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Apparent color–orientation bindings in the periphery can be influenced by feature binding in central vision

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ABSTRACT

A previous study reported the misbinding illusion in which visual features belonging to overlapping sets of items were erroneously integrated (Wu, Kanai, & Shimojo, 2004, *Nature, 429*, 262). In this illusion, central and peripheral portions of a transparent motion field combined color and motion in opposite fashions. When observers saw such stimuli, their perceptual color–motion bindings in the periphery were re-arranged in such a way as to accord with the bindings in the central region, resulting in erroneous color–motion pairings (misbinding) in peripheral vision. Here we show that this misbinding illusion is also seen in the binding of color and orientation. When the central field of a stimulus array was composed of objects that had coherent (regular) color–orientation pairings, subjective color–orientation bindings in the peripheral stimuli were automatically altered to match the coherent pairings of the central stimuli. Interestingly, the illusion was induced only when all items in the central field combined color and orientation in an orthogonal fashion (e.g. all red bars were horizontal and all green bars were vertical). If this orthogonality was disrupted (e.g. all red and green bars were horizontal), the central field lost its power to induce the misbinding illusion in the peripheral stimuli. The original misbinding illusion study proposed that the illusion stemmed from a perceptual extrapolation that resolved peripheral ambiguity with clear central vision. However, our present results indicate that visual analyses of the correlational structure between two features (color and orientation) are critical for the illusion to occur, suggesting a rapid integration of multiple featural cues in the human visual system.

1. Introduction

What does the world look like away from the point of fixation? We know that spatial acuity drops rapidly away from the fovea. Moreover, object identities and feature properties can be obscured by crowding effects (Levi, 2011; Pelli & Tillman, 2008; Whitney & Levi, 2011). While we experience the visual field as populated by coherent objects, the periphery might be characterized as a soup of features. Our perception of those feature may be based on summary statistics about their mean and distribution (Alvarez, 2011). Indeed, in the effort to determine what is out there, features in the periphery might combine incorrectly to indicate the presence of items that are not present at all (Balas, Nakano, & Rosenholtz, 2009). All of this is reminiscent of the pre-attentive world as envisioned by Treisman in her original Feature Integration Theory (FIT) (Treisman & Gelade, 1980). FIT proposed that features like color and orientation could only be 'bound' to each other and to an object once that object became the object of attention. This "binding problem" has been much discussed (Roskies, 1999) and remains controversial (Di Lollo, 2012; Wolfe, 2012). Under some circumstances, perceived binding is inaccurate and observers report "illusory conjunctions" (Treisman & Schmidt, 1982), incorrect combinations of features that are present in the display (as opposed to simply reporting colors, shapes, etc. that are not present at all). While Treisman's original illusory conjunctions were seen in brief presentations, illusory conjunctions can be persistent under the right circumstances (Prinzmetal, Henderson, & Ivry, 1995).

Wu, Kanai, and Shimojo (2004) introduced a "misbinding" illusion. It can be thought of as a particularly persistent form of illusory conjunction; one that can be scrutinized for an extended time without resolving itself into the correct bindings, in this case, of color and motion. In this illusion, central and peripheral portions of a transparent motion field paired color and motion in opposite fashions (Fig. 1A). For example, in the center, red dots might move up while green dots move down. In the periphery, these feature

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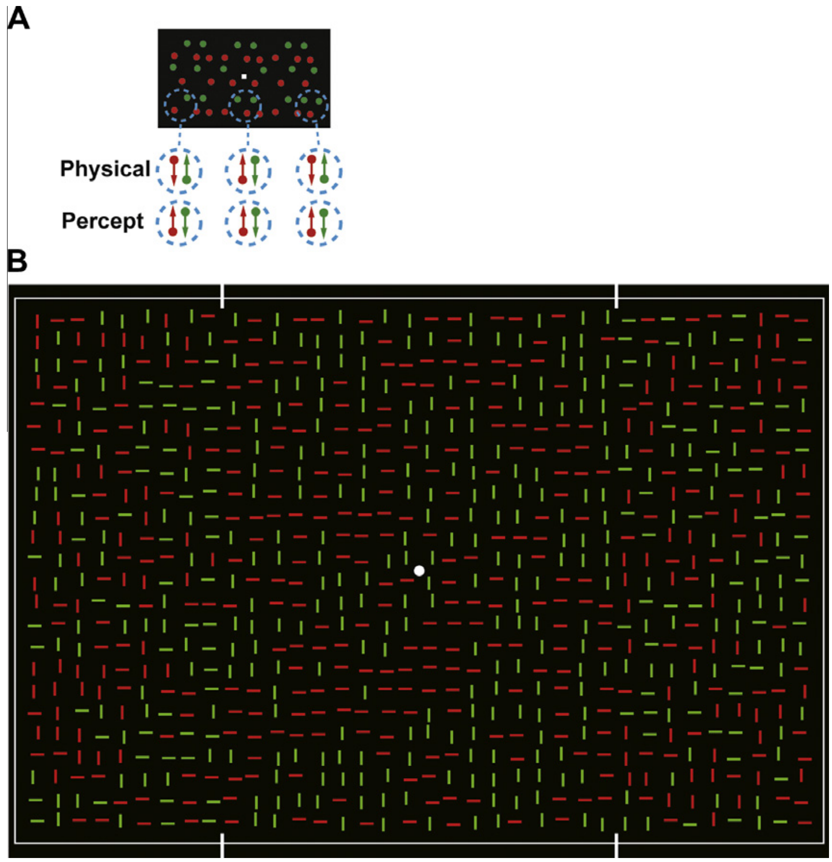

