Corner salience varies linearly with corner angle during flicker-augmented contrast: a general principle of corner perception based on Vasarely's artworks

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Abstract—When corners are embedded in a luminance gradient, their perceived salience varies linearly with corner angle (Troncoso *et al*., 2005). Here we hypothesize that this relationship may hold true for all corners, not just corner gradients. To test this hypothesis, we developed a novel variant of the flicker-augmented contrast illusion (Anstis and Ho, 1998) that employs solid (non-gradient) corners of varying angles to modify perceived brightness. We flickered solid corners from dark to light grey (50% luminance over time) against a black or a white background. With this new stimulus, subjects compared the apparent brightness of corners, which did not vary in actual luminance, to non-illusory stimuli that varied in actual luminance.

We found that the apparent brightness of corners was linearly related to the sharpness of corner angle. Thus this relationship is not solely an effect of corners embedded in gradients, but may be a general principle of corner perception. These findings may have important repercussions for brain mechanisms underlying the early visual processing of shape and brightness.

A large fraction of Vasarely's art showcases the perceptual salience of corners, curvature and terminators. Several of these artworks and their implications for visual processing are discussed.

Keywords: Alternating Brightness Star; Op-art; curvature; curves; junctions; filling-in; terminators; unfilled flicker.

> ***In basic research, intellectual rigor and sentimental freedom necessarily alternate.***
>
> ***– Victor Vasarely***

INTRODUCTION

Ibn al-Haytham (also known as al-Hazen) pointed out the importance of corners and curvature in visual perception almost 1000 years ago, when he wrote in his treaty

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Optics: “For sight will perceive the figure of the surfaces of objects whose parts have different positions by perceiving the convexity, concavity or flatness of those parts, and by perceiving their protuberance or depression” (al-Haytham, 1030/1989).

In the 1930s, Werner described angles as “those parts of contour which have stored within them the greatest amount of psychophysical energy”, and proposed that “angles are especially intense parts of contour, and there is invested in them a central significance for the construction of optical figurations” (Werner, 1935). Later, Attneave proposed that ‘points of maximum curvature’ (such as curves, angles, corners and terminators) contain more information than non- or low-curvature features and therefore they are more important for object recognition (Attneave, 1954).

Corners are not only important for object recognition and shape perception, but also for the perception of brightness and salience. In Vasarely’s ‘nested squares’ illusion (Hurvich, 1981; Jameson and Hurvich, 1975; Vasarely, 1970), a luminance gradient formed by concentric squares gives rise to illusory ‘folds’ at the squares’ corners (Fig. 1A). That is, the corners appear as more salient — either brighter or darker — than the adjacent flat (non-corner) regions of each individual square. However, Vasarely did not explore the role of corner angle in the perceived brightness of the corner. We thus previously developed a novel visual illusion, the ‘Alternating Brightness Star’ (Fig. 1B and 1C), which shows that sharp corners are more salient than shallow corners, and that corner angle and corner salience are linearly related (‘Corner Angle Salience Variation’ effect). The Alternating Brightness Star illusion also shows that the same corner can be perceived as either bright or dark depending on the polarity of the corner angle (i.e. whether concave or convex) and the direction of the luminance gradient in which the corners are embedded (‘Corner Angle Brightness Reversal’ effect) (Martinez-Conde and Macknik, 2001; Troncoso *et al.*, 2005). For an interactive demonstration of the Alternating Brightness Star illusion, visit http://smc.neuralcorrelate.com/demos/ABS-illusion.html.

Both Vasarely’s nested square illusion and the Alternating Brightness Star illusion are formed by nested corners embedded within luminance gradients. We wondered whether the linear relationship between corner angle and corner salience that we found in the Alternating Brightness Star may not be solely restricted to corners within luminance gradients, but hold true for all corners. This idea may seem counterintuitive at first: one might argue that, in a solid object, sharp corners do not appear more salient than shallow corners, and that corners in general do not appear more salient than edges. However, following the same line of reasoning, one might also claim that the edges of an object do not generally look more salient than the object’s interior, even though it is well established that early visual neurons respond to edges much more strongly than to uniform illumination (de Weerd *et al.*, 1995; Hartline, 1959; Hubel and Wiesel, 1959; Livingstone *et al.*, 1996; Mach, 1865; Macknik *et al.*, 2000; Ratliff, 1965; Macknik and Haglund, 1999).

