliciting a subjective contour along the ends of the nonplanar lines. Informal observations suggest that a slanted plane in front seems to produce a similar effect. We are grateful to Stephen Palmer for useful comments on the required properties of the occluding surface.

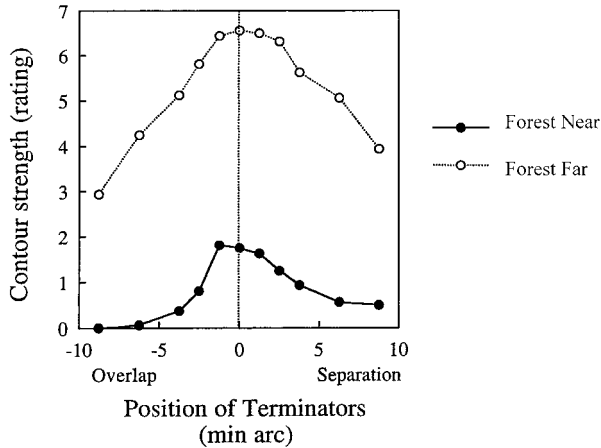


Figure 6. Experiment 1: Mean ratings of subjective contour strength as a function of the vertical shift of the forest relative to the plane. Open circles represent the case in which the forest is in front; filled circles represent the case in which the forest is in back. Note the clear difference between the forest-front and the forest-back cases, confirming the phenomenological observations described in the text. Also, note the only gradual weakening of the subjective contours as either the separation or interleaving is increased. min arc = minutes of arc.

explanation is the view that subjective contours are part of a more explicit process of surface recovery in which the visual system is successfully coding surfaces in the real world, constrained by the nature of images generated by objects and surfaces (Gillam, 1987; Nakayama & Shimojo, 1992).

Experiment 2

In Experiment 1, the forest was always on top and the plane below. Thus, forest and plane arrangements of contours were confounded with above and below positions. It is important for our argument to establish that the forest-near condition is weaker than the forest-far condition regardless of whether forest is above and plane below or vice versa. It would not be surprising, however, if position also had some effect, because occluding surfaces are more commonly below the elements occluded. Experiment 2 used abutting stimuli similar to those used in Experiment 1 with forest in front of–behind the plane combined factorially with forest above–below the plane.

Method

The method required the observer to decide on a given trial which of a pair of stimuli presented has the stronger subjective contour. Two different sets of lines were used. One set (A) was the same as that used in Experiment 1. The second set (B) consisted of different lines but with the same ranges of depth values as the first set. There were thus eight stimuli: Set A, forest above and near; Set B, forest above and near; Set A, forest below and near; Set B, forest below and near; Set A, forest above and far; Set B, forest above and far; Set A, forest below and far; and Set B, forest below and far. Each stimulus was presented in combination with each of the others 10 times for each subject (method of paired comparison).

The two members of each pair were presented sequentially. When the subject indicated his or her readiness, one stimulus appeared. The subject could then press a key on the keyboard to move to the other one. He or she

could go back and forth between the two members of a pair as many times as desired to decide which of the pair had the stronger subjective contour. A mouse button was pressed when the chosen stimulus was present on the screen.

The subjects were 10 individuals who had not taken part in Experiment 1 and were naive with respect to the aims of the experiment. They were shown examples of subjective contours using Kanizsa and Ehrenstein figures before the experiment.

Results and Discussion

The mean probability of each stimulus being chosen over the others is shown in Figure 8. Results were averaged across the two patterns. In calculating these probabilities, we did not include situations in which two forest-far conditions (A and B versions) were pitted against each other or two forest-near conditions (A and B versions) were pitted against each other. The results show, in support of Experiment 1, that by far the most important determinant of subjective contour strength was whether the forest was far or near relative to the plane (probability of .8 vs. .2). An analysis of variance showed a significant main effect for forest far versus near, $F(1, 9) = 24.37, p < .01$. The main effects of (a) above versus below position of forest and plane and (b) pattern (A or B) were not significant.