Fig. 1. The misbinding illusion and stimuli in the present study. (A) An schematic of the displays that induce color–motion misbinding (Wu, Kanai, & Shimojo, 2004). Transparent motion consisting of upward-red and downward-green dots was presented in the central field, while downward-red and upward-green dots were presented in the left and right peripheral fields. Subjects, however, did not notice the boundaries among the three fields. They reported a uniform transparent field made of upward-red and downward-green dots, resulting in erroneous color–motion paring (misbinding) in peripheral vision. (B) The misbinding between color and shape (orientation) tested in the present study. An entire array consisted of four types of bars produced by a combination of two colors, red (R) and green (G), with two orientations, horizontal (H) and vertical (V). As in the original color–motion misbinding effect, the central field has a clear (coherent) binding between color and orientation. All red bars are horizontal while all green bars are vertical, forming "double conjunctions" (R–H and G–V) of the two features. The left and right surrounds, on the other hand, contained equal numbers of the four types of bars (R–H, R–V, G–H, and G–V). As you can see, if you fixate in the central region, the clear bindings in the central field bias the perceptual bindings in the peripheral fields so that they accord more closely with the bindings in the center (R–H and G–V). When viewers are asked to compare numbers of R–H and R–V bars in the surrounds, their responses are biased toward larger "H" responses, despite an equal number of R–H and R–V bars in the surrounds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

pairings would be reversed, so that green dots move up and red dots move down. When observers viewed such stimuli, the color–motion bindings present in the central field were also perceived in the periphery. This illusion stems from a dominant influence of the contents of the central field on visual experience, and on perceptual grouping/segregation based on an integration of color–motion information (Noguchi et al., 2011). What is particularly interesting about this illusion is that the illusory conjunction continues to be perceived even when attended. Normally, selective attention would be expected to correct the misbinding. However, with the small, peripheral stimuli of Wu, Kanai, and Shimojo (2004), crowding and resolution issues appear to block accurate binding (Intriligator & Cavanagh, 2001). Unable to produce the correct bindings in the periphery, the visual system appears to accept the bindings of the central field as applying across the entire field.

In the current experiments, we extend the Wu, Kanai, and Shimojo (2004) findings by demonstrating that the misbinding illusion extends to color–orientation conjunctions. In two experiments, we used a richer set of conditions than employed by Wu et al., in order to employ the illusion as a means to determine the rules of misbinding.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

The first experiment consisted of two versions, Experiment 1a and 1b, with different types of stimulus arrays as described below. Eleven (seven males and four females) and 10 (five males and five females) subjects participated in Experiment 1a and 1b, respectively. All had normal or corrected-to-normal vision. Informed consent was received from each subject after the nature of the study had been explained. Approval for the experiment was obtained from the ethics committee of Kobe University, Japan.

2.1.2. Stimuli and procedure

All visual stimuli were generated using MATLAB 2007a and the Psychophysics Toolbox version 2.54 (Brainard, 1997; Pelli, 1997), implemented on a DELL OptiPlex GX280 running Windows XP, and presented on a CRT monitor (40 cm diagonal, resolution: 1024 × 768 pixels, viewing distance: 57 cm) at a refresh rate of 60 Hz. On each trial, we presented arrays of visual elements (width: 27 deg, length: 18 deg) for 200 ms (Fig. 1B). An array contained 864 stimuli placed on a 36 × 24 invisible grid (cell size: 0.75 × 0.75 deg) with a random spatial jitter of up to 0.9 deg both in vertical and horizontal directions. Each stimulus was chosen from 4 types of bars (0.09 × 0.47 deg) produced by a combination of two colors (red and green, 14.8 cd/m^2 for both) with two orientations (horizontal and vertical). A white fixation point (0.19 × 0.19 deg) was present at the center of the array.

