A new "tilt" illusion reveals the relation between border ownership and border binding

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The "association field" models of contour detection predict specific spatial conditions for linking or grouping neighboring elements into smooth contours. We previously suggested that the "association field" model may account for perceptual binding of near-collinear luminance edges of same contrast polarity and their consequent unification into a unique contrast border with illusory tilt. This approach is now developed into a new version of the tilt illusion, the *seesaw* illusion, in which the contrast border is perceived as inverting concave-convex illusory curvature when background luminance is inverted, indicating that contrast polarity must be incorporated into the notion of "association field" to account for the *seesaw* illusion. We found that although tile-edge segmentation into alternating black-white segments produces conflicting local tilts, the illusion remains, up to 16 arcmin edge distance. This occurs at extreme background luminance for long segments (where only congruent edge segments of higher contrast bind, the others being perceptually assimilated into the background surface) and, when segments are too short for their orientation to be detected, at all background luminance values except that equidistant from black and white stripes. Our findings provide further confirmation that these are striking border ownership phenomena, demonstrating that figure/ground organization precedes perceptual binding of edges through association fields.

Introduction

An important task for survival is to decide whether fragmented contours forming the retinal image belong to the contour of a single object. Performing this task may lead to illusory distortions of straight contours (see Westheimer, 2008 for a new account of these effects) that may appear either tilted, as in the Zöllner, Fraser and Café Wall illusions, or curved, as in the Hering and checkered illusion of Kitaoka (1998).

One particular kind of tilt illusion, shown in Figure 2A, first presented by Kitaoka, Pinna, and Brelstaff (2004) and later elaborated by Roncato (2006), occurs when near-collinear luminance edges of same contrast polarity bind: the resulting continuous contour perceived appears perceptually tilted. This illusion is not novel on the phenomenal level, but instead we have a new explanation to apply, based on the notion of local "association field" illustrated in Figure 1, defined as a set of local orientation signals that radiate by contour extrapolation in all directions (Field, Hayes, & Hess, 1993; Shipley & Kellman, 2003). Inspired by this model we have studied the spatial conditions by which local oriented edges are combined into a unique spatial contour using a yes-no detection paradigm (Roncato & Casco, 2003, 2006), and found the precise values of the spatial parameters (relative separation and/or alignment) that allow neighboring edge segments to bind into a smooth contour, in contrast with the values that degrade the perception and cause the edges to no longer conform to a smooth contour. Our previous results show that binding occurs between the association field projections propagating from the two edges, and that these edges are perceived as a unique contour with illusory tilt, providing that two conditions are met: first, the projections have to have the same contrast polarity and, second, their vertical and horizontal distances have to be short: their vertical misalignment (D2) has to be smaller than 7 arcmin and the horizontal gap (D1) has to be smaller than 13 arcmin. In this way, when the edges have the same contrast polarity and are sufficiently close, they perceptually bind throughout their association field projections and appear to be tilted, whereas whenever these spatial constraints are not fulfilled and/or the edges, having opposite contrast polarity, do not respect what we call the *contrast polarity rule,* the binding does not occur or else occurs with no illusory tilt.

The aim of the present study is twofold. First, we present a new illusion that follows the contrast polarity rule; it is derived by modulating the background luminance in configurations like those in Figure 2. This
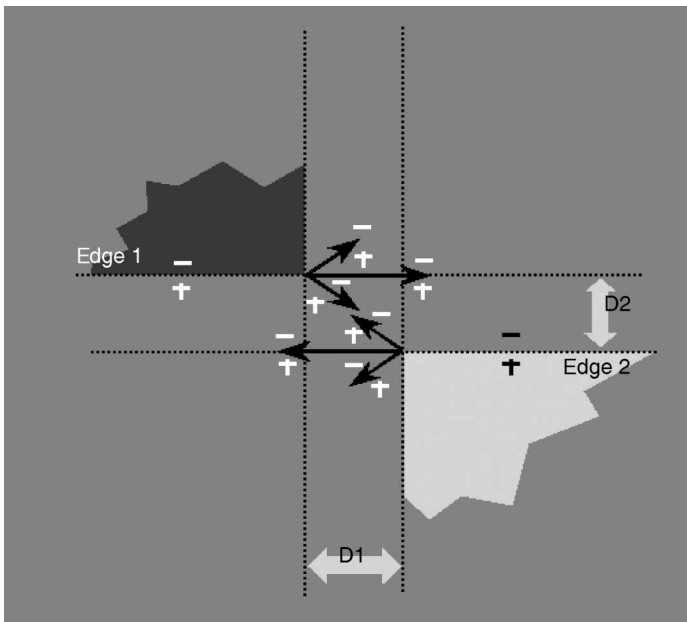
Figure 1. Edge 1 and Edge 2 separated by D1 and D2, and their association field projections (black arrows), labeled by ± to indicate contrast polarity. With appropriate D1 and D2, the two association field projections that are aligned, iso-oriented and of the same contrast polarity bind.

illusion demonstrates that, as distinct from other illusory distortions, the direction of perceived distortion depends on the direction of contrast between the edges and the background: as illustrated in Figure 3 (and demo), alternating the background luminance from light to dark alternates the contrast polarity, producing what we term a *seesaw* illusion, because the perceived curvature cyclically changes between convex and concave, confirming that contrast polarity is essential in binding contrast edges and has to be incorporated into the notion of "association field". Whereas contrast polarity has been shown to play a role in the formation of illusory edges resulting from the surface completion (He & Ooi, 1998), but Prazdny (1983) shows the opposite, the role of contrast polarity for binding of disconnected elements into contours is an open issue (Field, Hayes, & Hess, 2000) and our data show that for binding near collinear contrast edges, the local association field has to preserve the contrast polarity of the edges.

