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Irrational contour synthesis

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ABSTRACT

The mechanisms responsible for generating illusory contours are thought to fulfil an adaptive role in providing estimates of missing contour fragments generated by partial camouflage. One striking apparent counter-example to this view was described in Current Biology 21 (2011) 492–496, which showed that illusory contours could arise in motion displays depicting visible occluding discs occluding and disoccluding thin contours. These motion sequences generate illusory contours even though they play no necessary role in accounting for occlusion and disocclusion of the thin contours. The present work sought to more precisely characterize the quantitative dependence of these 'irrational' contours on the relative contrasts in the image. We show that the perceived strength of the illusory contours generated by these displays depends monotonically on the relative contrast of the occluding and occluded contours and that previous attempts to measure their strength with a method of adjustment appears to be contaminated by response bias. We further show that these illusory contours also arise when the occluding disks are rendered transparent and exhibit similar forms of contrast dependencies. These findings reveal a general methodological problem that can arise using methods of adjustment and provide quantitative data that may be used to identify the neural mechanisms responsible for IC genesis and their perceived strength.

1. Introduction

There has been an extensive body of empirical and theoretical research devoted to understanding illusory contours (ICs). This work includes psychophysical work dedicated to articulating the stimulus properties that evoke ICs, modulate their perceived strength, and determine their perceived shape (e.g., Anderson, Singh, & Fleming, 2002; Banton & Levi, 1992; Dumais & Bradley, 1976; Fulvio & Singh, 2006; Kanizsa, 1955; Kanizsa, 1979; Lesher & Mingolla, 1993; Petry & Meyer, 1987); computational work dedicated to formally modeling the perception of ICs (e.g., Grossberg & Mingolla, 1985a, 1985b; Lesher, 1995); and physiological work aimed at understanding the mechanisms that underlie the experience of ICs (e.g., von der Heydt, Peterhans, & Baumgartner, 1984; Ffytche & Zeki, 1996; Hirsch et al., 1995; Murray, Foxe, Javitt, & Foxe, 2004; Murray et al., 2002; Neumann & Sepp, 1999; Pillow & Rubin, 2002; Ramsden, Hung, & Roe, 2001).

It has been suggested that the formation of ICs can be understood by considering the adaptive functions that they could serve in natural environments. The boundaries of surfaces can be partially camouflaged by backgrounds that coincidentally match the color or texture of a nearer occluding surface. The genesis of ICs in such contexts would adaptively integrate these fragmented image contours into the coherent surface boundaries that were disrupted by camouflage. This adaptive function has been bolstered by work that treats completion processes as a rational solution to computational problems created by partial occlusion and camouflage by linking completion mechanisms to the statistics of natural scenes (Elder & Goldberg, 2002; Geisler, Perry, Super, & Gallogly, 2001).

There are at least two distinct initiating conditions for ICs that must be addressed by any theory of IC formation (see, e.g., Lesher, 1995). One of the most extensively studied and modeled involves the integration of disjoint oriented contour segments, such as the inducing elements of the classic Kanizsa figures. The ICs formed by these contours involves interpolating oriented image elements along paths that are locally specified by the inducing elements. Most models invoke some form of 'good continuation' to generate this path, either by enforcing completion 'rules' (such as 'contour relatability'; Kellman & Shipley, 1991), or by measuring scene statistics of camouflaged and partially occluded contour segments (Geisler et al., 2001). The other form of completion involves the formation of ICs generated by the termination of thin lines (Ehrenstein, 1941; Lesher, 1995; Lesher & Mingolla, 1993). The ICs generated in these displays are more difficult to model because there is no local orientation in the image to initiate the interpolation of the contours along the direction that ICs form (see

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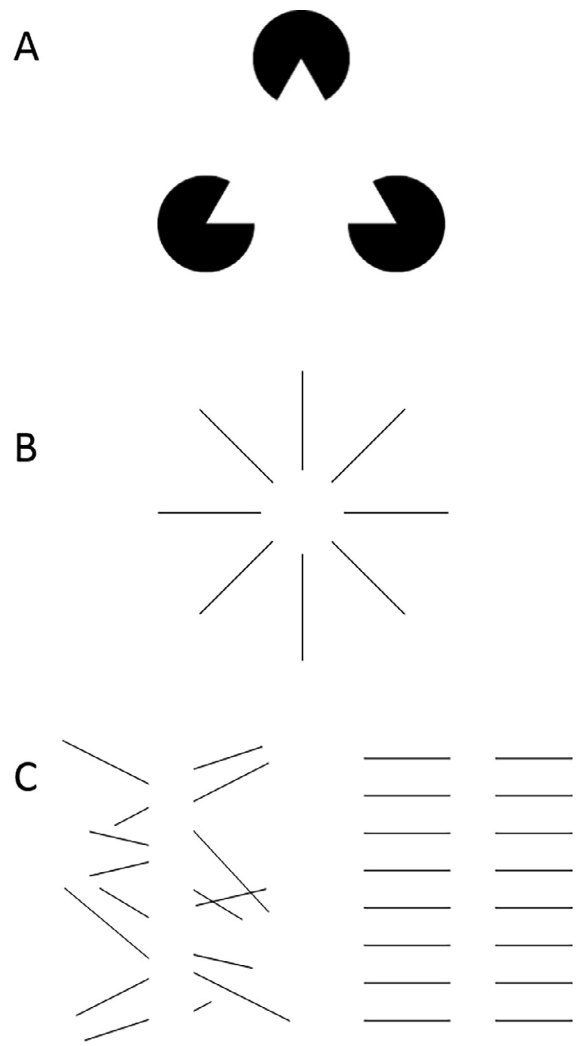