This experiment shows that the large effect of the near–far status of the forest with respect to the plane is robust under a change in the specific pattern of lines used. Also, this effect is preserved when above–below positions of plane and forest are reversed.

Experiment 3

Subjective contours are habitually demonstrated and studied with flat drawings. This is not unimportant in explaining the popularity of image theories and their concern with two-dimensional (2-D) relationships. We would argue that this is a degenerate case and that subjective contours will be considerably more powerful when an occlusion interpretation is supported by more effective 3-D information about the relationships among surfaces and contours in the scene. Our demonstrations support this claim. The stereoscopic forest-far condition (Figure 3C) produces a much stronger subjective contour than either the left or right eye image on its own, and the forest-near condition (Figure 3D) produces a much weaker subjective contour. However, given the importance of these claims for our scene-based account, it seemed desirable to support them experimentally. Therefore, Experiment 3 was conducted to compare the strength of subjective contours in our 3-D arrays with equivalent flat figures. We predicted that the forest-behind condition would exhibit increased strength of the subjective contour relative to the flat case, whereas the forest-front condition would exhibit reduced strength of the subjective contour relative to the flat case.

Method

The method of paired comparison was used, with four stereograms presented as in the earlier experiments. These stereograms were (a) a stereoscopic forest and plane (as defined in Experiment 1) with the forest nearer than the plane and with the images of plane and forest abutting, (b) the same stimuli but with the plane nearer than the forest (the stereogram just described with eyes reversed), (c) the left eye image of the first stereogram repeated for both eyes, and (d) the right eye image of the first