Each array consisted of three fields; a central field (13.5 × 18 deg, comprising 432 items) and two peripheral fields (left and right surrounds, 6.75 × 18 deg, 216 items for each). Boundaries among those three fields were marked by a pair of short vertical lines, one placed just above and another below the array. In the left and right surrounds, the array was composed of equal numbers of red (R) and green (G) bars (108 for each). Half of the green bars were horizontal (H) and other half, vertical (V). For the red bars, the ratio of V to H varied across trials from 0:100 to 100:0. The configuration of the central field was chosen from six conditions shown in Fig. 2. In the "No Stimulus" (or NS) condition, there was no visual stimulus in the central field (Fig. 2A). In the "Random" condition, equal numbers of the four types of bars (R–H, R–V, G–H, and G–V) were intermixed in the central field (Fig. 2B). These two conditions served as controls. In the "Double" conditions, all red bars were of one orientation and all green bars were of the other orientation. Thus the Double-1 condition (Fig. 2C) consisted of R–H and G–V bars, while the Double-2 condition (Fig. 2D) consisted of R–V and G–H bars. Finally, we tested two "Single" conditions (Fig. 2E and F) in which only red items were of homogeneous orientation. In Single-1, red was homogenously horizontal (R–H, G–H, and G–V). In Single-2, red was homogenously vertical (R–V, G–H, and G–V).

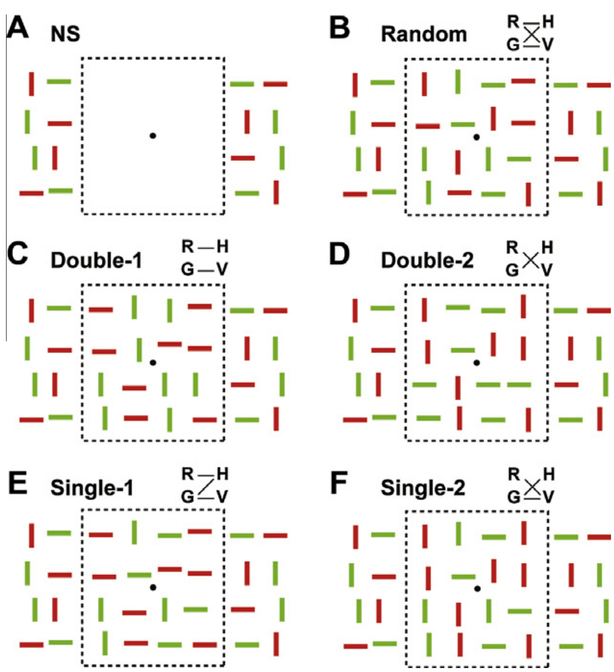

Fig. 2. Schematic illustrations of six types of the central field. In each panel, a rectangular area encompassed by dotted lines denotes the central field. (A) A control condition in which the central field had No Stimulus (NS). (B) Another control (Random) condition. As shown in a diagram above the dotted rectangle, random bindings of two colors (R and G) with two orientations (H and V) resulted in equal numbers of the four types of bars (R–H, R–V, G–H, and G–V) intermixed in the central field. (C) Double-1. All red bars in the central field were horizontal while all green bars were vertical, which formed the double conjunctions between colors and orientations. Those regular bindings induce the strong misbinding illusion in peripheral bars (Fig. 1). (D) Double-2. Another type of double conjunctions composed of R–V and G–H bars. (E and F) Single conditions in which double conjunctions of Double-1 and -2 were partially impaired. Although the central red bars were coherently paired with a given orientation (H in Single-1 and V in Single-2), the central green bars had random pairings with both H and V orientations. In all six conditions, left and right surrounds comprised equal numbers of red and green bars. The H:V ratio of peripheral green bars was fixed at 1:1, while the ratio was variable across trials for the red bars in the surrounds. Subjects attended to the red bars in either the left or right surround and compared the numbers of R–H and R–V bars there (H:V judgment task). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The task of subjects was to judge the ratio of R–H to R–V bars in the peripheral fields. Subjects pressed one key to indicate that number of *peripheral* R–H bars was greater than the number of R–V bars, and pressed another key to indicate the reverse. They were instructed to ignore stimuli in the central field and to attend to the surround (left or right, assigned randomly for each subject). They were also asked to ignore the green bars in the surrounds and were told – correctly – that the H:V ratio of those green bars was always 50:50 and thus would not help them with the task. As described above, the actual percentage of peripheral R–H bars (%R–H) was randomly varied across trials from 0% to 100%, and we measured the probability that subjects reported R–H bars as greater in number (%"H") for each level of %R–H. Misbinding illusions should appear as changes in the point of subjective equality (PSE) between R–H and R–V. Thus, Double-1 should bias the apparent orientation of peripheral red bars toward horizontal while Double-2 should bias the apparent orientation of peripheral red bars toward vertical.

Every trial began with fixation for 1 s, followed by a 200 ms presentation of the stimulus array. After 400 ms, subjects were prompted for a key press response. We ensured that the subjects maintained the fixation throughout the trial by monitoring their eye positions. Either left or right eye of each subject was recorded at 250 Hz using the Eyelink CL system (SR Research) and the Eyelink Toolbox on Matlab (Cornelissen, Peters, & Palmer, 2002). If a subject broke the fixation during a trial, the data from that trial were discarded and the same trial was repeated again at the end of the session.