Fig. 1. Examples of the different initiating conditions for illusory contours in static images. (A) A Kanizsa figure, where the illusory contours are interpolated along paths defined by oriented inducing elements. (B) Illusory contours generated by an Ehrenstein figure, where the illusory contour forms perpendicular to the inducing lines. Note that there is no measurable orientation at the end of the contour terminations that constrain the direction the illusory contour forms. (C) Variants of the stimuli generated by Gillam showing that illusory contours generated by the termination of thin lines with random orientations (left) is stronger than an array of lines where the terminations are all perpendicular to the inducing lines.

Fig. 1). Some early work suggested that there was a bias for contours to form orthogonally to the initiating contour segments (Kennedy, 1978), which inspired neural net architectures that embodied this constraint (Grossberg & Mingolla, 1985a, 1985b). However, subsequent studies have revealed the insufficiency of this constraint. One striking example was provided by Gillam (1987), who showed that columns of thin lines with different orientations generated stronger ICs than similar displays constructed using parallel lines oriented perpendicularly to the gap (Fig. 1c). A perpendicular bias predicts that ICs should be stronger for lines that were perpendicular to the gap, but this is not what is experienced. Gillam and Grove (2011) offered a computational level rationalization for the stronger ICs experienced with disorganized lines using a principle that they dubbed 'order from disorder'. They argued that the orderly arrangement of terminations of otherwise unrelated orientations is most plausibly explained by an occluding contour, whereas the orderly arrangement of parallel lines suggests a common process responsible for generating lines and their terminations.

The conceptual puzzles created by the termination of thin contours have had little influence on theories that interpret ICs as a rational (probabilistic) solution to the problem of camouflage. However, some motion displays have revealed a new class of ICs that are difficult to reconcile within such frameworks. Anderson, O'Vari, and Barth (2011) generated motion displays that depicted four discs outside of a thin, outline square, translating over and occluding the sides of the square (see Movie 1). Although all of the image data is fully explained by the visible occluding discs, extremely vivid ICs were observed forming *inside* the square; an IC was generated at the contour terminators generated by visible occluding discs for no apparent reason. Anderson et al. (2011) argued that these contours are difficult to reconcile with rational accounts of IC formation because their formation entails an extremely improbable event: two oppositely moving occluding surfaces generating the exact same pattern of accretion and deletion of the occluded contours.

The motion displays that elicit these apparently 'irrational' ICs hold potential theoretical importance for theories of IC formation. Because the function of these ICs is unclear, questions about why they exist may only be answered by having a thorough understanding of the neural mechanisms responsible for their genesis. Insights into these mechanisms may be gained by exploring and characterizing the image properties that modulate the strength of the ICs but there has been no subsequent work investigating this class of displays. One stimulus factor that modulates the vividness of the ICs is the luminance contrast of the occluded frame and moving occluding discs (Anderson et al., 2011). Luminance contrast refers to the *difference* in luminance between one image property and its surround scaled by some measure of overall energy. The vividness of the ICs shows a monotonic dependence on both the contrast of the thin occluded frame and the contrast of the moving occluding discs with respect to the background (Anderson et al., 2011); the IC is most vivid when there is low contrast for the occluding discs and high contrast for the occluded frame (and therefore high contrast for the thin line terminators at the disc-frame intersections). However, Anderson et al. (2011) did not measure the rate at which IC vividness varies as a function of contrast and determine whether the form of these contrast dependencies was linear or exhibits significant non-linearities.

The goal of the experiments reported here is to more thoroughly characterize contrast dependencies in the perceptual scaling of IC strength in these displays. The first two experiments assess the role of contrast polarity on the perceived strength of these ICs; the third was designed to test whether similar effects will generalize to displays where the accretion and deletion of the contour segments is a matter of degree by rendering the discs transparent rather than opaque.

2. General methods

2.1. Experiment 1

Previous work (Anderson et al., 2011) has shown that the strength of the IC increases as the luminance contrast between the occluding disc and occluded frame increases. The goal of Experiment 1 was to test whether IC strength also depends on the contrast polarity of the display. We have observed informally that the standard display (white frame on a black background) generates a stronger IC than its photographic negative (black frame on a white background). In order to test this hypothesis, the standard display and its photographic negative were presented side-by-side and the luminance of the occluding discs was varied. One display had a fixed disc luminance (either the standard or photographic negative) while observers adjusted the disc luminance of the other display to have matching IC strength. If the standard display generates a stronger IC than its photographic negative, then observers will use a smaller range of disc luminances in the standard display to match the IC generated by the photographic negative.