The second aim of our study was inspired by the consideration that edge segments whose "local association fields" interact are part of a figure. Our visual experience tells us that the visual system is compelled to interpret contrast borders as part of adjacent surfaces. The assignment of borders to regions is a basic task of vision (Kanizsa, 1979). Several physiological studies have shown that the response of cells selective for the contrast polarity of the border can depend strongly on contextual influences from outside their classical receptive field: the response of cells selective to contrast polarity in V1, V2 and V4 changes depending on whether the border is

presented as the right side of a light square or the left side of a dark square (Zhou, Friedman, & von der Heydt, 2000). These results suggest that even the earliest cortical response to contrast polarity cannot be dissociated from figure-ground segregation based on luminance contrast. These physiological data provide a theoretical construct for our second question, that is, whether binding of near collinear edges with the same contrast polarity presents contextual effects and is part of a more general process of perceptual organization. Based on the crucial property of the association field model in Figure 1 that the projections of the local association field preserve the contrast polarity of the edge, our second question is how contrast polarity is assigned to the association field projections. The projections could preserve the contrast polarity of closest segment of the edge (outer segment) or of the whole edge. In principle, when the edge belongs to a striped tile and is made up of black and white alternating segments, no curvature should be perceived on the basis of the local tilts of edge segments, because either they are too short (Figure 2B), or because these alternate in direction (Figure 2C). But, as Figure 3 and the demo show, when background luminance is not equidistant from the black and white stripes the illusion is restored. With long segments, although local tilts are conflicting because they alternate in direction, the illusory curvature is perceived at extreme background luminance (Figure 3, top). When the stripes are too narrow and edge segments are too short to provide local tilt information, the illusion is still perceived even at background luminance close (but not equal) to that intermediate (Figure 3, bottom) and this suggests a second contextual effect: the distortion is induced by the tile edge (tile-induced) not the stripe edge (locally-induced). To investigate the contextual effects that allow solution of these binding problems, we measured background luminance thresholds (which delimits the range of background luminances at which the illusion is perceived) as a function of the length of edge segments.

General methods

Stimuli

As in our previous studies the stimuli used in Experiment 1 (Figure 3) and Experiments 2a and 2b (Figure 4) were made up of rows of tiles that formed contrast edges with the uniform background. Stimulus area (187 × 110 mm) subtended 12.5 × 7.87 deg of visual angle. The tiles were arranged in counterphase, so that the right lower corner of the tile in the upper row met the upper left corner of the lower tile and vice versa. These two corners were covered by an oval shape (8 × 12 mm, 0.54 × 0.8 deg) containing a central horizontal bar (7 × 1.3 mm, 0.47 × 0.08 deg) whose longer axis was aligned with the tile
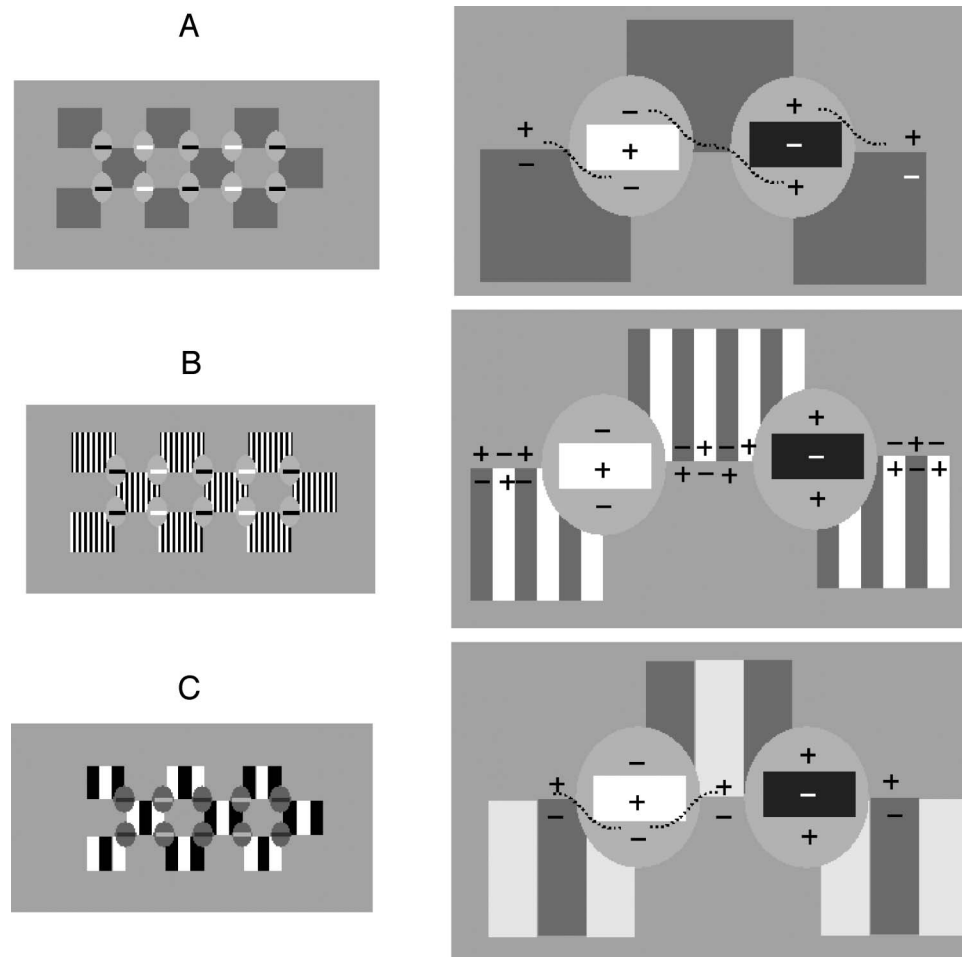
Figure 2. Tiles, arranged in counterphase, had their corners covered by an oval containing a central horizontal bar with the longer sides misaligned with respect to the tile edge. The enlargement on the right shows the contrast polarity and binding path of edges having same contrast polarity (dotted lines). Note that this path correctly predicts the overall direction of distortion. (A) Tiles of uniform gray (not used in the experiment). (B) Tiles made up of stripes that are too narrow to produce locally-induced tilts. If the curvature is perceived, it is "tile-induced," i.e., resulting from tile-background contrast polarity. (C) Widely striped tiles allow the binding between edges and horizontal bar to be "locally-induced". Note that although binding paths are in opposite directions, overall distortion is perceived at extreme values of background luminance.