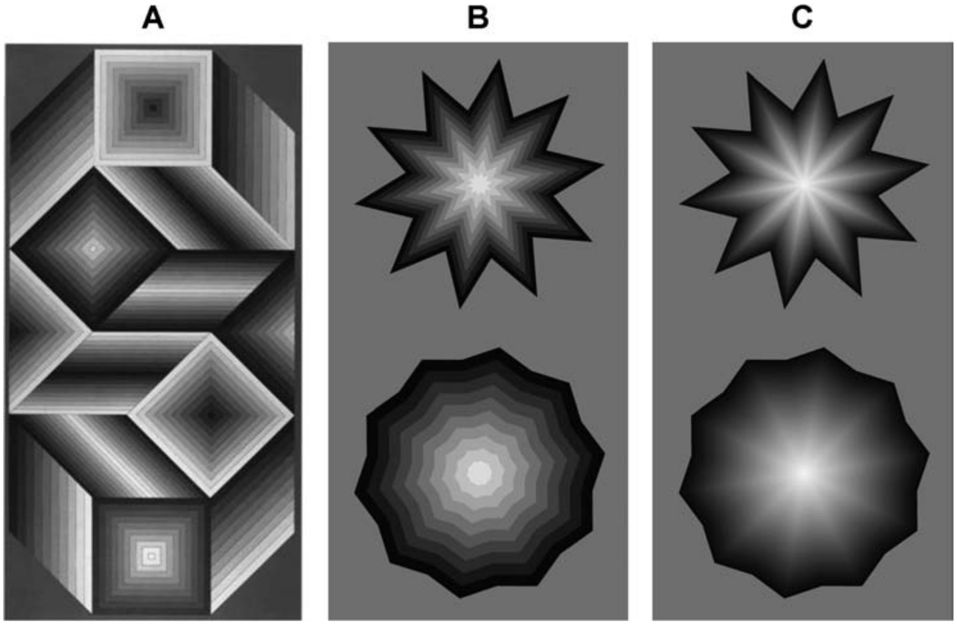

Figure 1. Corners generate illusory folds when embedded in luminance gradients. (A) Vasarely's 'Utem' (1981). Reproduced, with kind permission by the Vasarely Foundation, from Vasarely (1982). Note the four sets of nested squares. The two nested squares of decreasing luminance (from the center to the outside) have bright illusory diagonals. The two nested squares of increasing luminance (from the center to the outside) have dark illusory diagonals. The physical luminance of each individual square remains constant at all points; however the corners of the squares appear perceptually more salient than the straight edges, forming illusory X-shaped folds that seem to irradiate from the very center of each set of squares. (B) and (C) Alternating Brightness Stars (Martinez-Conde and Macknik, 2001; Troncoso *et al.*, 2005). The stimuli are formed by sets of concentric starts, in 10-step (B) or 100-step (C) gradients of decreasing luminance, from the center to the outside. Note that the illusory folds appear dark or bright depending on whether the corners are concave or convex (Corner Angle Brightness Reversal effect) (Troncoso *et al.*, 2005). Also, the illusory folds appear more salient for sharp (top) that for shallow (bottom) corner angles (Corner Angle Salience Variation effect) (Troncoso *et al.*, 2005).

The answer to this paradox may be that the interior of an object appears as bright as the object's edges due to 'filling-in' processes in the extrastriate cortex, which use the information from the object's edges to fill in the inside (de Weerd *et al.*, 1995, 1998; Macknik and Haglund, 1999; Macknik *et al.*, 2000; Pessoa and de Weerd, 2003; Spillmann and de Weerd, 2003; Spillmann and Kurtenbach, 1992). Nevertheless, certain stimuli, such as Mach bands (von Békésy, 1960; Mach, 1865; Ratliff, 1965), allow us to perceive that the edges of an object are in fact more salient than its inside. Here we propose that filling-in processes may normalize the perceived brightness of corners as well. This would explain why corners do not, in general, appear as more salient than edges, despite the fact that corners are very powerful stimuli to center–surround and other early visual system neurons (Troncoso *et al.*, 2005, 2007).

Here we present novel stimuli and illusions that (a) further display the perceptual salience of corners, and (b) demonstrate that the relationship between corner angle and corner salience (Corner Angle Salience Variation) is not limited to corners embedded within luminance gradients, but also applies to corners of solid objects.

Anstis and Ho discovered that simultaneous contrast (for instance, of a grey object displayed against a black or a white background) is greatly enhanced if the grey object flickers from white to black. They called this effect 'Flicker Augmented Contrast': "a flickering test spot looks almost white on a dark surround and almost black on a light surround" (Anstis and Ho, 1998) (see an interactive demonstration of Flicker Augmented Contrast at http://www-psy.ucsd.edu/~sanstis/SAFAC.html). In order to illustrate the perceptual salience of solid (i.e. non-gradient) corners, we developed a new variant of the Flicker Augmented Contrast illusion that amplifies the perceived contrast of corners. If our general model of corner processing in the early visual system (Troncoso *et al.*, 2005, 2007) is correct, then the strength of the Flicker Augmented Contrast illusion should vary parametrically with corner angle (Corner Angle Salience Variation).

