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Amodal representation of occluded surfaces: role of invisible stimuli in apparent motion correspondence

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Abstract. A series of demonstrations were created where the perceived depth of targets was controlled by stereoscopic disparity. A closer object (a cloud) was made to jump back and forth horizontally, partially occluding a farther object (a full moon). The more distant moon appeared stationary even though the unoccluded portion of it, a crescent, changed position. Reversal of the relative depth of the moon and cloud gave a totally different percept: the crescent appeared to flip back and forth in the front depth plane. Thus, the otherwise-robust apparent motion of the moon crescents was completely abolished in the cloud-closer case alone. This motion-blocking effect is attributed to the 'amodal presence' of the occluded surface continuing behind the occluding surface.

To measure the effect of this occluded 'invisible' surface quantitatively, a bistable apparent motion display was used (Ramachandran and Anstis 1983a): two small rectangular-shaped targets changed their positions back and forth between two frames, and the disparity of a large centrally positioned rectangle was varied. When the perceived depths supported the possibility of amodal completion behind the large rectangle, increased vertical motion of the targets was found, suggesting that the amodal presence of the targets behind the occluder had effectively changed the center position of the moving targets for purposes of motion correspondence.

Amodal contours are literally 'invisible', yet it is hypothesized that they have a neural representation at sufficiently early stages of visual processing to alter the correspondence solving process for apparent motion.

1 Introduction

We live in a three-dimensional world, full of nontransparent objects and surfaces. As a consequence, objects occlude other objects, and the boundaries and surfaces of occluded objects are often only partially visible. Thus, occlusion is one of the most fundamental facts about vision in daily life and is decisive in determining how light from the physical world reaches our eyes. Consequently, it sets a major obstacle which the visual system must overcome to accomplish its goal of identifying three-dimensional objects in the environment from purely viewer-centered visual inputs.

Recent studies in our laboratory suggest that the visual system takes account of occlusion-related real-world constraints for a wide variety of visual processes. Thus, occlusion has a role in perceptual grouping and object recognition (Nakayama et al 1989), solving the motion ambiguity problem (the 'aperture problem'; Shimojo et al 1989), seeing the depth of moving objects when targets are not seen simultaneously by both eyes (Shimojo et al 1988), seeing transparency and color spreading (Nakayama et al 1990), seeing depth and avoiding rivalry when regions in one image have no counterpart in the other (Shimojo and Nakayama 1990), and seeing subjective contours from unpaired monocular dots (Nakayama and Shimojo 1990). We now report a series of demonstrations and experiments which suggest that the 'amodal presence' (Michotte 1954; Kanizsa 1979) of an occluded surface strongly influences apparent motion.

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1.1 *Modal versus amodal contours*

In his important monograph, Kanizsa (1979) made the critical distinction between two types of contours which are not present in an image but which are perceptually 'completed' across image regions: *modal* versus *amodal* contours, corresponding to *occluding* versus *occluded* contours respectively. Probably the best way to obtain a graphic understanding of this distinction is to view stereograms where these two types of contours trade places in a particularly vivid way. Figure 1a is a stereogram designed so that both crossed and uncrossed free-fusers can experience opposite signs of stereoscopic depth, depending on whether the left and center images or the center and right images are fused. Viewed monocularly, each half-image usually appears as a flat cross-like figure. Addition of disparity, however, changes this dramatically. Different sets of subjective contours are formed, merely by the reversal of binocular disparity.

Vertical subjective contours are seen when the vertical bar is seen in front, whereas horizontal subjective contours are seen if the disparity is reversed. According to the theoretical framework outlined by Kanizsa (1979), subjective contours represent a visible or 'modal' completion, indicating an occluding edge. Kanizsa also outlined a more subtle yet complementary visual representation, the 'amodal' or occluded contour, an edge which continues behind an occluding surface. Although this contour is literally 'invisible', observers are aware of its continuation. Thus, when the vertical bar is seen in front (figure 1b, right), one is 'aware' that there is a horizontal contour providing continuity for the horizontal bar in back. Alternatively, when the horizontal bar is seen in front (figure 1b, left), one is now aware that there must be a vertical contour providing continuity for the vertical bar.

Physiological evidence has indicated a neuronal correlate for modal (or subjective) contours as early as area 18 in the primate visual system (Heydt et al 1984, 1989; Peterhans et al 1989). In addition, psychophysical evidence indicates that subjective contours can have functional roles which are comparable to the roles of real (physically-defined) contours (Ramachandran et al 1973; Paradiso et al 1989). The results of such studies suggest that modal or subjective contours are a consequence of vision-specific early cortical processing, rather than higher-level cognitive inference or reasoning.

The existence of and the level of representation for amodal contours, however, are much less established. Since these contours are literally invisible, one might suspect that, unlike modal contours, they may be based upon some kind of cognitive inference

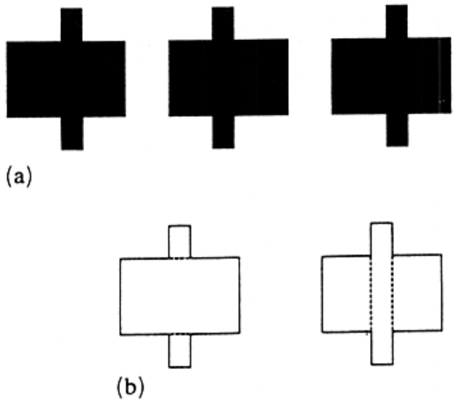


Figure 1. Amodal versus modal contours. (a) A stereogram specifically designed so that both cross-fusers and uncross-fusers can observe both signs of depth between surfaces. (b) Illustrations of modal contours (dashed lines) when the vertical limb appears in front (the right figure), and when it appears in the more distant plane (the left figure).