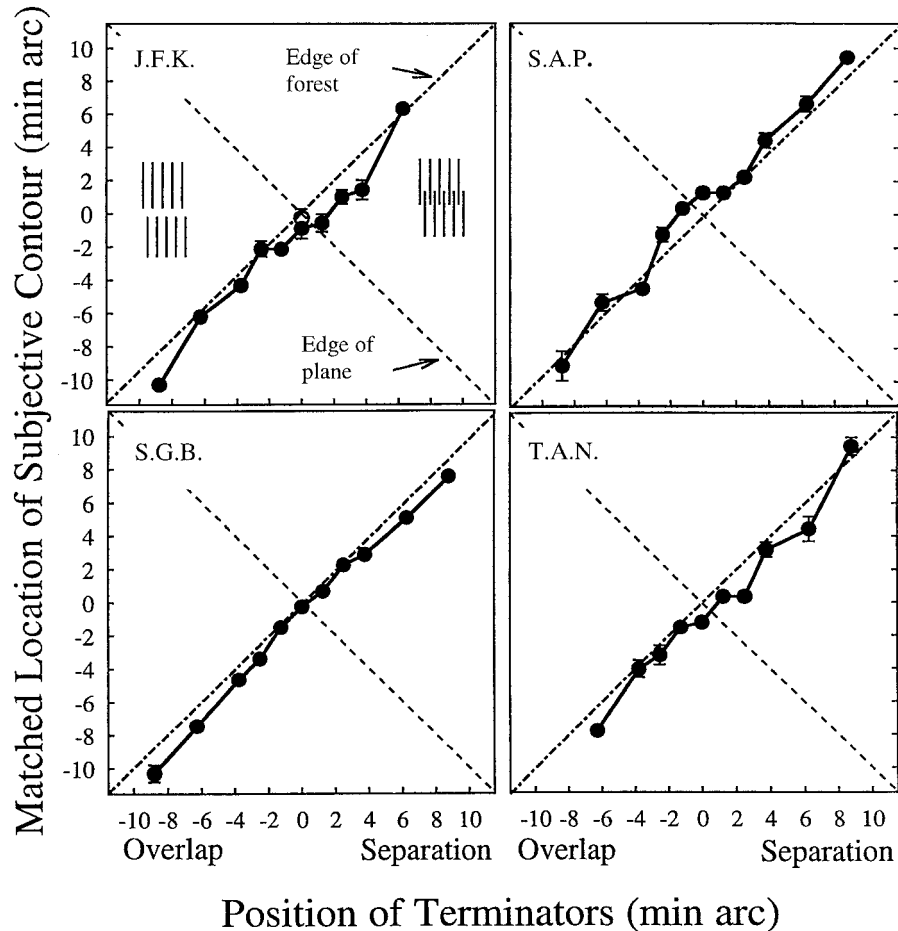


Figure 7. Experiment 1: Perceived location of subjective contours as a function of the shift toward separation (negative numbers) or shift toward increasing overlap (positive numbers), for subjects J.F.K., S.A.P., S.G.B., and T.A.N. Note that the position of the probe follows the forest edge, not the edge of the plane. min arc = minutes of arc.

stereogram repeated for both eyes. In the latter two cases, although viewing was binocular, the two images were identical for both eyes, and thus the percept was of a flat picture mimicking the situation for subjective contour stimuli viewed in books.

The individual sets of lines making up the forest and plane were similar to those used in Experiment 1 in that there were seven lines for the plane and seven for the forest. The specific orientations and spacings were different, but the range of depth values in the forest and the depth between forest and plane were the same as in Experiment 1. The method of presenting stimuli was the same as in Experiments 1 and 2, and the procedure was the same as in Experiment 2. There were 4 subjects, of whom 2 (T.S.C. and B.E.) were naive with respect to the predictions of the experiment. Each condition was presented to each subject 10 times in combination with each of the others. The participant had to indicate which of a pair of stimuli appeared to have the stronger subjective contour.

Results and Discussion

The proportions of choice for each condition in comparison with all others are shown in Table 1. In the case of 3 of the 4 subjects (including both of the naive subjects), the forest-near condition was almost never chosen over the 2-D conditions, and the forest-

far condition was almost always chosen over the 2-D conditions. For the other subject (S.G.B.), this was true for one of the 2-D stimuli but not the other. It is clear from these results that the addition of stereo depth information creates a much more compelling subjective contour than occurs for the image alone. Adding a depth difference between the two sets of abutting lines increases the contour strength relative to the flat case.⁵ Perhaps even more important for our present argument, however, is that adding 3-D layout information also strongly reduced the subjective contour relative to the flat image when the depth information rendered the spatial layout incompatible with an occlusion at the abutment. This

⁵ Informal observations indicate that a strong subjective contour can be obtained even when the forest in the far position is replaced by another plane. This is not surprising because this also represents an ecologically valid case of occlusion. We predict, however, following Gillam (1987), that the forest will produce an even stronger contour, because alignment among a set of nonplanar lines is less likely than for planar lines and therefore supports an occlusion response more strongly. This appears to be supported but will be tested in future experiments.

means that our stereo effects do not merely add richer occlusion information but also can veto an occlusion response.

General Discussion

Our findings can be summarized as follows. First, subjective contours appearing along a set of collinear abutting contour terminators in an image can be either enhanced or virtually eliminated by adding 3-D scene information using stereopsis. Second, when one set of image-abutting contours (situated at variable depths, making the contours nonplanar and incompatible with an occluding surface) was placed stereoscopically nearer than the other set, which was left planar, subjects gave very low ratings of subjective contour appearance (lower than for a flat image). On the other hand, when the depth relationships were reversed and the planar lines were nearer, a very strong subjective contour was seen, stronger than that for a flat image. Third, the subjective contours obtained in the 3-D case behaved quite differently from flat subjective contour figures when the collinear terminations were separated or overlapping rather than abutting. The contour persisted with full strength for several minutes of arc separation or overlap of the plane and the forest when the plane was in the nearer position. It was always seen along the terminations of the forest. This showed for the first time (to our knowledge) that subjective contours are delineated by the occluded rather than the occluding contours.