Here we test this prediction by using a 2-alternative forced choice (2AFC) design, equivalent to the design we previously used to quantify the strength of the Alternating Brightness Star illusion (Troncoso *et al.*, 2005).

METHODS

Subjects

Ten adult subjects with normal or corrected-to-normal vision (7 females, 3 males; 8 naïve subjects, 2 authors) participated in these experiments. Each subject participated in 10 experimental sessions, of about 1 h each, and was paid $15 per session. Previous to participating in this experiment, naïve subjects received training in a similar 2AFC brightness discrimination task (Troncoso *et al.*, 2005), but they remained naïve as to the hypothesis tested or the results obtained in the preceding study. Experiments were carried out under the guidelines of the Barrow Neurological Institute's Institutional Review Board (protocol number 04BN039).

Experimental design

Most of the experimental details were as in Troncoso *et al.* (2005). Subjects rested their head on a chin-rest, 57 cm from a linearized video monitor (Barco Reference Calibrator V). Subjects were asked to fixate a small cross ($1^\circ \times 1^\circ$) within a 3.5° fixation window while visual stimuli were presented (Fig. 2). To ensure proper fixation, eye position was measured non-invasively with a video-based eye movement monitor (EyeLink II, SR Research).

To test the magnitude of the illusory percept, we conducted a 2AFC brightness discrimination between flickering corners (Comparator stimuli) and non-flickering

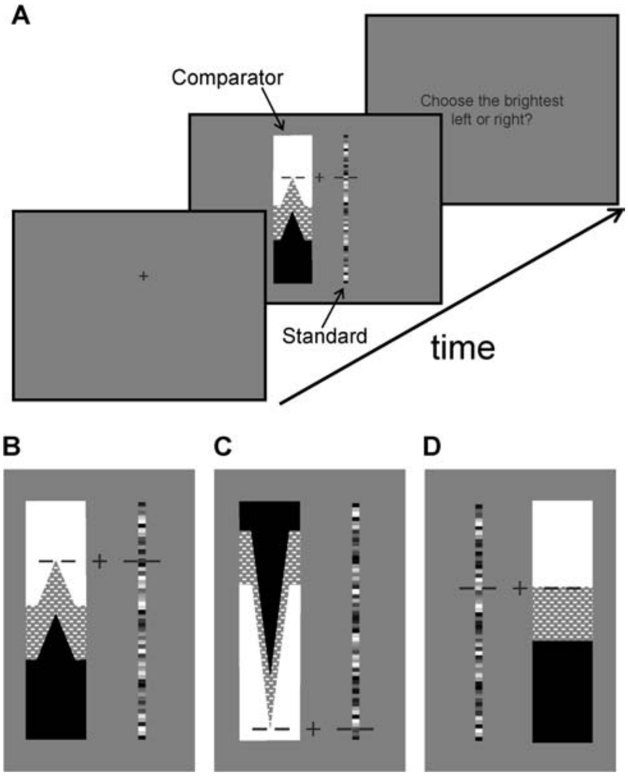

Figure 2. Experimental design. (A) Time course of a single trial. (B), (C) and (D) Three different stimuli presentations of the brightness discrimination task (out of 572 possible conditions, see Methods section for details). The patterned parts of the stimuli represent 15 Hz flicker between 15% and 85% grey (50% luminance over time).

scrambled luminance gradients (Standard stimuli). The Comparator stimuli (flickering corners) gave rise to illusory contrast enhancement; the Standard stimuli were non-illusory. At the beginning of each trial, a red fixation cross was displayed on the monitor. Once the subject fixated the cross, two sets of stimuli appeared simultaneously: the Standard and the Comparator (one to the right and one to the left of the fixation cross, see Fig. 2A).

The Comparator was a flickering corner with one of 13 possible angles: ±15°, ±30°, ±45°, ±75°, ±105° and ±135° plus 180° (flat). The corner flickered between 15% grey and 85% grey (50% luminance over time) at 15 Hz against a black (0%) or a white (100%) background. At this flickering rate, subjects had no difficulty lumping both phases of the flicker together and making judgments of the overall brightness of the flickering region (Anstis and Ho, 1998).

To construct the Standard stimulus, we took a non-illusory gradient (100 steps, 0.06° per step), we divided it into 11 luminance segments and we pseudorandomly scrambled the segments. To match the height of the Comparator we stacked 4 of these pseudorandomly scrambled gradients into a long vertical stripe that contained a total of 44 segments.