or reasoning regarding the spatial layout of the scene. Such processes are generally thought to occur at much higher levels of cortical processing. Yet there have been some indications from adaptation studies that occluded surfaces might have an early visual representation (Weisstein 1970; Gyoba 1979). Furthermore, in several recent papers, we have suggested that amodal presence is required for the specifically visual task of pattern recognition (Nakayama et al 1989b) and motion perception (Shimojo et al 1989), indicating that the amodal representation is indeed 'visual' because it is required for the solution of specifically visual tasks. In this paper, we address this issue by asking whether amodal presence plays a role in a yet another visual task, solution of the correspondence problem in apparent motion.

1.2 *The 'moon and cloud' effect: amodal presence blocks apparent motion*

Figure 2 illustrates what we call the 'moon and cloud' demonstration. The darker region (cloud) has a crossed disparity relative to the brighter region (moon), so that it appears as if the cloud were in front of the moon, occluding it. When the cloud changes its horizontal position relative to the moon (figures 2a and 2b) quickly and repeatedly without changing the relative disparity (ie the cloud is always in front), there is a clear impression of the cloud moving and the moon *staying stationary* behind it. This and the following observations were unanimously agreed upon by more than ten subjects (half naive as to the aims of our experiments). This occurred for disparities which ranged from 3.8 to 15.2 min visual angle at an observation distance of 70 cm.

Figure 3 illustrates the reversed-depth case of the moon and cloud demonstration in which the moon segment is in front of the cloud. Quick alternating exposures to figures 3a and 3b lead to a completely different perception—the unoccluded portion of the moon, now a crescent in front, appears to flip back and forth between the left and the right positions in front of the cloud. Note that figures 2 and 3 are identical except for the relative disparities of the two regions.

In terms of providing an interpretation of these findings, it seems reasonable to assume that "a crescent moving in front" is the only plausible interpretation of the visual input for the moon-in-front case (figure 3), whereas there is an apparent ambiguity in the moon-behind case. It can be either "a moving crescent" or "a full moon stationary with a moving cloud partially occluding it". Thus, it could be said that the visual system

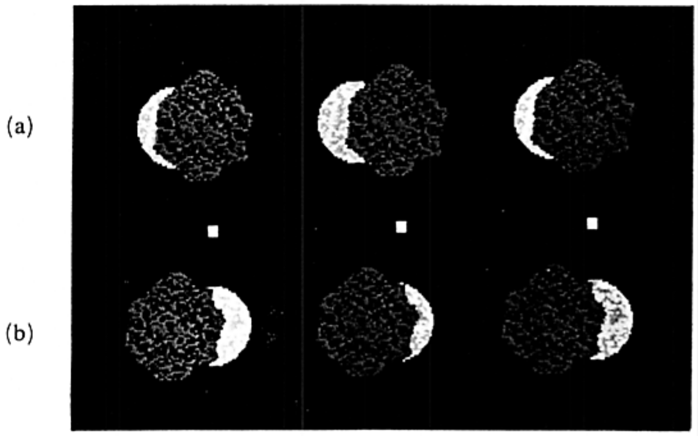


Figure 2. 'Moon and cloud' demonstration. The top (a) and bottom (b) figures are presented alternately. When the moon appears in the more distant plane (by a cross-fuser fusing the left two images, and by an uncross-fuser fusing the right two images), the moon is perceived as a stationary full moon.

is organized such that the "moon stationary" interpretation is *chosen* in the moon-behind case (figure 2). The idea behind such a choice, however, is somewhat at odds with the notion that apparent motion is a robust visual phenomenon: the appearance of an object in one frame followed by the object displaced in another frame ordinarily leads to the perception of apparent motion. Thus, an explanation would seem to be required as to why the partially visible segments of the moon do *not* appear to move in the moon-behind case.

Several additional observations under various conditions are also relevant:

(i) *Zero-disparity case.* When there was no relative disparity between the moon and cloud, the observation was similar to the moon-behind case (figure 2); ie the cloud appeared to move in front of the moon which appeared stationary, although there was an occasional weak impression of motion of the moon crescents. Note that even when the disparity is zero. there is a configurational occlusion cue (T-junction) so that the cloud appears as slightly in front of the moon in each frame (see Helmholtz 1909/1962; Guzman 1968). This suggests that it is not disparity per se, but general depth information that determines whether the moon appears to move or not.

(ii) *Cloud-invisible case.* By simply deleting the cloud from the zero-disparity stimuli, without changing the remaining moon regions, we could again create a vigorous apparent motion of the moon. This is consistent with our notion that configurational occlusion cues as well as disparity can abolish apparent motion of the object behind.

(iii) *Effects of a gap.* When there was a visible gap between the moon and cloud regions, a vigorous apparent motion of the moon was observed even in the moon-behind and zero-disparity cases. The gap could be as small as, or even less than, 3 min visual angle.