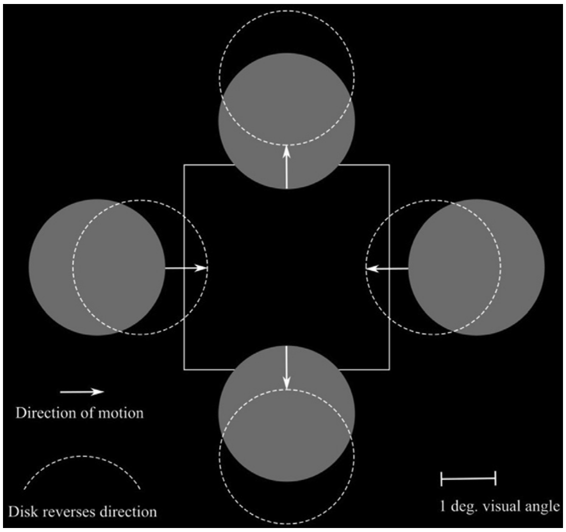

Fig. 2. Schematic drawing of our stimuli. The discs occluding the square frame moved to the positions depicted by the dashed outline and then reversed direction. Note that the discs that move vertically move in counterphase to the discs that move horizontally.

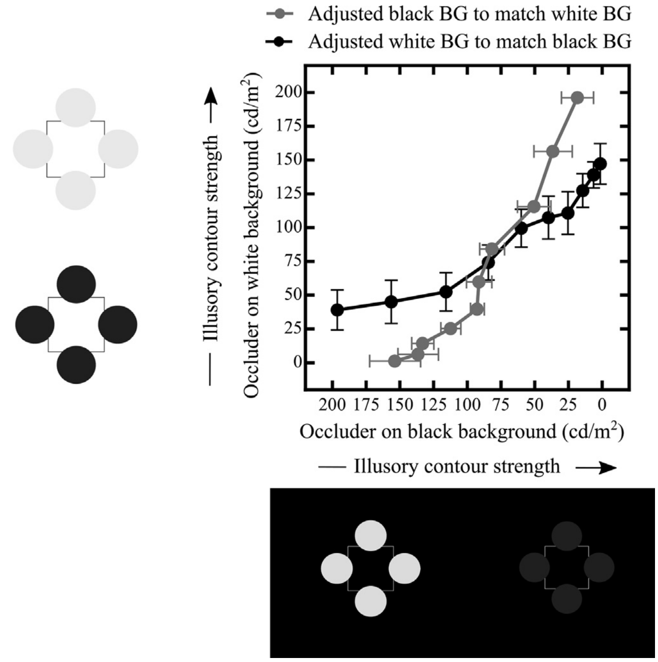

Fig. 3. Results of Experiment 1. Observers adjusted the disc luminance of either the standard or photographic negative to match the IC strength of the other display. The graph plots the luminance of the occluding disc for the standard display (horizontal axis) and photographic negative (vertical axis) at PSE in IC strength. Black data points with vertical error bars depict conditions where observers adjusted the photographic negative to match a fixed standard display. Grey data points with horizontal errors bars depict conditions where observers adjusted the standard display to match a fixed photographic negative. Error bars are standard errors of the mean of seven observers.

2.1.1. Methods

2.1.1.1. Observers. There were ten observers: three were lab members; and seven were psychology students who received some course credit for participating. All reported having normal visual acuity or corrected to normal. The experiments were approved by the University of Sydney and participants provided written informed consent and were debriefed about the aims in adherence with the Declaration of Helsinki.

2.1.1.2. Display and procedure. The stimuli were viewed in a black curtained room on a 30-inch flat screen LCD monitor (DELL U3014t) with a spatial resolution of 2560 × 1600 and a temporal resolution of 60 Hz. The display was calibrated using a SpectraScan 650 photometer (Photoresearch, Inc., Chatswoth, CA); the luminance maximum and minimum was 205.1 and 0.3 cd/m^2. The displays were viewed freely at a distance of approximately 700 mm.

Observers viewed a square frame and each side of the frame was partially occluded by a disc moving perpendicularly to the thin contour that it occluded. A schematic drawing of the display is shown in Fig. 2: the frame had a side length of 47 mm (3.84°); the contour of the frame was 2 pixels wide (2.34 arcmin); and the occluding discs had a diameter of 31 mm (2.53°). The discs moved with constant speed (34 mm/s) between the positions indicated in Fig. 1 (periodicity 0.84 Hz). To induce a more vivid percept of a nonrigid illusory contour, the vertically moving discs had a phase offset relative to the motion of the horizontally moving discs. Specifically, the position of the four discs was

$$x = \mathrm{r}\cdot\sin\theta$$

$$y = \mathrm{r}\cdot\cos\theta$$

$$r = 40\left|\frac{(t+\varphi)mod\ \lambda}{\lambda} - 0.5\right| + 28.5$$

where x and y are the horizontal and vertical coordinates of the discs (in mm), t is time (in seconds), λ is the periodicity of the motion $\left(\frac{1}{0.84}\right)$, and $\theta$and φ determine the direction and phase of motion for each disc. θ was 0°, 90°, 180°, and 270° for the top, right, bottom, and left discs respectively, and φ was 0 for the top and bottom discs and 0.2976 for the left and right discs.