The size of the Standard was 24° (h) × 0.5° (w). The Comparator size was 24° (h) × 4° (w). Both Comparator and Standard stimuli were centered at 3° eccentricity. Red indicator bars were displayed to the sides of the Standard and Comparator stimuli, to indicate precisely the parts of the stimuli to be compared (Fig. 2B). The vertical position of the indicator bars over the Comparator and Standard corresponded to the tip of the corner in the Comparator, irrespective of corner angle. The fixation cross was drawn between the indicator bars. The Standard stripe was drawn so that there was an equal chance that any of the 11 possible luminance segments would be pointed to by the indicator bars. The indicator bars were always aligned to the center of one of the luminance segments. After 2 seconds of presentation, all stimuli disappeared. The task of the subject was to compare the brightness of the pixel positioned precisely in the center between the inner ends of the indicator bars on the Standard stimulus, to the brightness of the same point on the Comparator stimulus. The tip of the flickering corner was compared against all possible luminances of the Standard, for all corner angles tested.

Since the discrimination point on the Comparator was always of 50% luminance over time, the physical difference between the Comparator and the Standard was a function of the luminance of the segment within the Standard stimulus pointed to by the indicator bars. Thus if a 50% luminance Standard segment appeared perceptually different from the Comparator, and this varied as a function of the corner angle of the Comparator stimulus, then the difference was not physical and it must have been caused by the illusory effects of corner angle.

Half of the subjects ($n = 5$) indicated which stimulus appeared *brighter* at the discrimination point (the Comparator or the Standard) by pressing the left/right keys on a keyboard. The other half of the subjects ($n = 5$) indicated which stimulus appeared *darker*, to control for potential bias due to the choosing of a brighter stimulus. These two groups were later averaged to control for criterion effects. The design was further counterbalanced for effects of criterion by giving subjects a bright-appearing Comparator in half the trials and a dark-appearing Comparator in the other half of the trials. The experiment was also counterbalanced for potential left/right and up/down criterion effects by presenting the Comparator half the time on the left, and half the time on the right, with the bright half of the background on the upper half of the Comparator half the time. Subjects were not required to wait until the stimuli turned off to indicate their decision, and could answer as soon as they were ready, in which case the stimuli were removed from the screen and the trial ended at the time of the subject's key press. Standard, Comparator and background all had the same average luminance (50% grey) in all conditions. If the subject broke fixation (as measured by Eyelink II), the trial was aborted, and replaced in the pseudorandom trial stream to be re-run later.

The summary of all conditions ($n = 572$) was as follows:

- 2 screen positions: left and right;
- 2 background configurations: white on top, dark on top;
- 13 corner angles: ±15°, ±30°, ±45°, ±75°, ±105° and ±135° plus 180°;
- 11 Standard luminances: 5%, 14%, 23%, 32%, 41%, 50%, 59%, 68%, 77%, 86% and 95%.

For each subject, each combination of background configurations (i.e. white-on-top *vs* black-on-top) and corner angle was presented 20 times, over 10 sessions (2 trials per session per combination).

Psychometric curves were obtained fitting the data with logistic functions using a maximum likelihood procedure (Wichmann and Hill, 2001).

RESULTS

We found that sharp corner angles generated qualitatively stronger illusory effects than shallow corner angles, as predicted by the Corner Angle Salience Variation effect (previously described for Alternating Brightness Star stimuli (Troncoso *et al.*, 2005, 2007)). This indicated that Corner Angle Salience Variation is not a property seen solely on corner gradients, but can be generalized to solid corners as well.

To objectively quantify the strength of the illusion, we calculated the Point of Subjective Equality (PSE) for each Comparator (i.e. its matching luminance in the non-illusory Standard). To do this, we determined the point on the psychometric curve (Fig. 3A) in which the comparator appeared more salient than the Standard in 50% of the trials (averaged over all subjects, and collapsed across the following conditions (see inserts 1–4 in Fig. 3A): convex corner against black background; concave corner against black background; convex corner against white background; and concave corner against white background). We calculated the illusory enhancement for each corner angle as the difference between 50% luminance (the objective luminance value of the stimulus) and the PSE for the angle tested (Fig. 3B). We found that the perceived salience of the corner varied linearly with the angle of the corner. Sharp angles generated stronger illusory salience than shallow angles (Corner Angle Salience Variation), as also found previously for corners embedded within luminance gradients (Troncoso *et al.*, 2005).

Figure 3C, D shows the same results, but conditions 1 and 2 (see figure inserts), corresponding to corners presented against black backgrounds (in which corners appeared perceptually bright) are plotted separately from conditions 3 and 4, corresponding to corners presented against white backgrounds (in which corners appeared perceptually dark). PSEs for corners presented against white backgrounds were lower than the PSE for the control (i.e. the 180° angle), whereas PSEs for corners presented against black backgrounds were higher than the PSE for the control. Note that the value corresponding to the 180° condition (when presented against a white background) is an outlier, as indicated by unfilled symbols in Fig. 3B (collapsed) and 3D (uncollapsed). Therefore the corresponding regression lines in