(iv) *Rectangular configuration.* In addition to the moon and cloud configuration, two rectangles of different heights were also used. Various disparity and height relationships between the two surfaces were tested. Blocking of apparent motion was again found, although more ambiguous than in the original moon and cloud configuration. (This weakness of the blocking effect may be attributed to the more regular rectangular configuration of the visible part of the target.) Also, this motion blocking effect was present *only when* the front rectangle was taller so that the horizontal contours of the more distant rectangle were end-stopped or 'T-junctioned' by the vertical edges of the

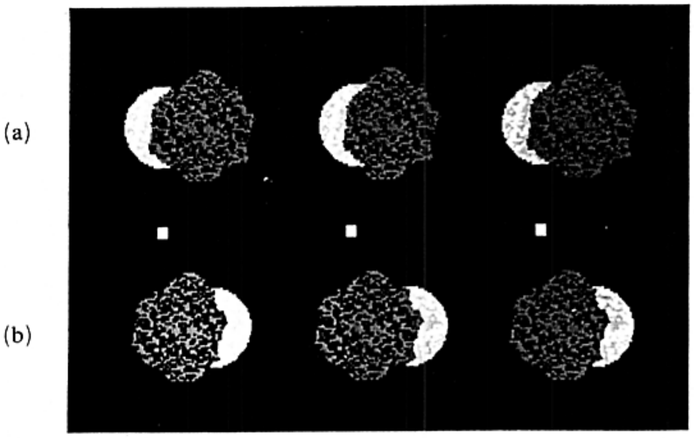


Figure 3. 'Moon and cloud' reversed-depth case. Similar to the demonstration in figure 2 except that the relative depth between the moon and the cloud is reversed (cross-fusers should fuse the left two images, uncross-fusers the right two images). The moon is perceived as a crescent flipping back and forth in front of the cloud when the top (a) and bottom (b) figures are presented alternately.

closer and occluding rectangle (see figure 4). The effects of disparities were qualitatively comparable to those in the moon and cloud demonstration.

These findings are generally consistent with previous demonstrations by other authors (Sigman and Rock 1974; Ramachandran and Anstis 1983a, 1986; Anstis and Ramachandran 1985). In these earlier studies, where monocular depth cues were used, it was found that targets which were seen as continuing behind another target tended to have their apparent motion attenuated. Considering all these observations, we can ask what it is about these configurations that inhibits apparent motion. Clearly, depth is important. In order for apparent motion to be blocked, the object in question must be seen as behind something else. Depth alone, however, is not sufficient because apparent motion is not blocked when there is a gap in the moon and cloud configuration. What appears to be necessary is that the more distant object be seen as occluded by the closer object and continuing behind it.

Here we return to our earlier discussion on the role of amodal completion in visual processing. Even though only a part of the moon is visible in each frame, the full moon can appear as amodally completed and present in the plane behind. Thus, without the visibility of the occluder, or without the benefit of T-junctions in the zero-disparity case, or with the existence of the gap, there is no opportunity for amodal completion and apparent motion is not blocked.

We now go on to describe our experiments on the effect of amodal presence on apparent motion correspondence.

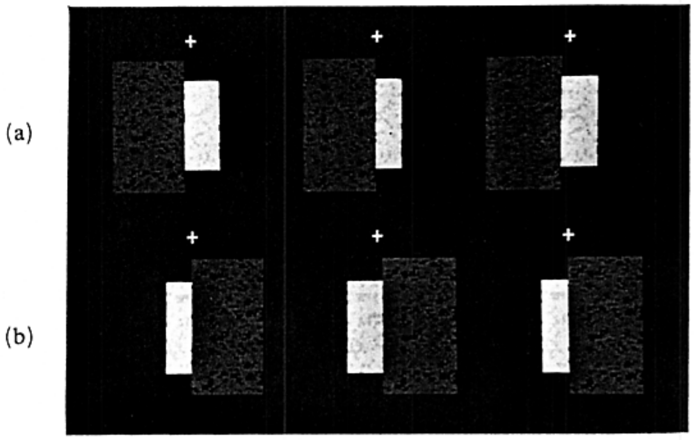


Figure 4. Rectangular version of the 'moon and cloud' demonstration.

2 Experiment 1: Amodal presence affects the correspondence solving processes

So far we have demonstrated the crucial importance of occlusion cues, such as binocular disparity and T-junctions, on apparent motion processes. In particular, our moon and cloud demonstration suggests that occlusion-related cues determine amodal presence or extrapolation, which then determines whether the visual target is perceived as moving or stationary. Even though the phenomena described are robust and immediate, it could be argued that the evidence favoring the existence of amodal presence is based mainly on phenomenological observations where 'reasoning' might possibly bias the perceived motion. Here we deal with this problem by designing a more quantitative study where it is difficult to see how spatial reasoning on the part of the observer would yield the predicted result.

The experiment that we describe concerns the correspondence solving processes for apparent motion. As shown in figure 5, when a single target is presented at time t_1 and another single target is presented at time t_2, correspondence between the two frames, or identity of the target across the frames, is obvious, and there is no room for ambiguity. However, when a pair of targets is presented at different positions in two frames, as illustrated in figure 5b, there are two equally plausible solutions to the correspondence problem, leading to either a horizontal or a vertical direction of perceived motion (illustrated in figure 5c). Relative dominance (percentage of horizontal as opposed to vertical motion) can be manipulated by changing the relative center-to-center length of the motion 'trajectory' in the horizontal and vertical directions (Gengerelli 1948). We call this the H/V ratio. Large H/V ratios favor vertical motion; smaller H/V ratios favor horizontal motion (see the solid curve in figure 6). This occurs because a relatively short spatial separation between frames has the advantage of trajectory facilitation or 'affinity' in the solution of the correspondence problem for motion (Ullman 1979; Burt and Sperling 1981). As such, there should be a critical H/V ratio at which the direction of perceived motion is equally likely to be horizontal or vertical (indicated by the filled arrow in figure 6).(1) Our research strategy was to measure this critical H/V ratio psychometrically, by means of a forced-choice procedure, to evaluate quantitatively the functional strength of amodal presence during apparent motion.