edges. This made the sides of the horizontal bar and the tile edges near to collinear. In this way, the segments of the tile edge (or its segments) could bind with either the upper or lower edge of the horizontal bar, depending on which of the two respected the contrast polarity rule, and this resulted in either clockwise or counter clockwise tilts.

In Experiment 1, the tiles, 13 × 13 mm (0.87 deg × 0.87 deg), were segmented into alternating black (.7 cd/m^2) and white (71.02 cd/m^2) vertical stripes, with height of 13 mm and width that depended on spatial frequency: low (1.7 c/deg), medium (3.4 c/deg) and high (10.9 c/deg). In Experiments 2a and 2b, the tiles size was 18 mm (1.21) × 13 mm (0.87). The edge of the tile was made up of the shortest side of the stripes and consisted of segments of alternating black-white luminance that, only in Experiment 1, swapped position from one tile to the next. In this way, corresponding edge segments of two contiguous tiles

had opposite color and thus produced at the corners non-congruent tilts of alternating direction. Tile mean luminance was 35.86 cd/m^2. The luminances of the oval region and that of the superimposed horizontal black (light) bar were: 16.5 and 5.6(38.6) cd/m^2, (Experiment 1a), 42.6 and 10.5(71.02) cd/m^2 (Experiment 1b). The black and white horizontal bar edges had close Weber contrast in Experiment 1a (1.9 vs. 1.4) and distant in Experiment 1b (3.0 vs. .7). Luminances of Experiment 2a were 23.9 and 7.1(39.1) cd/m^2.

Each stimulus consisted of two subpatterns, in mirror-like symmetry around the vertical axes. Each subpattern was composed of 14 tiles arranged in three rows. In the central row, the tiles were in counterphase with respect to those in the rows above and below. Thus, since the two subpatterns mirrored each other, the four central horizontal bars had the same color. All other conditions remaining
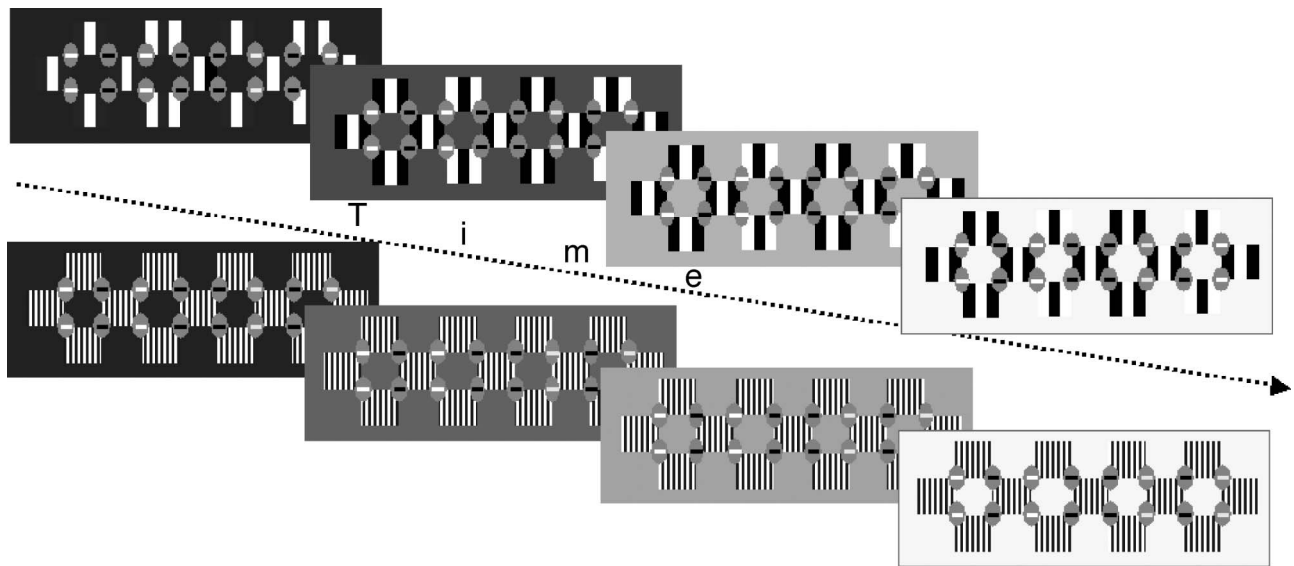
Figure 3. Four D*i* stimuli (see General methods), chosen from the series of 76 stimuli used in Experiment 1. Toward the right they form an "ascending series," i.e., the same stimulus appears against a background progressively lightening from black to white. The perceived convexity/concavity is illusory. Note the inversion of the illusory concavity/convexity effect when the background luminance changes from dark to light.