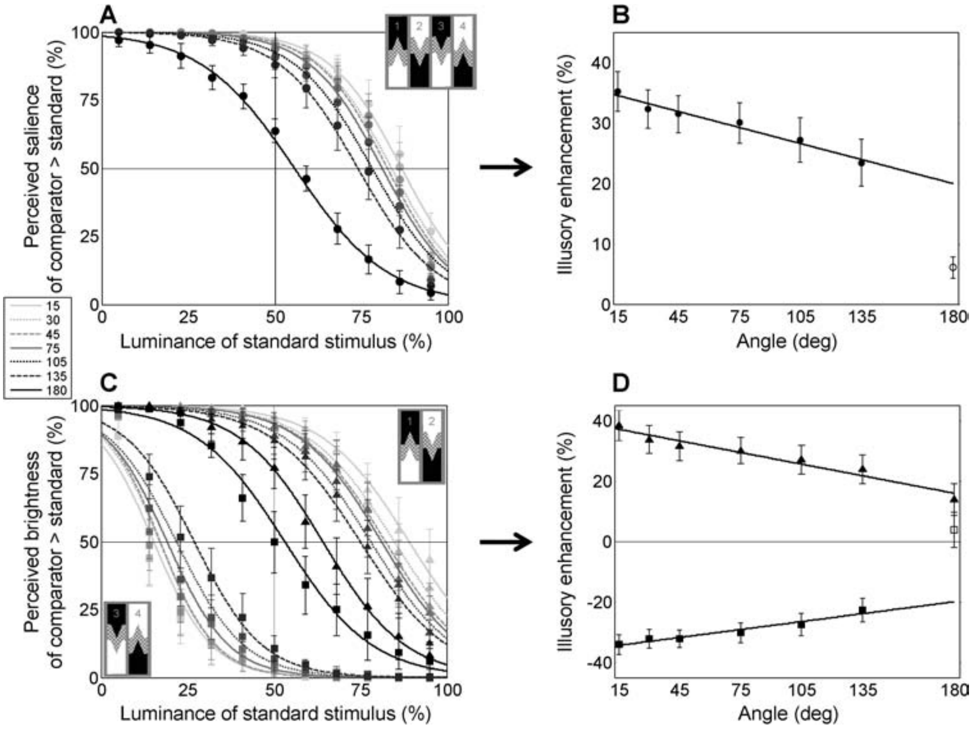

Figure 3. Results. (A) Psychometric functions for the different corner angles are plotted in different line styles. The conditions where the tips of the corners looked bright and dark are collapsed. (B) Illusory enhancement of the points of subjective equality (PSEs; the 50% chance crossing points from panel (A)) with respect to the objective value of the stimulus (50% luminance) for the different corner angles. The illusory enhancement decreases linearly as the corner angle becomes shallower (Corner Angle Salience Variation effect). (C) Same data as in (A), but the conditions where the tips of the corners looked bright (filled triangles), and the conditions in which the tips of the corners looked dark (filled squares) are uncollapsed (see inserts). The PSEs for conditions 1 and 2 (see insert) fall above the point of 50% luminance in the Standard stimulus. The PSEs for conditions 3 and 4 (insert) fall below the point of 50% luminance in the Standard stimulus (except for the 180° angle). (D) Illusory enhancement of brightness (filled triangles) and darkness (filled squares) perception, as a function of corner angle. Given that the value corresponding to the 180° condition (when presented against a white background) is an outlier (unfilled symbols in (B) and (D)), the corresponding regression lines have been fitted to all the other corner angles: 15°, 30°, 45°, 75°, 105° and 135°. Error bars in (A), (B), (C) and (D) represent the ± standard error of the mean for all subjects in each condition ($n = 10$). Psychometric curves in (A) and (C) were obtained fitting the data with logistic functions using a maximum likelihood procedure (Wichmann and Hill, 2001).

Fig. 3B and 3D have been fitted to all the other corner angles: 15°, 30°, 45°, 75°, 105° and 135°.

DISCUSSION

Our results show that the Corner Angle Salience Variation effect is not limited to corners embedded within luminance gradients (as in the Alternating Brightness

Star), but it also applies to solid corners. This suggests that the linear relationship between corner angle and corner salience may be a fundamental principle of corner perception, with important implications for the brain mechanisms underlying early visual processing of shape and brightness (Troncoso *et al.*, 2007). For instance, the results imply that the neural circuits underlying corner perception should generate activity that correlates linearly with corner angle. Thus the linear relationship between corner angle and corner salience may be a powerful tool in determining the neural mechanisms responsible for corner perception.