Consider the situation depicted in figure 7a, where an occluding surface is added between and in front of the motion targets. If we are correct in assuming that such a configuration would lead to amodal continuation of the targets behind the occluder (figure 7b), then we are faced with an interesting experimental situation. For purposes of motion correspondence, might not the continuation of a surface behind an occluder mean that the positions of the jumping targets be effectively displaced? Certainly this would be the case if we thought of the position of a target as being defined by its center of mass of both visible and invisible portions. It necessarily follows that the effective

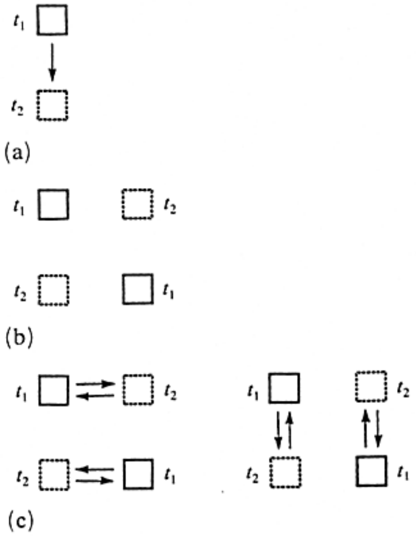


Figure 5. Bistable apparent motion display. Targets are presented alternately at time t_1 and t_2. (a) Unambiguous single pair. (b) Stimulus for bistable motion. (c) Illustration of bistable perception of motion. Arrows indicate direction of motion.

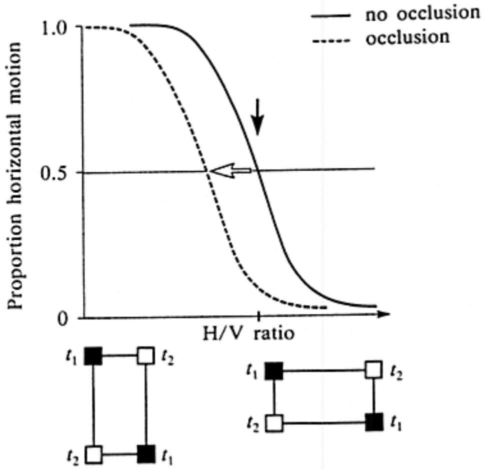
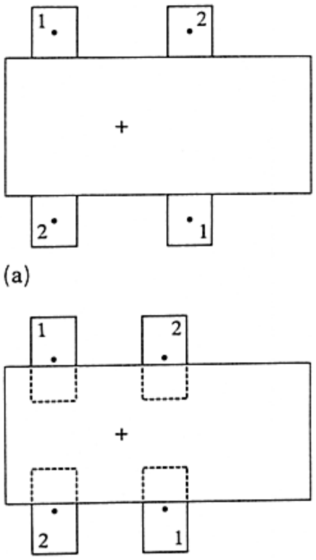


Figure 6. Theoretical motion dominance as a function of the horizontal/vertical (H/V) distance ratio, filled arrow indicates the critical H/V ratio in the no-occlusion case, where horizontal and vertical motion are equally likely. Empty arrow indicates the expected shift as a consequence of occlusion.

(1) It has been shown that the critical H/V ratio is somewhat smaller than 1 (Ramachandran and Anstis 1983a), indicating a bias towards vertical motion.

center of such a composite target (visible and invisible combined) can only be displaced vertically, making the centers closer in that direction than would appear from just the visible portions. Such an amodal completion would be expected to shift the motion dominance function leftward, indicating a greater bias towards vertical motion (see dashed line in figure 6).

To make a systematic assessment of the influence of amodal completion in the correspondence solving process for apparent motion, we used a variety of conditions. First, we placed the rectangular occluder in *crossed* disparity so that it would appear in front of the flashing targets, providing an opportunity for amodal completion to occur behind the occluder. This was compared to three control conditions. For our primary comparison, we presented the same rectangle in *uncrossed* disparity so that it appeared in back of the targets and would not allow amodal completion. In addition, we used conditions where the rectangular occluder was at zero disparity and where the occluder was absent. It should be emphasized that the primary comparison was between the crossed and uncrossed conditions because all stimulus parameters were identical except for the sign of disparity.



(a)

(b)

Figure 7. Visible targets and functionally equivalent visible surfaces. (a) The control condition where the targets alternate between position 1 and position 2 and where the central rectangle is seen as behind the jumping squares so that there is no opportunity for amodal completion. The figure is drawn to scale and represents the horizontal and vertical separation at which there is no horizontal or vertical motion bias. Thus the ratio of the distances between the target centers (dots) represents the critical H/V ratio. (b) The case where the central rectangle is in crossed disparity and is seen in front of the visible squares, thereby providing the opportunity for amodal completion behind it. Dashed lines represent the functionally equivalent surface, ie the size of the visible surface which would be required to maintain the critical H/V ratios seen in the control conditions.

2.1 *Method*

2.1.1 *Subjects and apparatus.* Six subjects, including three naive as to the aims of the experiment, participated. All had normal stereopsis. Stimuli were presented on a CRT display driven by a Commodore Amiga computer. A prism haploscope was used to separate retinal images between the eyes.