The frame was white on a black background in the 'standard display' and was black on a white background in the 'photographic negative'. The standard display and its photographic negative were presented side by side and centered in the left and right halves of the monitor. The luminances were 205.1 cd/m^2 and 0.03 cd/m^2 for the square frame and its background in the standard display (respectively), which were swapped to form the photographic negative (black frame on white background). The display on the left side of the screen was presented with a fixed disc luminance equal to: 1.4, 6.6, 15.3, 26.3, 42, 62.7, 88.6, 123, 165, and 205.1 cd/m^2. Observers adjusted the luminance of the discs on the right side of the screen to produce an IC that appeared equally strong as the IC on the left side of the display. The luminance of the discs on the right side of the display could be varied between 1.4 and 205.1 cd/m^2 and was assigned a randomly selected luminance within this range at the start of each trial. Different blocks of trials were used to adjust the standard display to match the photographic negative, or vice versa. There were 6 repeats and hence 60 trials in a block. The order of the blocks and trials within a block was a different random permutation for each observer.

2.2. Results and discussion

The results of Experiment 1 are shown in Fig. 3. The horizontal axis of the graph plots the disc luminance of the standard display (black background), and the vertical axis plots the disc luminance of the photographic negative (white background). The direction of the error bars is either horizontal or vertical depending on whether observers adjusted the standard or photographic negative (respectively).

The results support the observation that IC strength increases monotonically as the luminance contrast of the visible occluding disc relative to the background decreases; a low disc-background contrast in the standard display was matched to a photographic negative display that also had a low disc-background contrast. However, the results also reveal that observers' match setting depends on which display was the target (fixed on each trial) and which was the match (adjustable display). If observers used the same match values when the target and match display were switched, the two curves should be the same. However, the data show that observers used a smaller range of disc luminances in the adjustable displays to match the relatively large range of disc luminances tested in the fixed displays regardless of which display served as target and match. The simplest explanation of this result is that this pattern of data is caused by a conservative response bias; observers use a smaller range of luminance values in the matching pattern independently of which pattern serves as the match. Previous work (Anderson et al., 2011) employed a similar method of measuring IC strength where observers adjusted the standard display to match the IC strength of a fixed photographic negative display. However, because it was informally observed that the standard display could produce stronger ICs than the photographic negative display, they did not perform the complementary matching task where observers adjust the photographic negative to match a fixed standard display. The results of experiment 1 suggest that this method is contaminated by a significant conservative response method, and therefore does not provide an unbiased measure of the strength of the IC perceived in these displays. This suggests that a different method is needed to characterize how IC strength varies as a function of the component luminances in these displays.

2.3. Experiment 2

The goal of Experiment 2 was to determine how IC strength varies with the luminance of the occluding discs and the contrast polarity of the frame using a bisection task, which should be immune to the contaminating effects of response bias. The goal of this method is to characterize how the perceived strength of the IC is modulated by the intensity of the occluding (visible) discs. This psychometric function was constructed by having observers view three IC displays arranged in a horizontal sequence and psychophysically determining what disc luminance elicits an IC that appears half-way in strength between that of the left and right displays. The two outer displays depicted a weaker and stronger IC created by varying the luminance of the occluding discs. The middle display had a disc luminance between the two outer displays, and observers judged whether the IC of the middle display was more similar to the left or right displays. In a second condition, observers performed the same task, but were required to bisect the perceived brightness of the occluding discs. Note that this method only allows us to construct the shape of the psychometric function within each display type, and therefore does not allow us to directly assess how the strength of the ICs generated by different background and disc luminances are related to each other; this method only allows us to determine whether the psychometric functions generated by different combinations of background luminance, disc luminance, and frame luminance have the same shape.

2.3.1. Methods

2.3.1.1. Observers. Two of the authors (KT and PM) and one research assistant participated. On each trial, observers viewed three displays presented side by side (Fig. 4) and judged whether the central display had an IC more similar in strength to that of either the left or right side of the display.

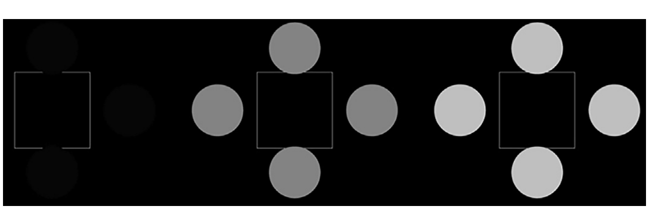

Fig. 4. Example stimuli for Experiment 2. Observers judged whether either the left or right display was more similar to the middle display in either IC vividness or disc brightness/lightness.

2.3.1.2. Stimuli. Six display types were constructed that varied the contrast polarity of the frame and occluding discs. The first condition was the standard display composed of a white square frame (205 cd/m^2) with black background (0.03 cd/m^2), and the second condition was the 'photographic negative' of the standard display with black frame (0.03 cd/m^2) and white background (205 cd/m^2). In both conditions, the luminance values of the discs were constrained to lie between the luminance values of the background and frame; hence, the discs had the same contrast polarity as the frame in both the standard display and its photographic negative. The other four conditions had a mid-gray (51 cd/m^2) background and varied whether the frame and discs had the same or opposite contrast polarity as each other. Specifically, the frame was either 'white' or 'black' and the luminance values of the discs were constrained to be either increments (lighter) or decrements (darker) relative to the grey background.