fixed, the perceived curvature switched in direction when the color of the four central bars switched from dark (D) to light (L). For each of these two stimuli, their mirrored subpatterns linked at the level of the central row (internal, *i*) or of the upper and lower rows (external, *e*), and this also produced a switch in the perceived curvature. To summarize, when perceived, the illusory curvature was either concave or convex, and this depended on the particular combination of background luminance and stimulus configuration (D*i*, D*e*, L*i*, L*e*).

Procedure

A group of 10 naïve subjects with normal vision participated in each experiment. Experiment 1 consisted of 12 sessions, resulting from the factorial combination
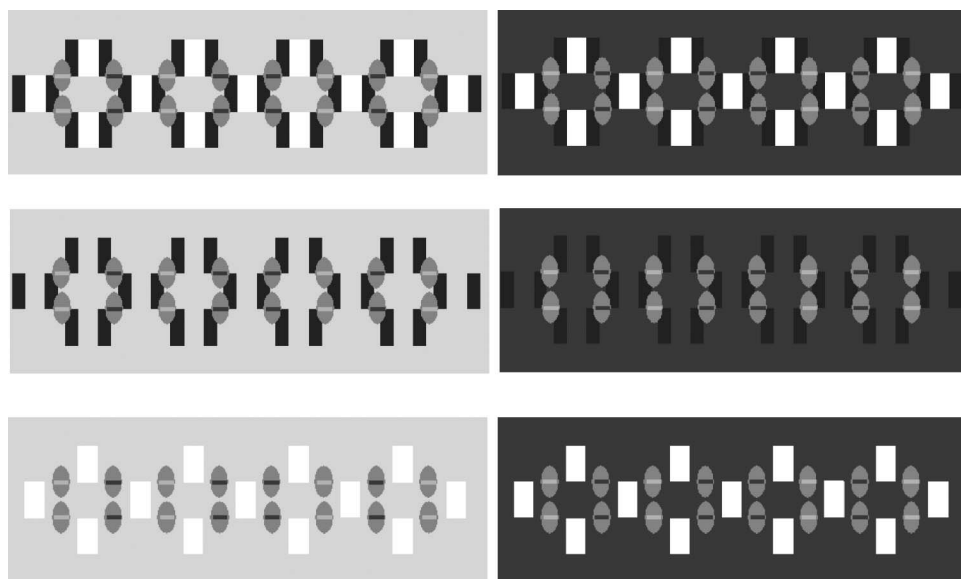

Figure 4. Examples of stimuli used in Experiment 2a. The two columns reproduce the same stimulus configurations with two different background luminances. The same stimulus configuration is reproduced in the three rows, but with either the center (middle row) or the outermost stripes erased in the stimulus. In the upper row, the distortion depends on tilts from segments of higher contrast: the black on the left and the white on the right. In the two other rows, the remaining stripe determines the tilt even if it is central.

of the four basic conditions and three spatial frequencies. By using the psychophysical method of limits, each stimulus was presented with 76 background luminance levels that were either increased or decreased in ascending and descending series, respectively. Average step luminance was .95 cd/m^2. In each trial observers were instructed to say "yes" continuously until no longer they perceived the curvature (as either concave or as convex). Thresholds were defined as the background luminance level at which subjects no longer perceived the curvature. In Experiment 2a, the session was made up of 48 trials—that is, from the factorial combination of the four basic configurations, each replicated six times to obtain six different pairs of stripe luminance (see Figure 4 for an example) and two background luminances. Subjects performed a binary choice task and had to say whether they perceived concave or convex curvature by pressing one of two alternative keys on the computer keyboard. Two of the configurations in Figure 4 (top and bottom right) were also used as stimuli in Experiment 2b. In Experiment 3 instead, the stimuli were the stripe/s in one tile of these two configurations. Using the method of limits, subjects had to say "yes" until no longer they perceived either the curvature (in Experiment 2b) or no longer perceived the darker stripe, in Experiment 3.