2.1.2 *Stimuli and procedure.* Four types of stimuli were used; (i) no occluder present (figure 5b), (ii) occluder with zero disparity, (iii) occluder with uncrossed disparity, and (iv) occluder with crossed disparity (see the inset of figure 8 for the configuration of the stimulus with occluder). The apparent motion targets were white (luminance approximately 120 cd m^{-2}) and subtended 41 min by 47 min visual angle at the observation distance of 95 cm. The vertical center-to-center separation (motion trajectory) was kept constant (2.9 deg) across the four stimulus conditions, but the horizontal separation was one of the following: 1.1, 1.4, 1.7, 2.0, 2.2, 2.5, or 2.8 deg. Thus, the H/V distance ratio varied from 0.39 to 0.98. The rectangular gray occluder was 2.1 deg by 4.7 deg in size, and its disparity relative to the targets was 16.8 min uncrossed, zero, or 16.8 min crossed. Its luminance was intermediate (approximately 40 cd m^{-2}), and it was textured by white dots to enrich the disparity cues. The background was 'black' (approximately 6 cd m^{-2}). A fixation cross 14 min by 17 min in size was added at the vertical center, and 1 deg lateral to the center of the left targets. To maintain stable binocular convergence, a blank field with the same binocular fixation cross was presented between trials. The motion stimulus consisted of a series of frames. The duration of each frame was 300 ms and six frames (three repetitions of the single motion pair) were presented for each trial. Thus, the duration of the motion display was 1.8 s.

A trial was initiated when the subject hit one of two buttons. After presentation of the apparent motion stimulus the subject made a judgement as to whether vertical or horizontal motion was dominant at the end of the 1.8 s display period, and accordingly chose one of the buttons to hit. All the subjects, including the naive ones, reported that they encountered a perceptually ambiguous motion only extremely rarely. As such, the task was very easy and judgements were made very quickly.

A block of twenty-eight trials with the no-occluder stimulus on its own was given at the beginning of the experiment to ensure that the subject experienced occasional reversals of motion dominance and fully understood the task. It consisted of four repetitions for each of the seven steps of horizontal center-to-center separation in a pseudorandom order. Then, the subject was given a second, practice, session consisting of one hundred and sixty-eight trials with all four types of stimulus (six repetitions × seven separations × four types of stimulus) in a pseudorandom order. This ensured that an identical combination of separation and stimulus type was not repeated more than twice in a row. We used this rather lengthy practice session to overcome the existence of hysteresis, the tendency of the visual system to resist alternation of motion dominance, particularly during the initial stages of an experiment. Subjects usually saw only either horizontal or vertical motion across many trials, with the direction almost unaffected by the wide range of H/V ratios used (also see Ramachandran and Anstis 1983a). This hysteresis would certainly have obscured the measurement of a critical H/V ratio. Fortunately, however, our pilot data also suggested that the hysteresis effect decays within one hundred to one hundred and fifty trials.

The main part of the experiment consisted of five sessions, each of which was equivalent in length and context to the practice session. Each session took about 15 min, and a break of at least 5 min was given between sessions. A maximum of three sessions were performed by a single subject in a single day. Data collection was completed within 1 week for each subject.

2.2 *Results and discussion*

Figure 8 shows the proportion of responses in which motion was judged to be horizontal, for the four stimuli, plotted as a function of H/V ratio for each individual subject. H/V ratios are based on the center-to-center distances between targets. As should be clear from the figure, the overall tendencies in the data were consistent with our occlusion predictions: The psychometric function for the crossed-disparity (occluder in front) condition was shifted leftwards relative to all other conditions. In other words, there was a general tendency in the crossed-disparity condition to show more vertical (less horizontal) dominance than in the other conditions, particularly at intermediate H/V ratios.

This conclusion was supported by further analyses. Probit analysis (Finney 1971) was applied to each condition for each subject to obtain the best-fitting psychometric function. From this the critical H/V ratio, where the proportion 'horizontal' responses is 0.5, could be obtained. These individual critical ratios were then pooled across subjects within each condition. Figure 9 shows the mean critical H/V ratio in each condition, together with the standard error across subjects. As is clear from the figure, the mean critical H/V ratio in the crossed-disparity rectangle condition is significantly smaller than in the other three conditions.

The results were thus highly consistent with our occlusion predictions: the effects of relative distance on correspondence solving in motion were susceptible to the occlusion-related three-dimensional layout. In particular, the consistent and significant difference observed between the crossed-disparity and uncrossed-disparity conditions supported our hypothesis. Again, note that this was the most critical comparison because all parameters, including the two-dimensional configurations and the amount of interocular disparity, were identical except for the sign of disparity.

The lack of any difference between the zero-disparity case and the no-rectangle control is of some interest because one might expect that monocular occlusion cues (T-junctions) would enable the target to 'leak' amodally behind the occluder. Yet, it should be remembered that the viewing in our experiments was binocular. Thus,