We have shown that subjective contours at abutting collinear line terminators may be present or absent depending on the 3-D layout of the lines. As previous investigators have indicated, such arrangements of terminators in an image are strongly associated with occlusion in the scene and, as such, constitute an important component of the layout information the visual system uses to detect an occluding surface. In flat arrays in which there is no depth, abutment is sufficient to produce the perception of surface overlay with an accompanying subjective contour (even though the direction of overlay is ambiguous). In 3-D scenes, more vivid subjective contours occur at abutting line terminations but only for

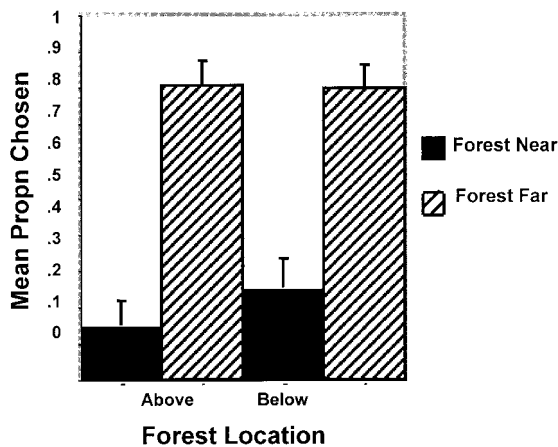


Figure 8. Probability of choice of forest as stronger subjective contour for forest above–below and near–far conditions in Experiment 2. Forest far shows a much stronger probability of being chosen than forest near for both above and below positions of the forest relative to the plane. Propn = proportion.

Table 1
Results of Experiment 3

Condition	Subject			
	B.J.G.	T.S.C.	S.G.B.	B.E.
Monocular LE	.53	.43	.53	.50
Monocular RE	.47	.37	.17	.40
Forest far	1.00	1.00	.97	1.00
Forest near	.00	.02	.33	.07

Note. Values are probabilities (among subjects B.J.G., T.C.S., S.G.B., and B.E.) of a particular stimulus being chosen over other stimuli with respect to subjective contour strength for the forest near, forest far, and two monocular stimuli corresponding to the left eye (LE) and right eye (RE) view, respectively, of the binocular pairs. Forest far was chosen more and forest near less than the monocular stimuli, with one aberration for subject S.G.B. (see text).

layouts that are consistent with occlusion of one set of lines by the other. The critical finding here is that when the nearer set of elements is nonplanar, it is not represented as an occluding surface, and the subjective contour becomes extremely weak or nonexistent.

An interesting and novel finding that emerges from the exploration of 3-D layouts is that although both sets of lines are necessary for a subjective contour to be experienced, there is a clear distinction between the status of the terminations of the occluded lines (the far set) and the terminations of the occluding lines (the near set). Subjective contours are formed at the terminations of the occluded but not the occluding lines, as shown by the separation and overlap results of Experiment 1. Yet, it is not the properties of the occluded set per se that produce the contour. The forest alone does not produce a sense of occlusion and a subjective contour. The necessary stimulus includes nearer planar elements in an appropriate location. Given that the details of the plane do not delineate the contour, we suggest that the exact boundaries of the plane are unimportant. They need only be located in the region of the visual field where they, in combination with end cuts bounding a more distant region, can support the perception of occlusion. This conjecture is supported by Figure 9, which shows the standard forest-far condition from Figure 3C with the planar lines replaced by a set of planar dots. The subjective contour survives the replacement. This is consistent with the view that the plane does not need collinear terminations and does not need to be composed of lines at all. On the other hand, Figure 9B shows that replacing the lines of the forest with nonplanar dots greatly weakens the subjective contour present. To appear occluded and to delineate a subjective contour, the forest requires collinear end cuts.