Stimuli were viewed on a flat screen computer monitor (Nec Multisync 95F) at 85 cm viewing distance. Each experiment was preceded by five practice trials used to familiarize participants with the stimulus configuration and task of judging the overall curvature without relying on local tilts.

Experiment 1

To address our first question of whether the perceived direction of curvature depended on the direction of contrast, we opposed the effect of contrast polarity, manipulated within session by varying background luminance, to the effect of the amount of contrast at the level of the edges participating to the binding process, i.e., those of the horizontal bar, manipulated across experiments. If contrast polarity is the crucial variable, background luminance but not contrast will be responsible for the perceived direction of curvature. Furthermore, the variation of spatial frequency of the striped tile enabled our second question to be addressed, i.e., whether the association field projections preserved the contrast polarity of closest segment of the edge (outer segment) or of the whole edge. In fact, only this second possibility explains two perceptual paradoxes: at low spatial frequencies (large edge segments of striped tile), no overall distortion should be perceived because locally-induced tilts are incongruent (due to a 180° phase shift from one tile to the next, as described under General methods), and yet the *seesaw* illusion is perceived at extreme background

luminance. At high spatial frequencies, although the *seesaw* illusion should not be perceived because edge segments are too short, the curvature is clearly visible, but only if background luminance is not exactly equidistant from black and white bars because this would abolish the contrast edge and cause the illusion to disappear. We put forward the hypothesis that at both low and high spatial frequencies, contextual (non-local) effects account for perceiving the curvature in a condition for which local tilts cannot account, and we attempt to define these effects.

Results and discussion

Background luminance thresholds are plotted as a function of tile frequency in Figure 5. The ANOVA executed to compare thresholds, with one between-group factor (Contrast) and four within-group factors (Background, Frequency, Color, Link) show a non-significant three-way interaction of Contrast × Background × Frequency, $F(2,36) = 2.1$, $p > .05$, indicating that the effect of dark (ascending series) or light (descending series) background depended on frequency in a similar way in Experiments 1a and 1b. This confirms our first hypothesis that is the contrast polarity, not the amount of contrast at the level of the horizontal bar (similar in Experiment 1a and very different in Experiment 1b), that is the crucial variable for perceiving the *seesaw* illusion. Indeed, the effect of contrast at the level of the horizontal bars did not differ in the two experiments, $F(1,18) = .5$, $p > .05$, and cannot account for the differences between experiments at the medium frequency, which could be due to the luminance of the ovals that was not equidistant from average luminance in Experiment 1a.

Our results also confirm our second prediction that although local tilts were non-congruent, providing that the background luminance was not exactly intermediate the curvature was perceived, although within a different range of background luminances at low and high spatial frequencies: large range at high spatial frequency and extreme values at low spatial frequency. Indeed, the effect of Frequency × Background (ascending vs. descending series) interaction was significant, $F(2,36) = 114.4$, $p < .001$. At high frequencies (short edge segments), threshold was close to, although not exactly, average luminance, indicating that a small difference between mean luminance of the tiles and that of background produced the illusion. At low frequencies, where the edge segments have well defined orientation, the curvature is still perceived provided the difference in luminance between either black or white stripes and background is so small that they are perceptually assimilated into a unique surface.

The interaction between spatial frequency and background luminance reveals two contextual effects. At high frequency, the edge segments are too short to induce local tilts, and yet the curvature is perceived on the basis of
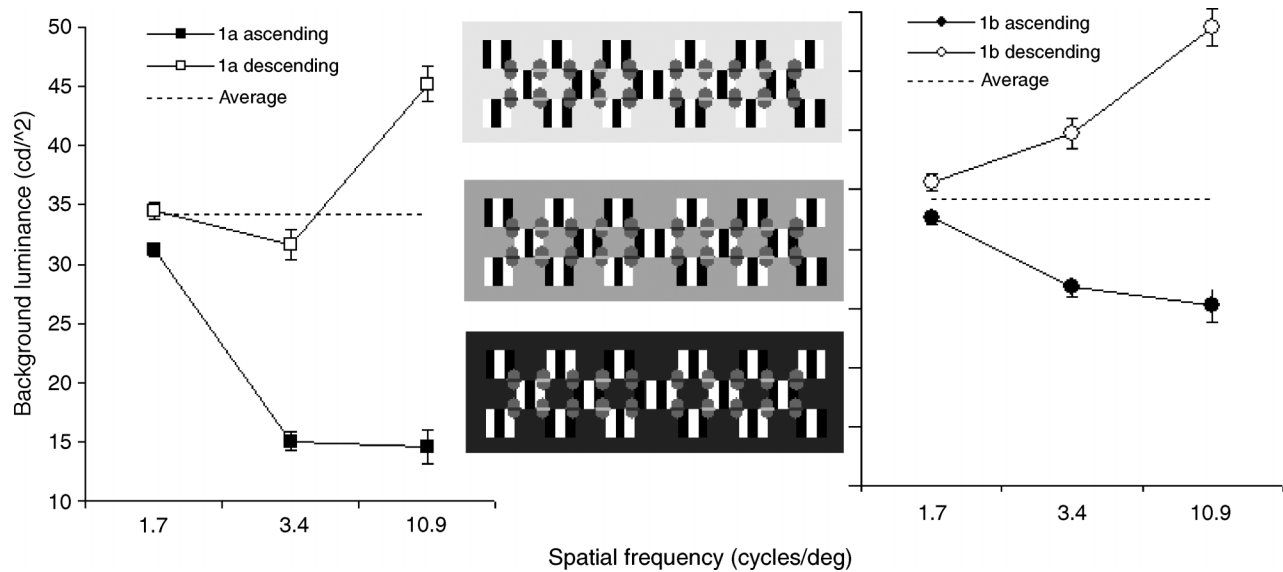
Figure 5. Results of Experiment 1a (left) and 1b (right). Background luminance thresholds—for which there is no longer the "concavity/convexity" effect—are shown for each tile frequency: 1.7, 3.4 and 10.9 cycles/deg in series starting from dark (black symbols) and light background (white symbols). The broken line indicates average luminance between black and white stripes. Bars indicate standard errors.