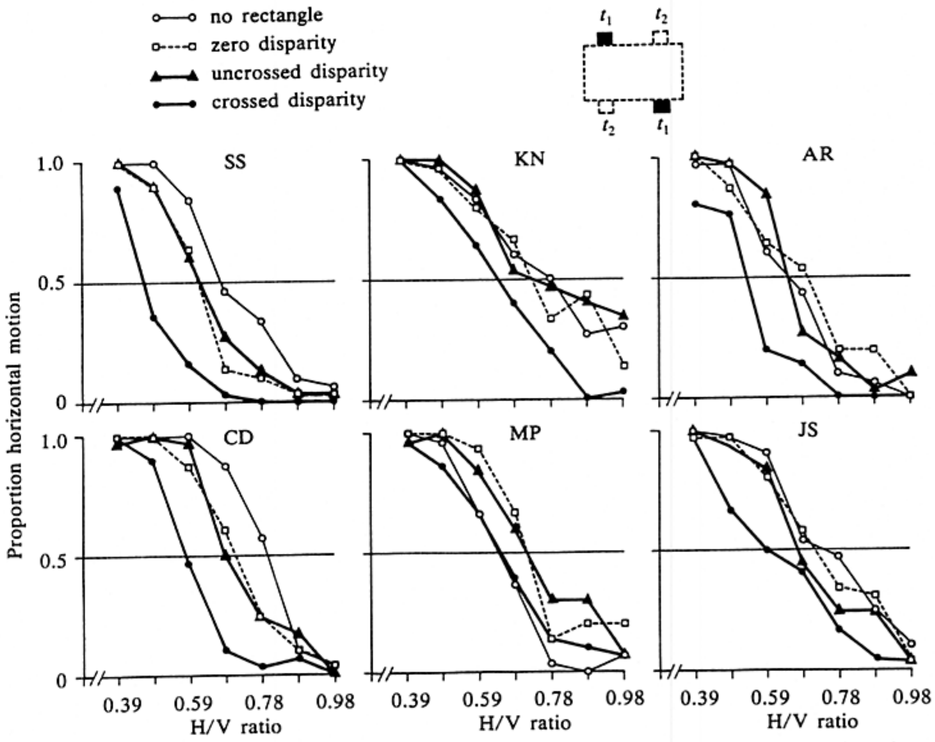


Figure 8. Proportion of responses in which horizontal motion was seen, as a function of the horizontal/vertical (H/V) distance ratio, in experiment 1. Data obtained in the four conditions are shown together for each of the six subjects. Each point reflects the data from thirty trials. The inset shows stimulus configuration in the with-occluder case.

stereopsis signalled that the targets and the rectangle were in the *same* depth plane, perhaps overriding monocular occlusion cues. That there was no amodal 'leakage' indicates the weakness of monocular cues relative to disparity cues in this situation. A similar finding was also obtained when amodal completion was examined in the solution to the aperture problem for motion (Shimojo et al 1989).

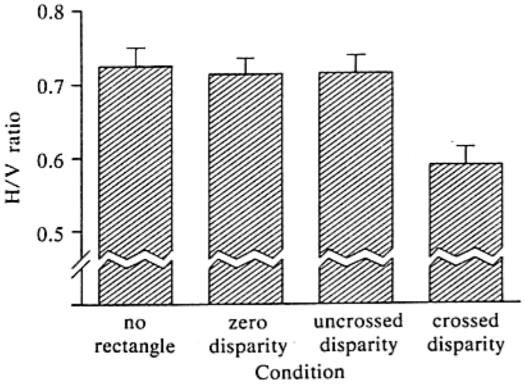


Figure 9. Mean critical horizontal/vertical (H/V) distance ratios. The critical H/V ratio was calculated by probit analysis, and mean ratios across subjects in each of the four conditions are shown here. The bars denote standard errors.

3 Experiment 2: Occluded contour versus occlusion of motion trajectory hypotheses

We have argued for the existence of amodal 'leakage' or extrapolation of a target's functional presence behind the occluder (figure 7b), such that the center position of the moving target is shifted vertically and thus biases the correspondence solving processes of apparent motion.

However, there is another conceivable explanation that is also related to occlusion, which we refer to as the *occlusion of motion trajectory* hypothesis. This idea is based on the fact that it is only in the crossed-disparity (occluder in front) condition that there is 'ecological' consistency regarding the trajectory of apparent motion and the continuous visibility of the object along this trajectory. In other words, there is often a physical inconsistency in most apparent motion experiments because an object moves across a space and yet it does not occlude objects along its path. By implication, motion interpretations that do not involve such an inconsistency might be expected to be favored. Such a consideration might possibly explain why vertical motion is preferred by the visual system in our crossed-disparity condition. Even though this interpretation is still related to occlusion, the underlying mechanism to explain such a process is considerably different from the one which we have proposed. Thus it was of importance to design an experiment to decide between these two alternatives.

Our choice of stimulus configuration for this experiment is illustrated in figure 10. The targets were disk-shaped instead of rectangular-shaped, so that amodal leakage or extrapolation of the target behind the occluder would be less likely (cf figure 7b). And yet, virtually all of the vertical trajectory of motion is covered by the occluder when the occluder disparity is crossed, just as in the original configuration in experiment 1. Thus, predictions from the two hypotheses are different: the occluded contour hypothesis predicts that the asymmetric disparity effects should now disappear so that all four stimulus conditions should yield very similar motion dominance functions because there is no amodal completion in any of the conditions. On the other hand, the occlusion of motion trajectory hypothesis predicts that the disparity effects should be essentially identical to those observed in experiment 1 (the crossed-disparity condition would enable the trajectory to continue behind the occluder).

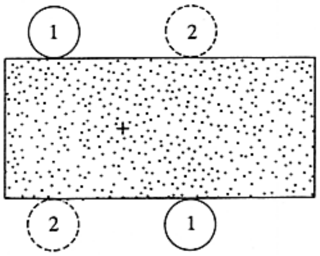


Figure 10. Example of the stimulus used for experiment 2. The disk-shaped targets alternate between position 1 and position 2.