Can these results be accommodated by the view that end-stopped cell-based models need only incorporate stereo to deal with 3-D occlusion? How could this work? First, stereo would have to record which set of contours is behind, and cooperation would be allowed only among end cuts of that set. Second, such cooperation would need to be immune to the random disparity values of the elements being linked. Third, cooperative processes among the end-stopped cells of the far set would occur only if the contours of the near set were planar. Fourth, under certain conditions of stereo depth (and only under those conditions), abutment

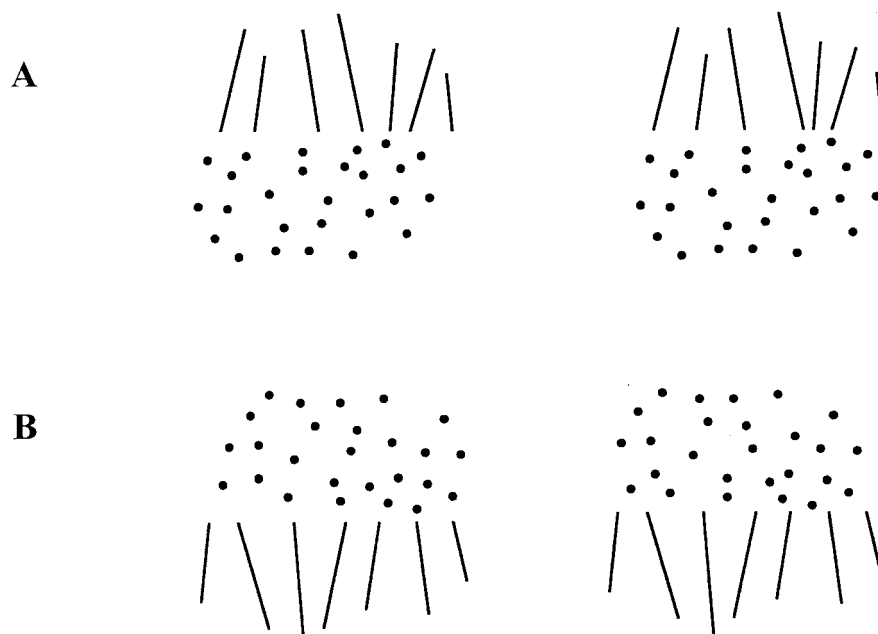


Figure 9. A: Stereogram with the plane composed of dots and the forest composed of lines. Crossed fusion is assumed, causing the plane to appear nearer. A subjective contour can be seen along the edge of an apparent plane whose depth is determined by the dots but whose edge is determined by the terminators of the lines of the forest. B: Plane composed of lines and forest composed of dots. No subjective contour is seen (see text for an explanation).

itself would cease to be critical, with subjective contours occurring for both overlapping and separated sets of contours. The subjective contour in this case cannot be predicted by the luminance contour associated with the region of overlap or separation, because it is precisely located at the edge of the far set of contours and not at some average position within the overlap or separation.

The point to be made here is that, considered purely as a set of stimulus conditions for producing subjective contours, these possibilities seem complicated and arbitrary as well as far removed from any known physiological implementation. It is only when they are considered with respect to their implications for spatial layout that they become less complicated and less arbitrary. This is what we mean by stating that it is at the level of determining surface layout that subjective contours can be explained.

In Figure 10, we have attempted to schematically model the flow of information underlying the perception of subjective contours in a 3-D situation such as the ones we investigated and as summarized in the four points just outlined. Although this schematic model is by no means complete, clearly it could form the basis of a neural network implementation.

Can it be argued that end-stopped cell models are designed for and should only be expected to deal with the 2-D case? The problem with this assertion is that there would then be inappropriate output of the model in 3-D arrays giving rise to the same image, such as the one shown in Figure 3B.

A commentator on an earlier version of this article suggested that end stopping could be considered one cue to occlusion (to which the models considered in the introduction apply) and stereo another, either adding to or subtracting from the output of the end-stopping module. But stereo is not a cue to occlusion as such.

It was important in the present studies only because it determined layout, which is critical in constraining the response of the visual system to collinear line terminators in the image. This is indicated in Figure 11. Figure 11A shows what occurs when the terminators of the forest in Figure 3A are replaced by a set of dots at random depths and the terminators of the plane by a set of planar dots. The nonplanar dots have the same standing disparity with respect to the planar dots as the line terminators in Figure 3C. Stereo information is therefore identical to that present in Figure 3C. But there is no sign of a subjective contour. The same is true of 3-D arrays of dots (see Figure 11B). It appears that there must be collinear terminations of extended objects for perception of occlusion and subjective contours to occur in arrays of the type we are considering. Stereo is important only as a carrier of layout information that places the terminations in a scene context and determines their significance with respect to surface layout.