Experiment 1a involved the two control conditions (NS and Random), to ensure that the bars in the central field themselves did not induce any perceptual and judgment biases of the task. Subjects performed four sessions of 90 trials, two NS and two Random, with order counterbalanced across subjects. Nine levels of %R–H (0%, 12.5%, 25%, 37.5%, 50%, 62.5%, 75%, 87.5%, and 100%, 10 trials for each) were randomly intermixed in each session. In Experiment 1b, all six conditions were randomly intermixed. Five levels of %R–H were tested (0%, 25%, 50%, 75%, and 100%) in each of the six conditions. A session consisted of 90 trials in which those 30 types of trials were randomly intermixed. Each participant completed six sessions.

2.1.3. Data analyses

For each condition for each subject, the function relating perceived %"H"s to actual %R–H were fitted by the sigmoid psychophysical function (Noguchi et al., 2011) in

$$F(x) = \mathrm{Min} + (\mathrm{Max} - \mathrm{Min})/[1 + e^{-a(x-b)}] \quad (1)$$

Here x was the %R–H, a and b were free parameters estimated with the Nelder–Mead method. The Max and Min indicated the maximum and minimum %"H" through all levels of %R–H, respectively. Magnitudes of the misbinding illusion were evaluated by measuring changes in the PSE (50% thresholds) of those curves. If there is the color–orientation misbinding, the Double-1 condition should increase %"H"s at all levels of %R–H, resulting in a leftward shift of the sigmoid function and a lower PSE. The Double-2 condition, on the other hand, should induce a rightward shift of the function and a greater PSE. After obtaining the PSE for each subject in each condition, PSEs were statistically compared across conditions using paired *t*-tests.

2.2. Results and discussion

Results from Experiment 1a were shown in Fig. 3A. We observed a shallower slope of the psychometric curves in Random than NS conditions. A paired *t*-test showed a significant difference in curvature of the psychometric functions (a in Eq. (1)) between the two conditions ($t(10) = 3.37$, $p = 0.007$). This indicates that subjects found the task in Random condition more difficult, probably because of the effort required to ignore the irrelevant stimuli in the central field. The PSEs, however, were comparable between the two conditions ($t(10) = 0.48$, $p = 0.64$). The random color–orientation bindings in the central field thus produced no perceptual bias on the H:V ratio in the peripheral red bars.

We then examined color–orientation misbinding by testing all six types of central fields (Experiment 1b). The PSEs in the two control conditions (NS and Random, Fig. 3B) did not differ again ($t(9) = 1.61$, $p = 0.14$), confirming the results of Experiment 1a. A one-way ANOVA with the Greenhouse–Geisser correction was then applied to test the difference in the PSE across the five conditions (Double-1, -2, Single-1, -2 and Random). We observed a significant main effect across the five conditions ($F(1.375, 12.373) = 6.284$, $p = 0.02$). Post hoc tests showed a significant decrease of the PSE in Double-1 compared to Random conditions (Fig. 3C and E, $t(9) = 3.08$, $p = 0.013$, uncorrected), and a significant increase in Double-2 compared to Random conditions ($t(9) = 2.51$, $p = 0.033$, uncorrected). The mean (±SE) magnitude of the illusion, quantified by a difference in the PSEs between the two Double conditions, was 33.2% (±10.4%), which was significantly larger than 0 ($t(9) = 3.18$, $p = 0.011$, one-group *t*-test, Fig. 3F). Those results are similar to those observed for color–motion misbinding (Wu, Kanai, &