tile-induced tilt, and results from binding of local association field projections that have a contrast polarity computed at the level of the whole tile edge. At low frequencies, the edge segments are long enough but produce locally-induced tilts that are non-congruent and even so the curvature is perceived, though only when background luminance is very far from tile mean luminance and close to either black or white stripes, which are perceptually assimilated to the ground whereas the other stripes—having high contrast with the ground—participate in the binding process.

The high spatial frequency effect demonstrates that contrast polarity is computed on the whole figure that the border delimits when segments are short. That is, although the binding occurs between short projections of the local association field by extrapolation of outer segments, the visual system assigns these projections the contrast polarity of the tile-edge, not of the outermost edge segment. The second interesting result is that although low spatial frequencies reintroduce non-congruent tilts, the illusion is still perceived in some appropriate contrast conditions between background and inner segments, i.e., when background is very similar to either the black or white segment such as to neutralize the tilts from these segments and allow only non-conflicting tilts.

Experiment 2a

Experiments 1a and 1b demonstrate that figure-ground organization precedes contour binding. Once the figure is segmented from the ground only congruent local tilts remain available and all are formed by edge segments of the same color. Let us now suppose that corresponding stripes in contiguous tiles (saying the central ones) all have the same color (no phase shift is applied, see Figure 4). The outermost ones also have the same color and therefore produce congruent tilts. What direction of curvature is perceived when two sources of congruent tilts are available? Is the curvature resulting from the outermost tilts preferred, or does the curvature depend on contrast of either inner or outer segments?

Method
Stimuli

Examples of the stimuli used are shown in Figure 4 and Table 1. The tiles were arranged in a symmetric pair of three-row configurations, using the same parameters as in Experiment 1: (a) the color of the central horizontal bars was either dark (D) or light (L) (see 1st to 3rd and 4th to 6th columns, respectively); (b) the two mirrored subpatterns linked at the internal (Di, Li), as in Table 1, or the external rows (De, Le). Each of these four basic stimuli was replicated with light (1st and 3rd rows) or dark (2nd and 4th rows) background (either 6.7 or 51.5 cd/m^2) and with six tile types: these comprised one central stripe (3rd and 6th columns), two lateral stripes either black or white (2nd and 5th columns) or of three stripes, black and white in alternation (1st and 4th columns), with the central stripe larger (8 mm, or 0.54 deg) than the two lateral ones (5 mm, or 0.34 deg), to give a total of 48 stimuli. Subjects viewed the stimuli for 2 sec and, at stimulus offset, a mask composed of randomly positioned vertical bars of random luminance was presented with no interval for 2 sec. Subjects were shown two repetitions of the 48 stimuli.

Table 1. Results of Experiment 2a. Percentages of clockwise (/) or anticlockwise (\) perceived tilt and standard errors calculated as follows: $(p_{success} \cdot p_{failure}/N)^{1/2}$, for each stimulus (only the basic subpattern is shown) in which: 1st and 4th columns: central and lateral stripes had opposite color leading to higher contrast in the inner or outer stripes, depending on background luminance levels: 2nd and 5th columns: the lateral stripes, either white (top rows) or black (bottom rows), the central isoluminant with the ground. 3rd and 6th columns: the central stripe, either black (top rows) or white (bottom rows), the lateral isoluminant with the ground.

Task

Observers had to execute a binary choice task, indicating whether they perceived illusory curvature as concave or as convex. By using this method we sought further direct support of the contrast polarity rule. Indeed, as distinct from the method of limits used in Experiment 1, which only allowed the background luminance limit to be recorded for perceiving concave (convex) curvature, the binary choice method forced choice between concave and convex, and this allowed the inversion of curvature with background luminance to be tested directly.