Finally, we would like to comment on the notion that models of perceptual processes do not have to consider the complexities of perception because these can be attributed to a later cognitive level. We regard it as arbitrary to take specifiable stimulus parameters that have been shown to influence the percept and remove them from consideration with respect to a mechanism by designating them as cognitive. Is layout information cognitive and end-cut information not cognitive? When supposedly later processes determine whether a subjective contour is present, what is the role of the earlier mechanism? Does it create a contour that is removed by a higher process? This is precisely the kind of outcome Marr (1982) has argued against in his principle of least commitment.

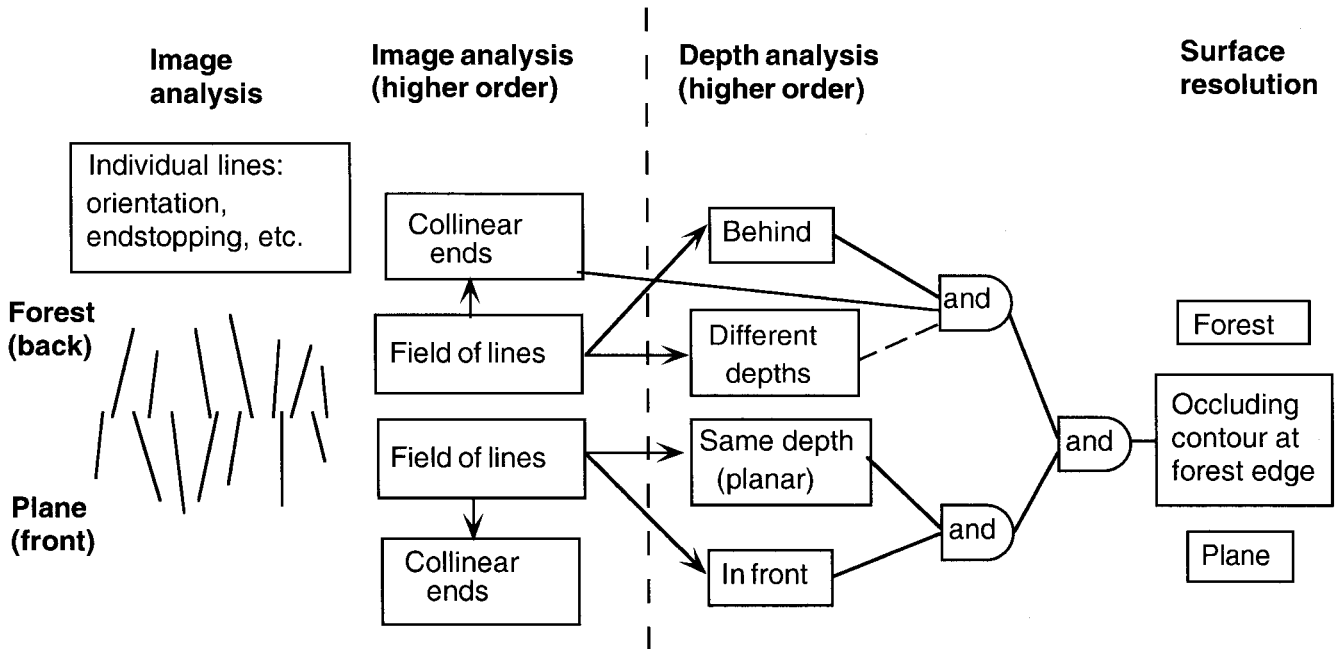


Figure 10. Outline of the processes underlying the perception of subjective occluding contours as indicated by our experiments. We depict four stages. Those to the left of the vertical dashed line are similar to those proposed by previous models of subjective contour formation (e.g., Heydt et al., 1989) and are not sketched in detail. Novel are two later stages, one of depth and the other of surface resolution. AND gates delineate the requirements for a subjective occluding contour to appear at the edge of the forest. The scheme reflects our experimental finding, that collinear end cuts of the back set are critical, but collinear end cuts of the front set are not. In addition, the planar status of the front set is critical. The dashed line indicates that the variable depths of the forest lines may play a role, but we did not test this. We have included only those connections relevant to the creation of an occluding contour.