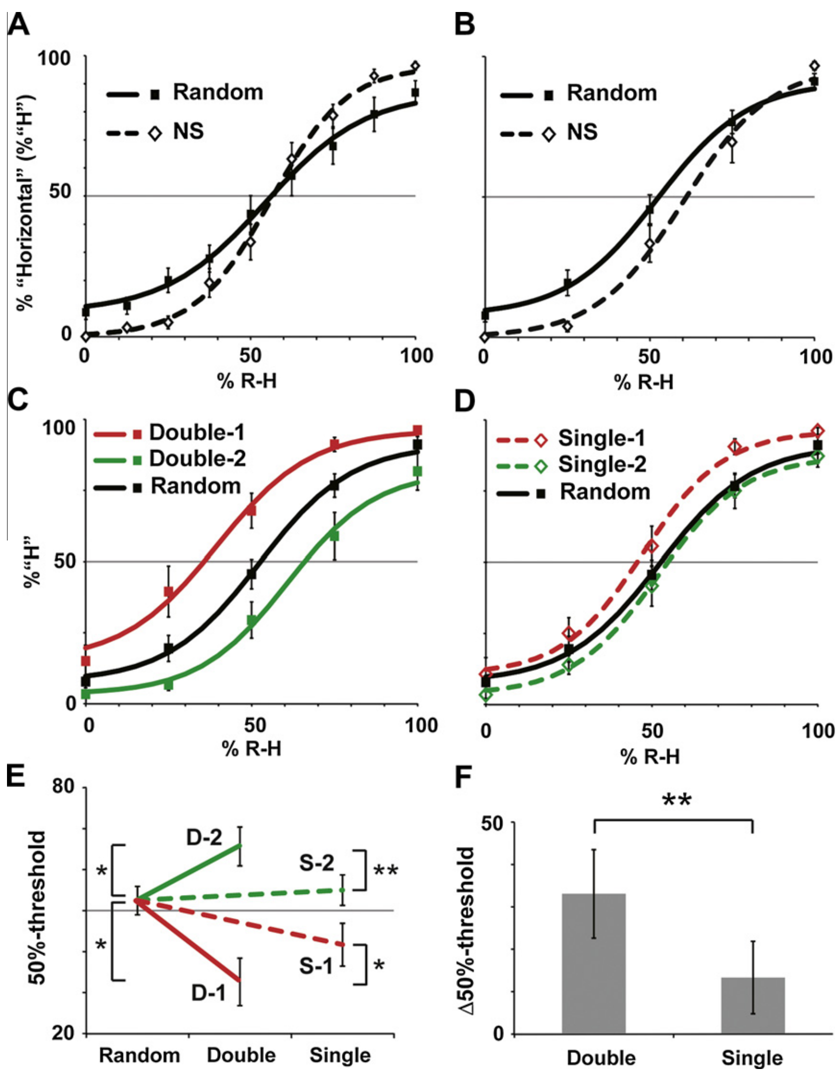

Fig. 3. Results of Experiment 1. (A) Experiment 1a (NS vs. Random). We plotted changes in percentages of R–H bars (%H) reported by the subjects as a function of actual R–H percentages (%R–H). The 50% threshold (PSE) of those psychometric curves did not differ between NS (dotted) and Random (solid), indicating that the central display with the random color–orientation bindings elicited no misbinding in the surrounds. (B) The NS and Random conditions in Experiment 1b. Consistent with Experiment 1a, no significant difference in the PSE was observed between the two conditions ($p = 0.14$, see text). (C and D) Double and Single conditions in Experiment 1b. Compared to the control (Rand) condition (black), the central field in Double-1 (R–H and G–V) induced an increase in %"H"s at all levels of %R–H (red solid line), while the %"H"s were decreased overall in the Double-2 condition (R–V and G–H, green solid line). Those perceptual biases, represented by horizontal shifts of psychometric curves, became smaller in Single-1 (red dotted line) and Single-2 (green dotted line). (E) The PSEs in Experiment 1b. Conventions of colors and lines are the same as in panels (C and D). (F) Magnitudes of the misbinding illusion, as measured by differences in PSEs between Double-1 and -2 (left bar) and between Single-1 and -2 (right bar). In this and subsequent figures, all error bars denote standard errors (SEs) across subjects. $^{*}p < 0.05$, $^{**}p < 0.01$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Shimojo, 2004), indicating that the misbinding illusion can also take place between color and orientation information.

One alternative account of these results might be that subjects included the red bars of the central field in their assessment of the percentages of R–H and R–V bars. For example, the central field in Double-1 had more R–H bars than did the Random condition. If subjects included those bars in their assessment of the H:V ratio, they would overestimate the number of R–H bars in Double-1 as seen in Fig. 3C. The Single conditions were included in order to examine this "miscounting" possibility. The Single conditions partially disrupted the coherent color–orientation correspondences of the Double conditions by mixing G–H and G–V bars. The numbers of R–H or R–V bars was the same as in the Double-1 or Double-2 conditions. The miscounting hypothesis would thus predict the same results in the Single and Double conditions.

Results for Single-1 and -2 conditions are shown in Fig. 3D. Compared to Double conditions, the changes in PSEs were significantly smaller in Single conditions (Double-1 vs. Single-1, $t(9) = 3.17$, uncorrected $p = 0.011$, Double-2 vs. Single-2, $t(9) = 3.52$, uncorrected $p = 0.006$, Fig. 3E). The magnitude of illusion, quantified by a difference between PSEs (Fig. 3F), also diminished significantly in Single compared to Double conditions ($t(9) = 4.23$, $p = 0.002$). The magnitude of the illusion in the Single condition did not differ from zero ($t(9) = 1.56$, $p = 0.15$). Thus, at best, only a small part of the PSE shifts observed in the Double conditions can be attributed to miscounting, rather than to misbinding. These results support the hypothesis that "misbinding" is stronger when color and orientation are perfectly correlated (Double conditions) than when color and orientation are imperfectly correlated (Single). The results do not support the alternative hypothesis that performance was driven by including the central red items in the calculation of red V to H ratios.