2.3.1.3. Procedure. On each trial, observers viewed a 1x3 array of displays that were all the same display type; the only difference between the three displays was the luminance of the occluding discs. The left display elicited a stronger IC than the right display (because its occluding discs had weaker contrast with the background than the right display) and observers judged whether the IC vividness of the central display was more like the left or right display. The luminance of the discs for the central display was varied in 12 linearly spaced steps using the method of constant stimuli with 8 repeats (see Table 1). A Weibull function was fit to each observer's data to determine the disc luminance of the bisector display. The six display types were tested in separate blocks of trials and three blocks of trials were performed for each display type. The first block of trials for each display type bisected the interval formed by the strongest variant of the display possible given the monitor gamut and the weakest variant of the display. The bisector computed from the first block creates two half-intervals that were again bisected in the two subsequent blocks of trials. These half-intervals were constructed using the bisector value from the first block averaged across observers (so that all observers viewed the same stimuli). The order of the trials within a block was a different random permutation for each observer. Table 1 gives the disc luminance values for the first block of trials for each of the six conditions. The value to the left of the equals sign is the absolute value of the luminance difference between the occluding disc and the background. The first value to the right of the equals sign is the background luminance and the second value is the disc luminance. Two values are given for the discs of the middle display and indicate the range of its variation.

In a second set of trials, observers performed a second bisection task where they were instructed to bisect the perceived brightness/lightness of the occluding discs rather than the strength of the ICs. The purpose of this experiment was to determine whether observers were performing the IC bisection task by simply bisecting the perceived lightness/brightness of the discs rather than bisecting the perceived strength of the ICs.

2.3.2. Results and discussion

The results reveal that IC strength varies monotonically with disc luminance for both the standard display and its photographic negative. The six graphs in Fig. 5 plot the PSEs of IC strength for each combination of surround luminance, frame luminance, and disc polarity. The horizontal axis depicts the luminance difference between the disc and background; larger differences generate a stronger visible occlusion signal, and hence a less vivid IC. The data at the far left and right in each graph represent the fixed luminances of the stimuli generating the strongest and weakest IC (respectively); the three middle points represent the three bisections performed by the observers (i.e., the 75%, 50%, and 25% bisections). The solid lines depict the bisections for the IC judgments, whereas the dashed lines depict the bisections of the disc luminance. Error bars represent standard errors of the PSEs (points of subjective equality) for the 3 observers. It is clear that for all of the

Table 1
Disc luminance in cd/m^2 for Exp.2. The value to the left of the equals sign is the luminance difference between the disc and background.

Background	Frame	Disc	Left display	Middle	Right display
black	white	increment	0 = |0.3–0.3|	[0.1 121] = |0.3 − [0.4 121]|	121 = |0.3 − 122|
white	black	decrement	84 = |205 − 122|	[84 205] = |205 − [121 0.3]|	205 = |205 − 0.3|
gray	white	increment	0 = |51 − 51|	[0 74] = |51 − [51 125]|	74 = |51 − 125|
gray	black	increment	0 = |51 − 51|	[0 74] = |51 − [51 125]|	74 = |51 − 125|
gray	white	decrement	0 = |51 − 51|	[0 47] = |51 − [51 4]|	47 = |51 − 4|
gray	black	decrement	0 = |51 − 51|	[0 47] = |51 − [51 4]|	47 = |51 − 4|

conditions in the top display containing the 'white' frame that observers' IC bisections are not the same as their disc luminance bisections; the strength of the IC falls off more slowly than the perceived luminance of the discs. The F and p values were $F(1,2) = 138$, $p \ll 0.01$ for the top left graph, $F(1,2) = 202$, $p \ll 0.01$ for upper middle, and $F(1,2) = 215$, $p \ll 0.01$ for top right. However, the same is not true for the black frame; the bisection data of the discs and ICs are essentially identical for all of the values tested and only reach statistical significance for the condition with white background ($F(1,2) = 67$, $p < 0.05$). The F and p values for the conditions with a black frame on a gray background were $F(1,2) = 8.7$, $p = 0.1$ for the lower middle graph and $F(1,2) = 1.040$, $p = 0.415$ for the lower right graph.

There are two notable outcomes of this experiment. First, the results demonstrate that the perceived strength of the IC is not solely a function of the perceived brightness/lightness of the visible occluding discs; the vividness of the IC also depends on the luminances of the background and the frame. These dependencies are particularly evident for frames that are lighter than their backgrounds. Second, the perceived strength of the IC falls off more slowly than the perceived contrast of the occluding discs when the occluded frame is white; but when the occluded frame is black, the perceived strength of the IC is well predicted by the perceived contrast of the occluding discs. The different dependencies of IC strength on disc luminance exhibited by white and black occluded frames reinforces our previous argument that it is not appropriate to use the 'standard' display (white frame on black background) to measure the strength of the IC of displays where the frame and background polarities are inverted. We discuss some possible reasons for these different dependencies in the general discussion.

2.4. Experiment 3

The previous Experiments, as well as those reported previously (Anderson et al., 2011), only considered displays where the occluded contour (the square frame) was completely hidden by the occluding discs (i.e., the occluding discs were completely opaque). This generates two types of occlusion signals: a spatial discontinuity that generates contour terminators and an accretion/deletion signal generated by the motion of the occluding discs. In all of the previous displays, the discs completely occluded the contours.