Results and discussion

Table 1 summarizes the results, which confirm those of the Experiment 1, i.e., with large stripes, the curvature is perceived when background is close to either the black or white stripes. When either the central or lateral stripes are missing (2nd, 3rd, 5th, 6th columns), direction of perceived curvature corresponds to local tilts resulting from congruent contrast polarity of the edges of the horizontal bar and of the stripes. Of particular interest is the direction of perceived curvature when both black and white stripes are visible (1st and 4th columns), which could be dictated either by stripe position (outermost tilts win) or by stripe contrast. These results are unequivocal. When both are available, perceived curvature depends on the tilts resulting from either white or black stripes, depending on contrast. The tilts originating from edge segments with higher contrast win, regardless of whether they have an inner or outer position in the edge. So, for the width of stripe tested, either the central or the outer stripes can participate in the binding process, depending on contrast: stripes of lower contrast are not segmented from the ground, and only those of higher contrast participate in the binding process. This is a crucial result
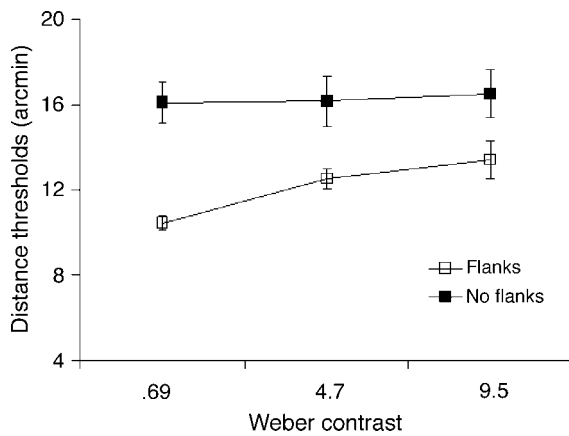
Figure 6. Results of Experiment 2b. The maximum distance that allows the curvature to be perceived is plotted as a function of contrast, in stimuli with only the central stripe or both lateral and central stripes present.

because it confirms our prediction that the direction of curvature depends on whether the central or outer stripes are interpreted as belonging to the uniform background. In other words, this finding confirms that the segmentation of figure from the ground precedes the binding process.

Experiment 2b

The results of Experiment 2a reveal that the contrast of the tile's edge can be a strong factor affecting the illusion. However, the distance between the tile and the horizontal bar (proximity factor) could also play a role. Experiment 2b analyzed the relative contribution of contrast and proximity. We used two of the stimuli in Figure 4 (top and bottom right) with the light stripe contrast varying in three levels (.69, 4.7, 9.5). We gradually increased the distance between the horizontal bar and the central light-stripe from 9 to 22 arcmin, by decreasing the width of the stripe from 26 to 0 arcmin (14 steps at intervals of 1 arcmin). We measured thresholds, defined as the maximum distance that allows the curvature to be perceived.

Results

Figure 6 shows mean thresholds as a function of contrast for the two stimuli. In the absence of the gray stripes, the illusion was perceived up to 16′ distance, in line with our previous findings, at all contrasts. Only with the gray stripes present, the maximum distances decreased with contrast, $F(2,18) = 5.9$, $p < .02$. Note that, although stripe width increases with proximity, proximity rather

than width is the factor affecting the illusion, since even a very narrow light stripe presented alone produced the illusion.

Experiment 3

We have claimed that the border ownership of the stripes is a factor affecting the *seesaw* illusion. Using the basic configuration of a white stripe flanked/not flanked by a narrower gray stripe, Experiment 3 tested this suggestion directly. The white-gray stripes configuration is more readily interpreted as a light figure on a background of non uniform gray rather than a gray figure on a light-dark background. In terms of border ownership, where the bounding border of the stripes belongs only to the figure and is more readily owned by the white, sensitivity for the border of the gray stripe should be higher when presented alone than when flanked by the white stripe, with both dark and light background. Instead, brightness induction and simultaneous contrast decrease sensitivity with light and dark background respectively.

Method

The lighter and darker backgrounds were different in luminance from the gray stripe of 12.4 cd/m^2 in nine steps of .2 cd/m^2 each, leading to Weber contrast variation from 0 to 0.129 and from 0 to .148, respectively. Weber contrast thresholds for the gray stripe were measured when this was isolated (and interpreted as figure) or when flanked by the white stripe (44 cd/m^2). Note that the white and gray stripes have the same (positive) and opposite contrast polarity with light and dark background respectively.
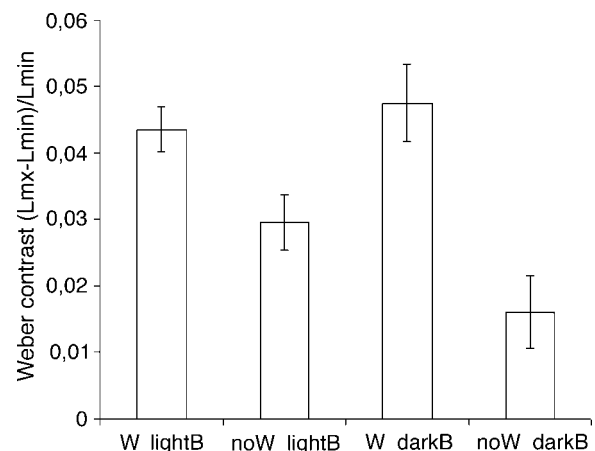

Figure 7. Contrast Weber thresholds for each of the stimuli used in Experiment 3 for the conditions with (W) and without white stripe (noW) and background either light (lightB) or dark (darkB).