The relationship between corner angle and corner salience in solid corners had been previously reported in a short note by von Békésy, who qualitatively described the varying extents of apparent saturation in individual yellow gelatin wedges cut at different angles (von Békésy, 1968). However, no quantification of this effect was carried out. Here we took advantage of the Flicker Augmented Contrast paradigm to enhance the simultaneous contrast produced by varying corner angles, and to objectively quantify the Corner Angle Salience Variation effect in solid corners. We used Flicker Augmented Contrast because, upon qualitative observation, the effect of corner angle on solid corners appeared to be substantially stronger in Flicker Augmented Contrast corners than in non-flickering corners. Therefore by using Flicker Augmented Contrast we were able to magnify the strength of the effect and to establish its existence more easily and clearly. Our results confirm and extend previous findings on Flicker-Augmented Contrast (Anstis and Ho, 1998). However, these experiments have no bearing on the potential mechanisms underlying the Flicker-Augmented Contrast illusion *per se*, but on how different shapes (namely, corners of different angles) modify perceived brightness under Flicker-Augmented Contrast.

Another visual illusion, 'Unfilled Flicker' (Macknik *et al.*, 2000), also demonstrates qualitatively that corners of solid objects are more salient than straight edges. The Unfilled Flicker illusion shows that a slow-flickering stimulus appears filled-in (just as a non-flickering solid object appears filled-in), but if one flickers the object fast enough, the filling-in effect is foiled to some extent, and the solid object appears like an empty frame (allowing one to see that the edges of the object are more salient than its interior). For an interactive demonstration of the Unfilled Flicker illusion, visit http://macknik.neuralcorrelate.com. The Unfilled Flicker illusion also shows that corners are more salient than straight edges (previously unreported). This is illustrated by the fact that, even when filling-in partially fails in the Unfilled Flicker condition, its spatial extent is nevertheless larger for corners than for edges. That is, when the fast-flickering object appears like an empty frame (due to partial failure of filling-in), the inside of the object is nevertheless filled-in for a longer distance — measured from the object's contour to its center — when starting from the object's corners than when starting from the edges. Figure 4 schematically depicts the Unfilled Flicker percept.

Various artworks by Victor Vasarely also show that solid corners are more salient than straight edges. Previous to developing the 'nested-squares within luminance

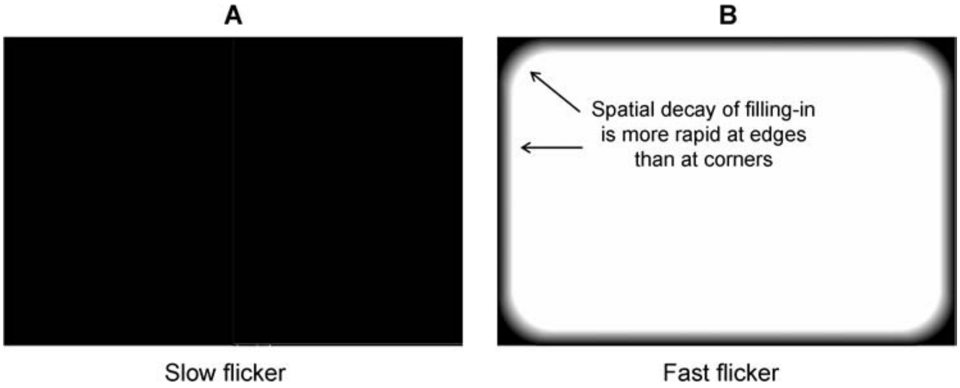

Figure 4. Schematic representation of the perception of the Unfilled Flicker illusion (Macknik *et al.*, 2000). (A) A slow-flickering black rectangle presented against a white background appears to be filled-in: the interior appears as salient (i.e. as black) as the edges of the rectangle. (B) When the same rectangle is flickered very fast (6.67 Hz or higher, 33% duty cycle), filling-in is partially foiled, so that the solid rectangle now appears to be an empty frame. Filling-in decays more rapidly across space (from the contour of the rectangle towards its center) for the edges than for the corners.

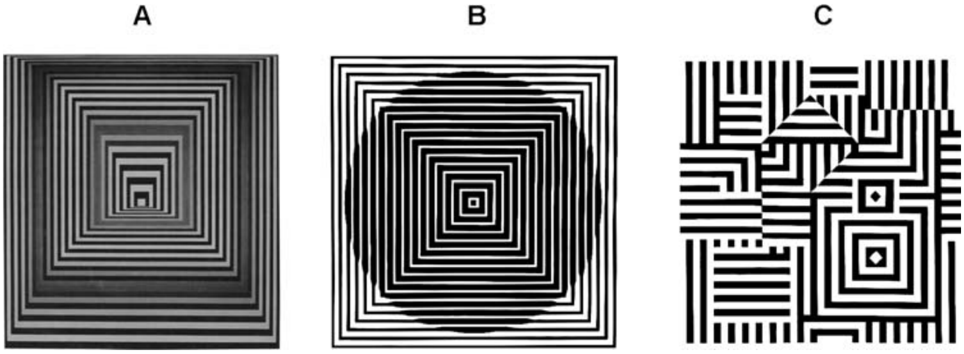

Figure 5. Vasarely's nested-square patterns of 'solid' corners (i.e. corners not embedded within luminance gradients). One can observe subtle illusory folds running across the diagonals of the nested squares. (A) From Vasarely (1970). (B) Vasarely's 'Interference' (1958) (Vasarely, 1965). (C) 'Riu-Kiu-C' (1960). Reproduced with kind permission from the Vasarely Foundation.