The purpose of Experiment 3 was to determine whether illusory contour genesis required the complete occlusion of the contours, or whether their formation required a discontinuous change in the magnitude of contrast. The latter stimulus could be created by rendering the occluding discs as transparent. Three forms of luminance discontinuities can be generated at the points where the discs intersect the frame depending on the luminance and opacity of the discs: I-junctions, when the discs are opaque and camouflaged by the background (i.e., when the background and discs have the same luminance); T-junctions, when the discs are opaque and clearly visible; and X-junctions, when the discs are transparent, which allows the frame contour to be visible through the discs. The preceding experiments show that both I- and T-junctions can elicit ICs and that IC strength increases with the luminance difference (contrast) across the junction stem. The purpose of Experiment 3 was to test whether X-junctions associated with transparent discs can also generate ICs, and if so, whether IC strength again depends on the luminance contrast of the disc and partially occluded frame. Our pilot data revealed that transparent discs can also generate vivid ICs (see Movie 2). We therefore sought to characterize the strength of the IC of the transparent display by varying the opacity of the occluding discs and measuring its strength by matching it to an IC formed by an opaque disc.

2.4.1. Methods

Two of the authors (KT and PM) and one research assistant participated (the same observers as Experiment 2). They viewed two displays side by side and judged which had the stronger IC. Both displays had the same white (205.1 cd/m^2) or black background (0.3 cd/m^2). The right display had opaque discs and the luminance of the opaque discs was varied from 0.3 to 176 cd/m^2 in 7 linearly spaced steps. The left display had transparent discs and their opacity was varied from 0.4 to 0.9 in five linearly spaced steps. However, if the entire disc was rendered as transparent, the opacity manipulation would cause both the luminance of the disc and the luminance of the occluded frame to vary. The results of the previous experiments have already demonstrated that the strength of the IC varies as a function of the strength of the visible occluding disc. We therefore held the luminance of the discs that covered regions of the background fixed as a function of disc opacity (15 cd/m^2 on the black background and 162 cd/m^2 over the white background), and varied the intensity of the occluded frame as a function of disc opacity to assess the impact of varying the perceived visibility of the occluded line (note that this is consistent with varying the lightness of the disc as a function of its opacity, both of which have been shown to affect perceived opacity (Singh and Anderson, 2002)). In the black background condition, increasing the opacity of the discs reduced the luminance of the white frame seen through the transparent discs. The luminance of the white frame beneath the transparent discs was equal to 180, 168, 153, 133, and 109 cd/m^2 for each level of opacity respectively. In the white background condition, increasing the opacity of the discs increased the luminance of the black frame seen through the transparent discs from 89 to 150 cd/m^2.

The observer's task was to select whether the display depicting the transparent surface appeared to generate a stronger IC than the display depicting the opaque discs. Each combination of the five transparent discs and seven opaque discs were compared with eight repeats in two blocks of 280 trials. The standard display (black background white frame) was presented in one block of trials and the photographic negative (white background black frame) was presented in a separate block. The order of the trials in a block was a different random permutation for each observer, as was the order in which the blocks were presented.

2.4.2. Results

The results reveal that IC strength varies approximately linearly with disc opacity for both the standard display and its photographic negative. In order to calculate the disc luminance at the PSE in IC strength between the two flanking displays, a psychometric function (Weibull function) was fit to each observer's data, which were used to compute PSEs for each observer. The data points in Fig. 6 depict the mean PSEs of the observers. For both the standard display and the photographic negative, the strength of the IC falls off approximately