Again, we do not deny a role for end-stopped cells in vision. The encoding of retinal properties in early vision undoubtedly plays an important part in what is finally perceived. It is likely that end-stopped cells play a role in the perception of line length, and they may well be critical in signaling collinearity of line ends in the image, which we have found to be necessary (although not suffi-

cient) in forming subjective contours across configurations of lines such as the forest and which we have incorporated into our schematic model shown in Figure 10. Our argument is that the perception of surface occlusion and subjective contours cannot be accounted for by the properties of these cells and their cooperation. This is at best just one component of the input to a process by

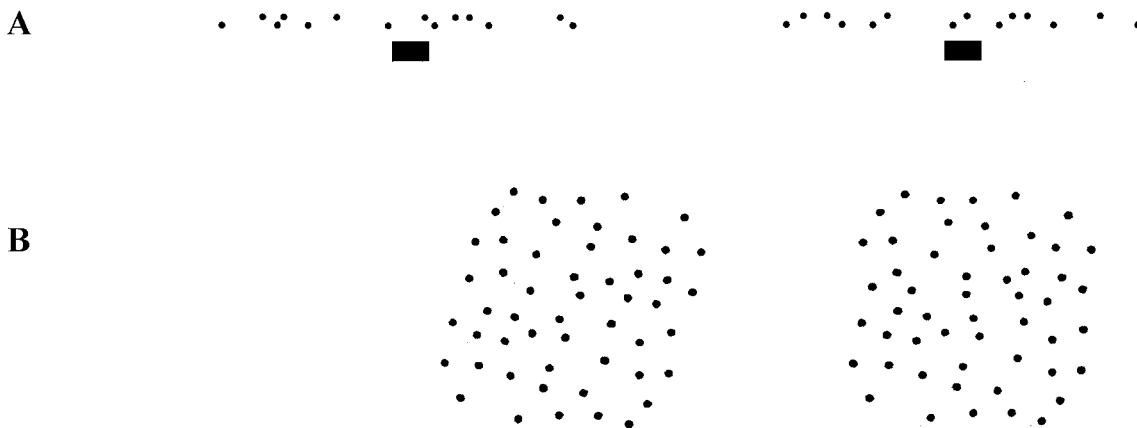


Figure 11. A: Terminations of the forest in Figure 3C replaced with dots. There is no subjective contour. B: Both plane and forest replaced with dots. There is no subjective contour. These demonstrations illustrate that stereoscopic information alone does not produce a subjective contour (see text).

which explicit contours are either organized or not organized into surfaces and whose complex depth relationships are critical in determining whether perceived occlusion and, thus, subjective contours occur at collinear terminations.