3.1 *Method*

3.1.1 *Subjects and apparatus.* Three subjects, including one naive as to the aim of the experiment, participated. All had taken part in experiment 1, but one (AR) was still kept naive as to the purpose and the specific predictions of the experiments. The apparatus used in experiment 2 was identical to that in experiment 1.

3.1.2 *Stimuli and procedure.* An example of the stimulus configuration used is illustrated in figure 10. Each target had a diameter of 44 min arc. Except for the configuration of the targets, other stimulus parameters and procedures were identical to those in experiment 1.

3.2 *Results and discussion*

The results are shown in figure 11. Unlike the situation in experiment 1, there was no obvious difference between the crossed-disparity and the uncrossed-disparity conditions in any of the three subjects tested (compare figure 11 with the top row of figure 8).

Probit analysis was again applied to obtain critical H/V ratios. Within-subject paired comparisons by *t*-test revealed that the critical ratio in the uncrossed-disparity condition was *not* significantly different from the ratio in the crossed-disparity condition in any of the three subjects. To test more directly the difference between experiments 1 and 2, or the effect of configuration of the target, paired comparisons in

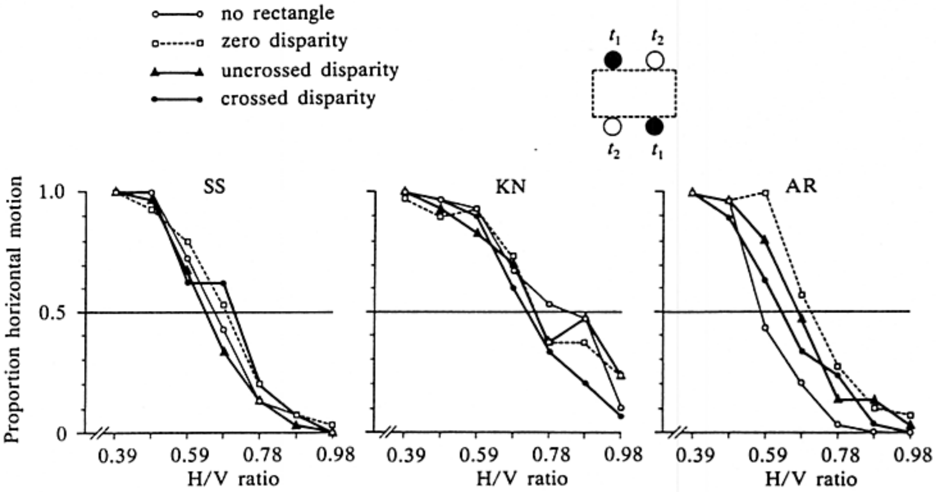


Figure 11. Proportion of responses in which horizontal motion was seen, as a function of the horizontal/vertical (H/V) distance ratio, in experiment 2, where targets were disks (see inset). Data obtained in the four conditions are shown together for each of the three subjects. Inset shows stimulus configuration in the with-occluder case.

individual subjects were made by t-test between comparable conditions in the two experiments. The results revealed that the critical H/V ratio in the uncrossed-disparity condition was significantly larger in experiment 2 (disk-shaped targets) than in experiment 1 (rectangular targets) in all of the three subjects ($z = 9.86, 4.26, 5.69$; $p < 0.01$ in two-tailed tests). No significant difference was found between the two experiments in any other condition in any subject, except for the no-occluder condition in subject SS.

In summary, the results of experiment 2 are inconsistent with the predictions of the occlusion of motion trajectory hypothesis. It seems unlikely that this hypothesis is correct or sufficient to explain the disparity effects observed in experiment 1. The disk-shaped configuration here was in a sense similar to the gap variation of the moon and cloud demonstration. In both cases, there is little in the way of an occluding edge in direct contact with the object behind and, therefore, no opportunity for amodal extension behind the occluding surface. Thus no occlusion-specific effect on motion was expected or observed.

Our results are also consistent with early findings on apparent motion (Wertheimer 1912). Among other demonstrations, Wertheimer mentioned an observation which is closely related to the trajectory issue described here. When the apparent rotating motion of a bar was optimized, the impression of motion was so vigorous and smooth that most observers could not tell whether the motion was real or illusory. Furthermore, when a distractor was added to the middle of the motion trajectory in the same depth plane, there was no impression of the moving bar crossing the distractor at any moment, and yet the quality of 'pure motion' was not at all degraded. Based on this and other phenomenological observations, Wertheimer argued for the unique Gestalt quality of motion perception, which could not be reduced into a sequence of elements such as stationary encodings of positions. These findings suggest that the presence of a physical stimulus in the middle of the trajectory does not affect the quality of motion perception. Thus, Wertheimer's observations are consistent with our own, indicating that the occlusion of motion trajectory hypothesis cannot account for our results.

4 General discussion

Kanizsa (1979) has presented a number of intriguing demonstrations which suggest that amodal presence is the outcome of relatively early visual processing rather than being the result of cognitive inference or high-level knowledge. Our results support his position, and we extend the concept in several significant ways:

(i) We have demonstrated the effects of amodal presence in the motion domain. This is important because motion is generally accepted as a uniquely-visual module of early cortical processing.

(ii) We suggest that the observed effects on correspondence solving for motion are closely related to the optogeometric constraints dictated by occlusion. The effects are very specific to the crossed-disparity case, which is the only condition consistent with an occlusion layout.

The results also confirm and extend our earlier results, where we found that amodal completion is strongly influenced by binocular disparity cues. Thus, we have shown that amodal presence enables disconnected image fragments to be linked for purposes of pattern recognition (Nakayama et al 1989b) and that a similar linkage occurs in solution of the aperture problem for motion (Shimojo et al 1989).