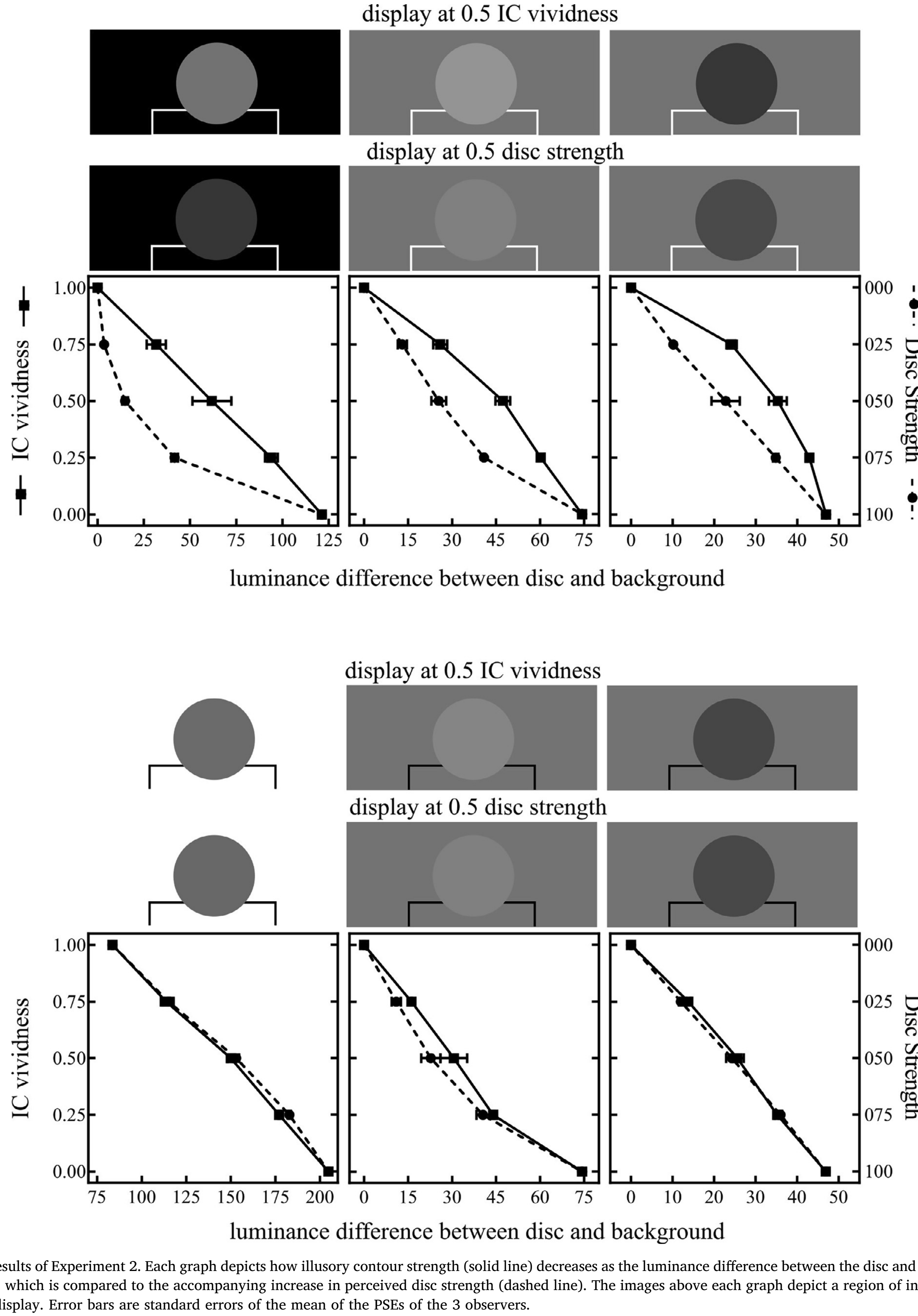

Fig. 5. Results of Experiment 2. Each graph depicts how illusory contour strength (solid line) decreases as the luminance difference between the disc and background increases, which is compared to the accompanying increase in perceived disc strength (dashed line). The images above each graph depict a region of interest of the bisector display. Error bars are standard errors of the mean of the PSEs of the 3 observers.

linearly as the opacity of the occluding disc is reduced, i.e., the strength of the IC decreases as the strength of the accretion/deletion signal decreases. These results demonstrate that the visibility of the frame beneath the occluding discs does not abolish the IC. Instead, these results show that the IC can be generated by all forms of luminance discontinuities formed by the accretion/deletion of contours in this display

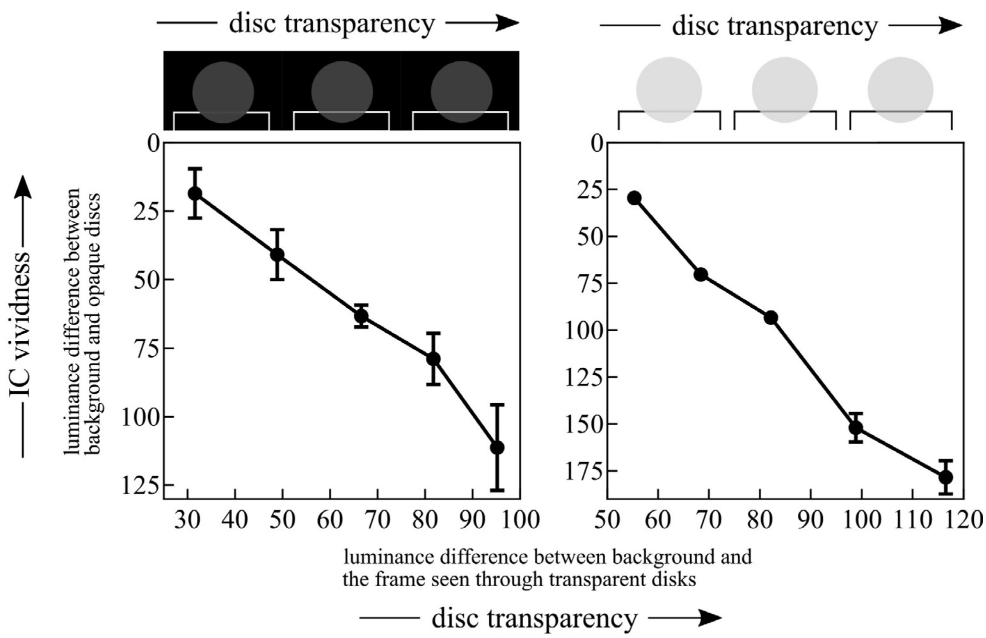

Fig. 6. Increasing disc transparency reduces the vividness of the IC. Error bars are standard errors of the means of the observers.

(i.e., I-junctions, T-junctions, and X-junctions).

3. General discussion

The experiments described herein were designed for two purposes: to precisely characterize the quantitative dependences of IC strength generated in the displays originally described by Anderson et al. (2011), and to test whether similar ICs would also occur when the visible occluding discs were rendered transparent. We consider each in turn.