3. Experiment 2

Experiment 1 showed that central fields with double conjunctions induced illusory bindings of color and orientation in the periphery. There are at least two factors which could facilitate perceptual extrapolation from the center to peripheral fields, resulting in the bias of the H–V judgment observed in Experiment 1. One possibility is the perfect correlation of color and orientation in the central portion of the field. In Double-1, for example, all red bars in the central field were horizontal while all green bars were vertical. The other possibility is the fact that the Double conditions were simpler and more uniform than the Random or Single conditions. While the Random and Single conditions in Experiment 1 had three or four types of bars in the center (e.g. R–H, R–V, G–H, and G–V in the Random condition), the central fields in the Double conditions had only two types of bars (R–H and G–V in Double-1, and R–V and G–H in Double-2).

To discriminate between these two possibilities, in Experiment 2 we compared the Double and Single conditions with two new Uni-orientation conditions, shown in Fig. 4A and B. In those conditions, the central field consisted of two types of bars with the same orientation, but different color (R–H and G–H in Uni-1 and R–V and G–V in Uni-2). If the simplicity or uniformity of the central field elicited the misbinding observed in Experiment 1, the same results should be also seen in the Uni conditions. Indeed, the entire display should come to appear to be more homogeneously of one orientation. In contrast, if the orthogonal pairings of color and orientation are critical, the central displays in Uni conditions should induce no illusion in the peripheral fields, because red and green bars shared the same orientation in those displays.

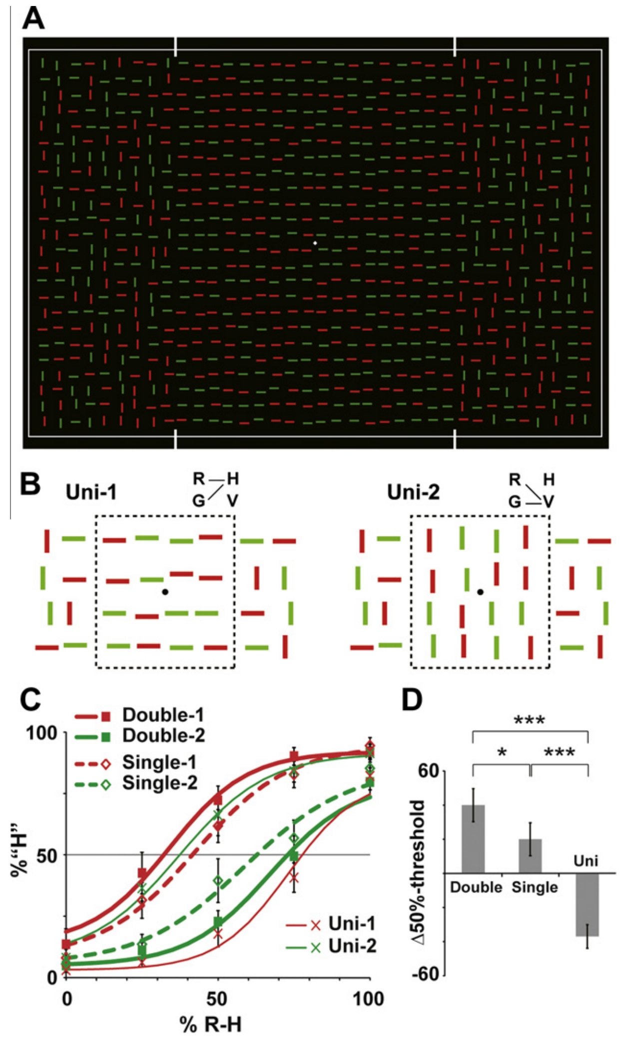

Fig. 4. Experiment 2. (A) An example display of Uni condition. The central displays in this condition consisted of red and green bars in the same orientation (in this case, horizontal). In contrast, equal numbers of four types of bars were intermixed in the peripheral fields. (B) Stimulus configurations in Uni-1 and Uni-2. In Uni-1, all central bars are horizontal while they were vertical in Uni-2. (C) Psychometric curves for the H:V judgment task on the peripheral red bars. We found that the Uni conditions (red and green thin lines in (C)) induced a perceptual bias opposite to those in Double (thick lines) and Single (dotted lines) conditions. Homogeneous horizontal bars (Uni-1) biased the perceptual H:V ratio of red bars in the surround into a V direction, resulting in decreases in %"H"s at all levels of %R–H (thin red line). (D) Magnitudes of illusion in Double, Single, and Uni conditions. $^{*}p < 0.05$, $^{***}p < 0.001$, corrected for multiple comparisons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. Methods

Nine subjects (four males and five females) participated in Experiment 2. We replaced the NS and Random conditions with by Uni-1 and Uni-2 in which all bars in the central field had the same orientation (H or V, respectively). As before, subjects were asked to compare the number of R–H and R–V bars in the surrounds, neglecting the central field. Trials in six conditions (Double-1, Double-2, Single-1, Single-2, Uni-1, and Uni-2) were randomly intermixed in a session of 90 trials. Each participant performed six sessions. Other details were identical to Experiment 1.