4.1 *The functionally equivalent surface: a quantitative estimate of amodal completion*

The concept of amodal completion implies that at some level of visual-neural representation, an 'invisible' surface continues behind an occluder. The idea is as yet a qualitative one with no specification as to the spatial extent of this invisible surface.

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Our experiment enables us to treat the concept more quantitatively, to estimate the 'size' of this invisible representation.

Our finding is that the motion system appears to act as if the existence of the occluded surface alters the effective starting and finishing positions of the apparent motion targets. Since we cannot literally 'see' the occluded surface, our approach is indirect. Rather than characterizing the invisible surface itself, we estimate the size of an *equivalent visible surface* which would functionally have the same effect on the ambiguity-solving processes for apparent motion.

To make such an estimate, we assume that the motion dominance function (relating the probability of seeing horizontal motion to the H/V ratio) remains constant for small changes in scale and that the effective H/V ratio is determined by a 'center-of-mass' calculation. With these assumptions and the critical H/V ratio data obtained in experiment 1, it is a simple mathematical exercise to calculate the amount of surface extension behind the occluder which would have the effect of moving the center points of the targets to preserve the motion dominance function between the occlusion and no-occlusion conditions.

In figure 7a we show the targets and their centers for the control case where the central rectangle was in back of the targets and thus there was no opportunity for amodal completion. In figure 7b we schematize the occlusion case where the targets were behind the occluder. The target separations shown in both figures are the ones for which there was no horizontal or vertical motion dominance (interpolated from the probit analysis functions summarized in figure 8). The dashed lines in figure 7b indicate our equivalent visible surface, added such that the combined visible and 'equivalent' surfaces would have their centers positioned to maintain the same H/V ratio as in the control conditions (as in figure 7a). Distances in this figure are drawn to scale and are calculated from grouped data on all six observers. Our analysis indicates that the size of the functionally equivalent surface is substantial, being about two thirds of the target size itself in this particular case. Thus our technique provides a way to quantify the magnitude of amodal surface completion, one that may be useful in future studies.

4.2 *Relation to current concepts of apparent motion*

Besides having a number of implications for occlusion-related visual processing, our current findings have significant implications for theories of apparent motion. Based on the earlier work of Braddick (1974), Anstis (1978, 1980) made a distinction between two kinds of apparent motion. One is short-range motion, in which motion perception is based on luminance information alone and can precede form perception. The other, and more relevant to the current study, is long-range motion, in which primitive form perception can precede motion perception. In fact, if a form or figure segregates from a ground by almost any kind of visual property at different positions between two frames, it is sufficient for apparent motion to occur (Pantle 1973; Ramachandran et al 1973). According to Ullman (1979), this kind of apparent motion is based on correspondence of 'tokens'. The characteristics of tokens and the affinity (correspondence strength) between them have been studied extensively (Green 1986, 1988; Green and Odom 1986), but what defines correspondence between tokens is still not fully understood. Our contribution in this context is that we have demonstrated the critical role of invisible yet amodally present surfaces in the token representation for apparent motion.

4.3 *Neurophysiological representation of hidden lines and surfaces?*

Current approaches to the neurophysiological foundations of perception have focused on the relation between the visibility of stimili and associated neuronal responses. For example, it has been of interest to relate visual thresholds as measured by psychophysical experiments to the properties of units at various stages in the visual pathway.

Yet the results of the present investigation, as well as other work in our laboratory, indicate that neuronal activity in the visual system might also reflect the presence of *invisible* stimuli. In other words, contours or surfaces concealed behind other surfaces might have a specifically visual–neural representation. Our work on the relation between grouping and depth indicates that the visual system can link separate image fragments so that isolated elements can appear as a continuous surface lying behind a closer surface (Nakayama et al 1989b; Shimojo et al 1989).

Does this mean that the observer has a literal representation of a hidden surface, explicitly represented as an object with a defined extent and locus, or does it mean that the representation is less spatially explicit and more 'propositional', providing information that a given surface patch or line continues behind an occluder but not representing the spatial nature of this continuation in any explicit homomorphic detail?

Whatever the representation is, the results we present here force us to consider the possibility that the issue of occlusion is handled relatively early in visual processing, early enough to have a major effect on the perception of motion. Because motion-analyzing mechanisms have been found in cortical area MT (Zeki 1978; Maunsell and Essen 1983; Albright 1984; Mikami et al 1986; Movshon et al 1986), this raises the possibility that occlusion-related processing occurs even earlier, perhaps in V2 or V1. The representation of subjective contours in cortical area V2 (Heydt et al 1984; Heydt and Peterhans 1989; Peterhans and Heydt 1989) supports this view.

Do cells in V1 and V2 have receptive-field properties that could begin to address the issue of whether a surface continues behind another or whether it ends abruptly? Elsewhere (Shimojo et al 1989), we have argued that the combined output of binocular disparity cells and end-stopped cells could make the distinction between a real line terminator and an extended line rendered invisible because of occlusion. Our suggestion was that the activity of end-stopped cells might be gated by disparity-sensitive cells with receptive fields in the end-stopped zone of these cells. If crossed-disparity cells were activated it would indicate line continuity behind an occluder; whereas, if uncrossed-disparity cells were activated it would indicate the termination of a real line in the world. Thus, it is conceivable that the combination of two relatively simple receptive-field types could begin to represent occlusion and surface continuation in early cortical areas.

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