References

- Bakin, J. S., Nakayama, K., & Gilbert, C. D. (2000). Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *Journal of Neuroscience*, *20*, 8188–8198.
- Bradley, D. R., & Petry, H. M. (1977). Organizational determinants of subjective contour: The subjective Necker cube. *American Journal of Psychology*, *90*, 253–262.
- Ehrenstein, W. (1987). Modifications of the brightness phenomenon of L. Hermann (A. Hogg, Trans.). In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 35–39). New York: Springer. (Original work published 1941).
- Finkel, L. H., & Edelman, G. M. (1989). Integration of distributed cortical systems by reentry: A computer simulation of interactive functionally segregated visual areas. *Journal of Neuroscience*, *9*, 3188–3208.
- Gillam, B. (1987). Perceptual grouping and subjective contours. In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 268–273). New York: Springer.
- Grosz, D. H., Shapley, R. M., & Hawken, M. J. (1993, October 7). Macaque V1 neurons can signal illusory contours. *Nature*, *365*, 550–552.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. *Psychological Review*, *92*, 173–211.
- Harris, J. P., & Gregory, R. L. (1973). Fusion and rivalry of illusory contours. *Perception*, *2*, 235–247.
- Heitger, F., Rosenthaler, L., Heydt, R. von der, Peterhans, E., & Kübler, O. (1992). Simulation of neural contour mechanisms: From simple to end-stopped cells. *Vision Research*, *32*, 963–981.
- Heydt, R. von der, & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex: I. Lines of pattern discontinuity. *Journal of Neuroscience*, *9*, 1731–1748.
- Heydt, R. von der, Peterhans, E., & Baumgartner, G. (1984, June 15). Illusory contours and cortical neuron responses. *Science*, *224*, 1260–1262.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, *195*, 215–243.
- Kanizsa, G. (1974). Contours without gradients or cognitive contours? *Italian Journal of Psychology*, *1*, 93–112.
- Lawson, R. B., Cowan, E., Gibbs, T. D., & Whitmore, C. G. (1974). Stereoscopic enhancement and erasure of subjective contours. *Journal of Experimental Psychology*, *103*, 1142–1146.
- Marr, D. (1982). *Vision*. San Francisco: Freeman.
- Marr, D., & Poggio, T. (1976, October 15). A cooperative computation of stereo disparity. *Science*, *194*, 283–287.
- Nakayama, K., & Shimojo, S. (1992, September 4). Experiencing and perceiving visual surfaces. *Science*, *257*, 1357–1363.
- Nakayama, K., Shimojo, S., & Ramachandran, V. S. (1990). Transparency: Relation to depth, subjective contours, luminance, and neon color spreading. *Perception*, *19*, 497–513.
- Nelson, J. I. (1975). Globality and stereoscopic fusion in binocular vision. *Journal of Theoretical Biology*, *49*, 1–188.
- Ramsden, B. M., Hung, C. P., & Roe, A. W. (2001). Real and subjective contour processing in area V1 of the primate: A cortical balancing act. *Cerebral Cortex*, *11*, 648–665.
- Redies, C., Crook, J. M., & Creutzfeldt, O. D. (1986). Neuronal responses to borders with and without luminance gradients in cat visual cortex and dorsal lateral geniculate nucleus. *Experimental Brain Research*, *61*, 469–481.
- Rock, I., & Anson, R. (1979). Illusory contours as the solution to a problem. *Perception*, *8*, 665–681.
- Schumann, F. (1900). Beiträge zur Analyse der Gesichtswahrnehmungen. Erst Abhandlung. Einige Beobachtungen über die Zusammenfassung von Gesichtseindrücken zu Einheiten [Contributions to the analysis of visual perception: First paper. Some observations on the combination of visual impressions into units]. *Zeitschrift für Psychologie*, *23*, 1–32.
- Sheth, B. R., Sharma, J., Rao, C., & Sur, M. (1996, December 20). Orientation maps of subjective surfaces in visual cortex. *Science*, *274*, 2110–2115.
- Soriano, M., Spillmann, L., & Bach, M. (1996). The abutting grating illusion. *Vision Research*, *36*, 109–116.
- Sperling, G. (1970). Binocular vision: A physical and neural theory. *American Journal of Psychology*, *83*, 461–534.
- Spillmann, L., & Dresch, B. (1995). Phenomena of illusory form: Can we bridge the gap between levels of explanation? *Perception*, *24*, 1333–1364.
- Treisman, A., Cavanagh, P., Fischer, B., Ramachandran, V. S., & Heydt, R. von der. (1990). Form perception and attention: Striate cortex and beyond. In L. Spillmann & J. S. Werner (Eds.), *Visual perception: The neurophysiological foundations* (pp. 272–315). San Diego, CA: Academic Press.

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