For data analyses, we compared the magnitudes of illusion among Double, Single and Uni conditions. First, we obtained the magnitude of illusion in Double condition by comparing the PSEs of Double-1 and -2. The same procedures were applied to Single and Uni conditions. We then contrasted the magnitudes across the three conditions with a one-way ANOVA.

3.2. Results and discussion

Changes in %"H" as a function of %R–H are shown in Fig. 4C. The PSE in Double-1 was significantly smaller than that in Double-2 ($t(8) = 4.12$, $p = 0.003$, Fig. 4D), which replicated the misbinding effect in Experiment 1b. The same tendency was also observed in Single condition, although a difference between Single-1 and -2 did not reach significance ($t(8) = 2.07$, $p = 0.07$). In contrast, this relationship was reversed in Uni conditions; the PSE in Uni-1 was significantly larger (not smaller) than that in Uni-2 ($t(8) = 5.34$, $p = 0.0007$). One-way ANOVA on the magnitude of illusion (differences between the PSEs, Fig. 4D) indicated a significant main effect ($F(2,16) = 42.7$, $p < 0.001$) among three types of the central field (Double, Single, and Uni), and post hoc comparisons with Bonferroni corrections reveled significant differences between Double vs. Single (corrected $p = 0.028$), Double vs. Uni ($p = 0.0002$), and Single vs. Uni ($p = 0.0007$).

These results show that the misbinding in Experiment 1 was caused by the double conjunctions of colors and orientations, not by the simplicity or uniformity of the central display. These results also provide further evidence against the miscounting hypothesis. If the miscounting hypothesis had been true, the red horizontal bars in the central field in Uni-1 would have biased the judgments into "H" direction while the actual results are in the opposite direction. The results of the Uni conditions suggest a contrast effect. With uniformly horizontal items in the center, the flanking surrounds, with a mix of horizontal and vertical elements, appears to contain more vertical items. As in the original color–motion misbinding (Wu, Kanai, & Shimojo, 2004) the misbinding of color and orientation in Experiment 1 appears to be a generalization of the bindings of the central field to the periphery.

4. General discussion

The classic view of binding is of a local effect. A subject attends to a specific object and that permits the binding of its features, say, color and orientation, making the conjunction of those features available for later report. Under some circumstances, the wrong features might be appear to be bound, creating an illusory conjunction (Treisman & Schmidt, 1982). Though Treisman and Gelade (1980, p. 100) originally argued that features were "free-floating", meaning that illusory conjunctions could be created from features anywhere in the visual field, it subsequently became clear that "the visual system does not combine things that are far apart" (Prinzmetal, Henderson, & Ivry, 1995, p. 1373); the probability of illusory conjunctions drops with the distance between the features. In this context, the misbinding illusion is of interest because it is a global effect in which the structure of the central field creates illusory conjunctions in the periphery. Experiments 1 and 2 showed that the correlation of color and orientation in the central portion of the visual field biases the apparent correlation of those features in the periphery. When the central field consisted of red verticals and green horizontals, the peripheral field was also perceived to consist of red verticals and green horizontals.

4.1. Mechanisms of the color–orientation misbinding illusion

The original study of misbinding (Wu, Kanai, & Shimojo, 2004) proposed that the illusion occurred when the visual system extrapolated unambiguous color–motion binding from the central field to resolve ambiguous color–motion binding in peripheral fields. The present findings, using color–orientation misbinding, show that extrapolation from the central to peripheral fields is too simple. If the extrapolation theory were true, the illusory binding should have been observed in Uni as well as Double conditions. Experiment 2, showed that this is not the case.

Thus, we presume that the present color–orientation misbinding emerges from the interplay between visual extrapolation and the process of perceptual segmentation based on conjunctions of multiple features. Fig. 5A shows a schematic illustration of the proposed visual processing in Double-1 condition. When we are faced with a visual scene in which two features are intermixed (e.g. red and green bars in an horizontal and vertical orientations), the clear double conjunctions may prompt us to perceptually segregate the whole scene into two surfaces (in this case one red horizontal surface and one green vertical surface) (Noguchi et al., 2011). Given ambiguous information about the state of the peripheral fields, the visual system extrapolates the clear information from the central field to the periphery (Kanai et al., 2006; Wu, Kanai, & Shimojo, 2004). In this case, the color–orientation binding in the center spreads into the left and right surrounds, changing a perceived binding of the peripheral bars to increase the apparent frequency of R–H bars (the misbinding effect).