gradients' series ('Arcturus' (Vasarely, 1970)), Vasarely experimented with patterns of interleaving black and white nested squares, without using the intermediate gradations of luminance between black and white that characterize the post-'Arcturus' nested squares. Figure 5A–C shows three examples: in these, the illusory folds generated by the concentric squares are more subtle than in Fig. 1A, and they look more similar to illusory contours — such as those in Kanizsa's triangle — than to illusory brightness folds. Nevertheless, it is evident that an alignment of successive corners gives rise to a more salient percept than an alignment of straight edges.

A recurrent theme in Vasarely's art is the generation of illusory percepts from deflections or discontinuities in edges, such as corners, curves and terminators.

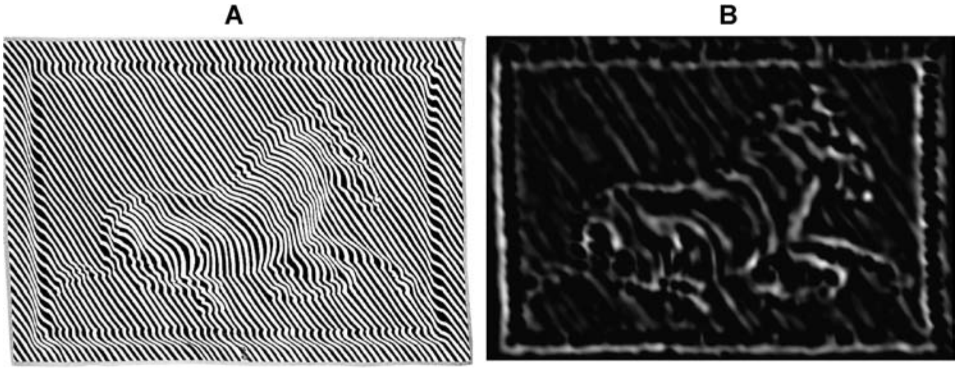

Figure 6. Vasarely's 'Zebra' (1938), from Aknai and Sarkany (2000). (A) The zebra has no actual contour: our brain samples the points of maximum curvature (i.e. the deflections in the diagonal lines), and connects them together to create the percept of a galloping zebra. Reproduced with kind permission from the Vasarely Foundation. (B) The image in (A) has been convolved with a center–surround filter. This simple transformation, which is also performed by the center–surround receptive fields of the visual system, makes the contour of the zebra highly salient.

Note that the zebra in Fig. 6 is solely constructed from small deflections in the parallel lines that run diagonally across the surface of the image. The zebra has no actual contour: our brain samples the most salient parts of the image (i.e. the points of maximum curvature), and connects them together to create the percept of a galloping zebra. When the image is convolved with a center–surround DOG filter (Enroth-Cugell and Robson, 1966; Rodieck, 1965) (i.e. to enhance local contrast; see further discussion below), the contour of the zebra pops out (Fig. 6B).

In 1975, Jameson and Hurvich proposed that the illusory diagonals in Vasarely's classic nested-squares (in which corners are presented within a luminance gradient) "are generated as pure physiological-contrast light" (Jameson and Hurvich, 1975). A few years later, Hurvich suggested that this illusion could be accounted for by center–surround receptive fields (Hurvich, 1981). Hurvich's hypothesis was that the contrast between the center and the surround regions of the receptive field would be stronger along the corner gradients than along the edge gradients of the nested squares, resulting in increased perceived brightness at the corners. We previously proposed (Troncoso *et al.*, 2005, 2007) that center–surround models could be applied more generally to corner gradients of all angles (i.e. as in the Alternating Brightness Star) and even to solid corners, such as in the examples discussed here. Because surface corners increase local contrast, sharp corner angles result in higher local contrast than shallow corner angles and flat edges. Given the geometry of center–surround and other early receptive fields, sharp solid corners may create hotspots of high local contrast (see also Fig. 6 of Troncoso *et al.*, 2005). This would result in all sharp corners appearing more salient than shallow corners and straight edges. This does not eliminate or diminish the need for higher-level circuits — such as those provided by curvature-selective neurons in the extrastriate cortex

— to further process and analyze corner and curvature information, especially in the context of shape processing and object recognition.