Our results revealed that the method of adjustment used by Anderson et al. (2011) to characterize the strength of the IC was likely contaminated by a form of response bias. Observers use a smaller range of contrasts in the displays that they adjust irrespective of which display serves as target and the match (i.e., the data depend on which display serves as the standard and which serves as the match). The simplest explanation of this pattern of data is a conservative response bias, where observers use a subset of the scale available to them (as occurs generically when people use rating scales). We employed a bisection task to avoid this bias. Our data show that there are clear differences in how the strength of the IC varies as a function of disc luminance for the 'standard' display and its photographic negative. Whereas the IC strength was well predicted by the perceived contrast of the occluding discs when the occluded frame was 'black' (i.e., the lowest luminance), the same was not true for displays where the occluded frame was 'white' (i.e., the highest luminance): IC strength declined less rapidly than the perceived contrast of the occluding discs relative to its background. These different dependencies cannot be gleaned from a method of adjustment task where one display is used as a measurement tool of perceived IC strength for another. A method of adjustment only determines whether there is a monotonic mapping between two displays, and therefore cannot be used to determine the perceptual scaling of ICs.

Why do the ICs generated by white occluded frames (and terminators) persist over a broader range of luminances than black occluding frames? One possible explanation is that the perceived contrast of the terminators (and the occluded frame) appears stronger when the frame is white than when it is black. This difference is most salient when the display with the black background and white frame is compared to its photographic negative (i.e., a white background and black frame). Although the luminance difference between the two is identical, the total luminance from the white background/black frame display will be much greater than the total luminance generated by the black background/white frame display. Any divisive normalization used to transform luminance differences into contrast that is sensitive to such overall intensity differences will cause the contrast of the white frame relative to the black background to be substantially higher than its photographic negative. These differences may also reflect different states of luminance adaptation; the brighter stimuli may reduce sensitivity to luminance differences, which in turn diminishes the strength of the ICs.

The most important aspect of the different pattern of data obtained with the two different polarity conditions is that it shows that observers were not simply matching the perceived contrast of the discs; if they did, the bisections for the ICs and the discs would be the same in all conditions tested. This is not what our data show. Thus, we are confident that the data captures the perceived strength of the ICs in these different displays. Presumably, this strength will be reflected in the neural populations that generate these ICs. If so, the neural substrates that generate these ICs should exhibit the same quantitative dependencies as those exhibited in our psychophysical studies. These quantitative signatures could therefore be used to identify the neural loci where these ICs are generated.

The results of Experiment 3 provide additional insights into the stimulus conditions that generate ICs. We found that ICs will also form when the occluding discs are rendered transparent. This demonstrates that the ICs generated in these displays do not require the accretion and deletion of contour segments, but rather, can be generated by a sufficiently large discontinuous change in the *magnitude* of contrast along a line. Similar results have been reported previously for stereoscopically induced ICs (Anderson, 1994; Anderson & Julesz, 1995; Malik, Anderson, & Charowhas, 1999), where they showed that inter-ocular differences in the magnitudes of contrast could elicit stereoscopic ICs.

One the most influential ideas in vision and cognitive science was Marr's articulation of the different 'levels of analysis'. As someone working at the forefront of machine vision, he placed greatest conceptual weight on computational level analyses that characterize the problems that the visual system is organized to solve. This idea is also evident in theories that treat perception as Bayesian inference, which attempt to treat percepts as 'solutions' to the 'natural tasks' that the visual system evolved to solve (Geisler et al., 2001). The broader theoretical problems involved in identifying and testing the 'natural tasks' that shaped our perceptual systems has been recently discussed at some length (Anderson, 2015), but the displays described herein and previously (Anderson et al., 2011) seem difficult to reconcile within this framework. The occlusion and disocclusion of the contours forming the outline square is fully given by the clearly visible occluding discs, yet the visual system nonetheless generates an additional illusory figure at the same contour terminators. The simultaneous occlusion and disocclusion of a figure by two surfaces moving in different directions is an extraordinarily improbable occurrence, and thus seems hard to rationalize within any probabilistic framework.

It has been previously noted that the occlusion and disocclusion of thin lines is inherently ambiguous (Anderson & Sinha, 1997; Anderson & Barth, 1999; Bruno and Gerbino, 1991); there are an infinite number of shapes and motion directions of an occluding surface that could generate such events. However, the stimuli described herein and previously (Anderson et al., 2011) appear unique in two ways. First, these stimuli are not ambiguous in any typical use of the term; the surfaces causing the occlusion and disocclusion of the square outline are clearly visible, so there is no ambiguity that is 'resolved' by the genesis of ICs. Second, vision science is replete with ambiguous stimuli that elicit multistable percepts. The different candidate solutions are typically experienced sequentially, and alternative solutions are suppressed from conscious awareness. The genesis of ICs in the stimuli described herein is equivalent to two simultaneous interpretations of the same image data: a visible occluding figure and a second camouflaged occluding figure. It is unclear why the visible occluding surfaces fail suppress alternative solutions, and why this suppression is such a weak function of the contrast of the visible occluding surfaces. It seems unlikely that a computational level theory or Bayesian analysis will be found that can offer a cogent rationalization of these phenomena; it seems more likely that the answer will require a detailed understanding of the neural mechanisms responsible for their genesis. If so, these phenomena demonstrate that some robust perceptual phenomena cannot be understood as 'implementing' a solution to a computational level problem; they can only be explained by a thorough understanding of the mechanisms responsible for their genesis.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2019.02.014.

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