Results

Results are shown in Figure 7. The ANOVA revealed a significant stimulus × background interaction, $F(1,9) = 36.2$, $p < .001$]. Post hoc comparisons indicate higher sensitivity for the gray stripe on a dark background ($p = .003$). Contrast thresholds were higher when the white stripe was present than when it was not, $F(1,9) = 162.5$, $p < .001$]. As predicted by border ownership, the increase was significant for both light ($p = .002$) and dark background ($p = .001$), ruling out alternative explanations in terms of simultaneous contrast and brightness induction.

Conclusions

Results of Experiment 1 demonstrate that the *seesaw* illusion depends directly on the contrast polarity at the level of the tiles (stripes) and background. This is confirmed in Experiment 2a using a binary choice task where the subject is forced to choose between concave and convex. In this regard, the *seesaw* illusion is new and different from other illusions not based on contrast polarity, such as the Fraser, Zöllner, Hering and other tilt illusions. Note that contrast polarity not always has been considered essential for contour binding. Prazdny (1983) for example thought it not to be essential for the formation of an illusory edge, though this idea was challenged by He and Ooi (1998). Field et al. (2000) demonstrated that contrast polarity was not essential for grouping based on association field. Instead, we have shown a drastic behavioral consequence of having near collinear edges of same compared with different contrast polarity: if contrast polarity is not the same, the edges do not bind.

The second new result is that the contrast polarity rule is applied on the basis of context luminance. That is, when spatial frequency is high, binding between two near-collinear edges is based on contrast polarity of the figure edge, not of the outermost segment. Consequently, although the binding occurs between projections of the local association field extrapolating from the outer segment, the visual system assigns these projections the contrast polarity of the whole edge. This implies that the process enabling contrast polarity to be assigned to the figure-edge at early level is linked to and affected by the processing of surface luminance in the tile. On the other hand, both experiments show that when the stripes in a tile are large, the contrast polarity rule applies to the stripes with higher contrast. To achieve this, background luminance values have to be extreme. Otherwise, if the background luminance was intermediate between the black and white stripes, the illusion would not be perceived because both black and white stripes produce local tilts, but in opposite direction. To have congruent tilts producing

either concave or convex curvature, one stripe color (that closer to the background luminance) has to be excluded from application of the contrast polarity rule. This implies that this rule is applied only after the figure (stripes with the largest luminance difference from the background) is segmented from all the remaining surfaces. In Experiment 1, this occurs with background luminance close to black and to white, at the beginning of ascending and descending series. In Experiment 2a, this occurs in the configuration in which stripes of only one color are present or, if both black and white stripes are present, by coding those of higher contrast as figures (even if they are not close to the edge) and the others as ground (even if outermost). The results of Experiment 2a are therefore also seen to confirm the suggestion that figure-ground organization precedes boundary interpolation, because otherwise there would be no illusion.

Our results are consistent with the physiological evidence of early coding of surface information in V1. Various data indicate that the perception of surface brightness is mediated by neurons responding to the entire spatial extent of the surface. Results from Kinoshita and Komatsu (2001) indicate that global luminance information significantly modulates the activity of surface-responsive V1 neurons, which respond to homogeneous surfaces at least three times as large as the receptive field as stimuli. fMRI data (Haynes, Lotto, & Rees, 2004) show that the response to changes in the luminance of uniform surfaces occurs early on in the human visual cortex. Our results are in strong agreement with these neurophysiology and neuroimaging findings because the application of the contrast polarity rule, which follows figure-ground segmentation, can only be based on cells selective for contrast polarity which are present very early in the central visual system. Our results are in line with the findings of Zhou et al. (2000), in that they strongly suggest that border ownership phenomena occur at the level at which neurons are selective to contrast polarity, i.e., at the earliest stages of central visual processing.

By showing that luminance assigned at the border results from global luminance level in the background and average luminance level in the tile, our results provide information about the powerful mechanisms for organizing the incoming information into figures segmented from the ground according to the Gestalt laws of perceptual organization (Rubin, 1921). The perceived *seesaw* illusion occurring with striped tiles suggests that figure/ground organization precedes binding but that the two operations occur at a very early level in the central visual system. It is worth considering whether other tilt illusions can be explained by the notion of association field. The illusory tilt obtained by shifting the phase of aligned gabors (Popple & Levi, 2000) can be accounted for by the association field model. Similarly, illusion of shifted edges by Kitaoka et al. (2004) can be explained by this model, since it consists of pairs of near-collinear edges of same contrast polarity. In particular conditions, the

integration of association fields resulting from co-linear edges—such as the Münsterberg illusion and the checkered illusion of Kitaoka (1998)—can also produce illusory tilts. However, in contrast with the *seesaw* illusion, these tilt illusions do not invert direction of tilt when the background luminance switches from dark to light gray.

Our demonstration that segmented edges of alternated contrast polarity can bind represents a significant step forward in understanding common phenomena in the visual world where the sign of contrast may alternate along a contour.

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