The same reasoning relating corners to center-surround geometry may be applicable to curvature in general (i.e. to all discontinuities in edges, such as curves, angles and terminators — any point at which straight lines are deflected). For instance, because terminators generate hotspots of high local contrast for early receptive fields (when compared to non-terminated lines and edges), one should expect an alignment of terminators to give rise to illusory folds or contours. This is illustrated in the classic Abutting Grating illusion (Fig. 7C) reported by Kanizsa, in which one can perceive an illusory border defined solely by the adjacent terminators of two contiguous surfaces (Kanizsa, 1974). Before Kanizsa discussed the Abutting Grating illusion in 1974, Vasarely had already developed abutting-grating-like contours (Fig. 7A) and other patterns that involved the alignment of terminators. Figure 7A and 7B shows some of Vasarely's artworks illustrating this concept. All the objects

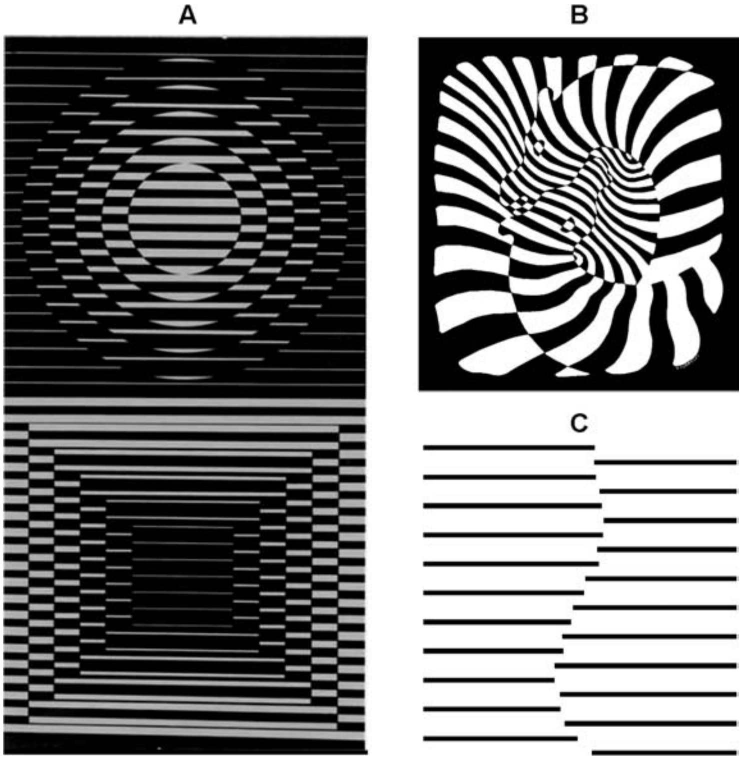

Figure 7. Abutting gratings. (A) Abutting-grating-like images by Vasarely (1970), reminiscent of the Abutting Grating illusion described by Kanisza (C). The images contain no actual concentric circles (top) or squares (bottom). (B) Vasarely' 'Zebres' (1939) (Aknai and Sarkany, 2000). (C) The classic Abutting Grating illusion (Kanizsa, 1974). (A) and (B) Reproduced with kind permission from the Vasarely Foundation.

represented in these patterns — the concentric circles, the concentric squares, the zebras — are defined by the alignment of terminators.

To conclude, one could say that art, illusions, and visual science have always been implicitly linked. Visual artists generally use their implicit knowledge of perception — especially illusory perception — to achieve specific results in their artworks. For instance, if the painter uses perspective and proportions adequately, a flat canvas will convey a sensation of depth. The birth of the Op-art (for 'optic art') movement, founded by Victor Vasarely, made the link between art and illusory perception an artistic style in and of itself.

The Op-art movement was born simultaneously in Europe and the US in the 1960s with a special focus on visual illusions as an art form *per se*. The term Op-art was coined by *Time Magazine* in 1964 and became very popular after the exhibition 'The Responsive Eye' was held at the MoMA in New York, in 1965. However, many of the previous works by Victor Vasarely exemplify what would be later called Op-art (see some of Vasarely's early art in Figs 5–7). Motion illusions were a very strong component of Op-art, as one can appreciate in many of the works of Victor Vasarely and Bridget Riley. However, many other aspects of perception were also explored, such as geometrical relationships, impossible figures, and other illusions concerning brightness, color and shape perception. Some of the illusions created and systematically explored by Victor Vasarely are excellent examples of how the visual arts have sometimes preceded the visual sciences in the discovery of fundamental vision principles, through the application of methodic — albeit perhaps more intuitive — research techniques. One of our goals in this paper was to acknowledge how some of Vasarely's best known series, the 'nested squares' paintings (and other related artworks), have given us significant insight into how corners, angles, curves and terminators affect the appearance of shape and brightness in our brains.

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