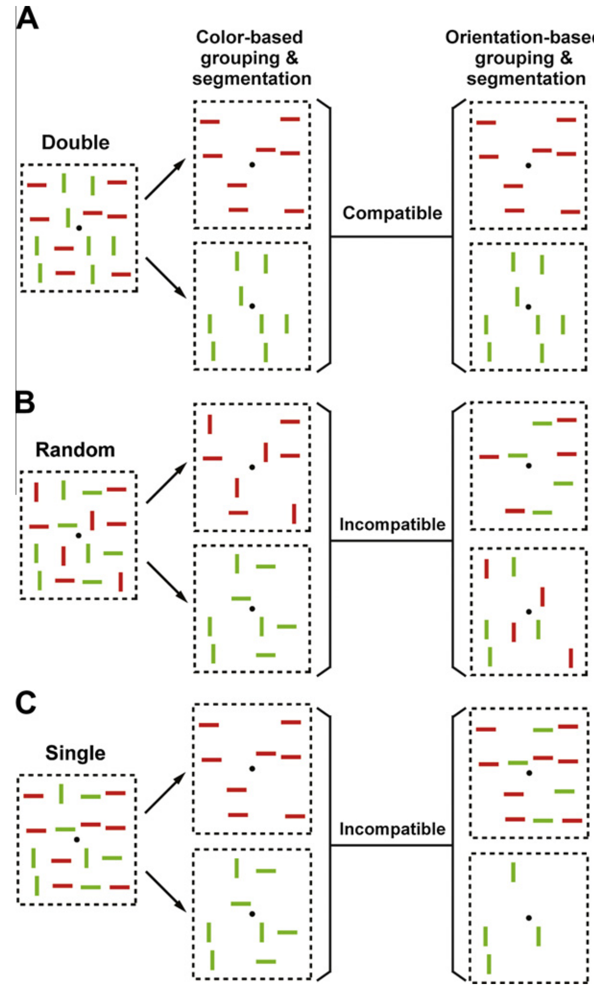

Fig. 5. The perceptual segregation account of misbinding illusions: When faced with the central field in Double trials (A), the visual system segments the entire scene into two surfaces (or proto-objects). The coherent binding of color and orientation in the center is extrapolated to the periphery (Wu, Kanai, & Shimojo, 2004). This surface-segregation, however, does not work in the Random (B) and Single (C) conditions, because color and orientation are imperfectly correlated. The misbinding illusion is reduced or eliminated in these conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

It is important to note that perceptual segmentation, based on conjunctions of features, is elicited when the scene has clear double conjunctions (Noguchi et al., 2011; Additional Experiment 1a). When the central field contains all four combinations of color and orientation (Random trials in Experiment 1), the visual system seems to give up on segregating the field into two (or four) surfaces, perhaps because the segregation based on color information disagrees with that based on orientation information (Fig. 5B). Consequently, no misbinding effect in the peripheral bars was induced in Random condition, as shown in Fig. 3 (black line). Likewise, when the central display like Uni-1 trials was presented, the visual system recognized it as a single collection of horizontal bars. Rather than an extrapolation of horizontal, this situation gives rise to contrast with the mixed orientations in the periphery. The contrast effect biases the H–V judgments toward V (Fig. 4B, thin red line).

4.2. A relationship of the filling-in with the misbinding illusion

Because misbinding is a form of persistent illusory conjunction, it may be useful to think about this as analogous to the 'filling in' of the blindspot (Kawabata, 1983; Ramachandran, 1992) or color spreading in neon-color phenomena (Bressan et al., 1997). The visual system is predisposed to attribute properties to entire regions. If information appears to be better in one part of a region than another, the system will tend to generalize information from that part to the region as a whole. Prinzmetal and Keysar proposed something very much like this in their "Functional theory of illusory conjunctions and neon colors" (Prinzmetal & Keysar, 1989). They showed that both illusory conjunctions and neon color spreading followed the perceptual structure of the display. In the present work, the bindings of the central field spread to the periphery, where information about conjunctions is less reliable. A similar account might be phrased in terms of Bayesian theories of perception (Mamassian, Landy, & Maloney, 2002). Since the central field is a more reliable source of information, the feature conjunctions in the central field are taken as the perceptual prior for the peripheral fields.

It is controversial whether perceptual filling-in results from symbolic tagging and labeling of surface regions in higher order cortex (passive filling-in) (Dennett, 1992), or from active neural interpolation in lower order visual areas (active filling-in) (Pessoa, Thompson, & Noe, 1998). A point to discriminate those two types of filling-in would be whether the filling-in process involves higher order cognitive factors such as attention (De Weerd, 2006). On this point, converging evidence indicates that the present misbinding illusion stems from the feedforward visual processing in a pre-attentive stage (e.g. perceptual grouping and visual extrapolations) rather than attentive analyses of visual stimuli. First, the original study of the misbinding showed that the illusory binding was not modulated by attention (Wu, Kanai, & Shimojo, 2004). Regardless of whether subjects attended to the central or peripheral field in the display, the illusory binding occurred as long as they kept fixation at the central portion of the transparent motion field. Conversely, moving the fixation from central to peripheral portions of the field quickly eliminated the illusory binding. This would seem to indicate that the misbinding illusion emerges from mechanisms dependent on the retinotopy (central dominance) of the visual cortex and suggests that misbinding is the product of bottom-up visual processing, rather than the top-down mechanisms mediated by attention. This view has been further strengthened by another study reporting that a magnitude of the misbinding illusion was unchanged even under a dual-task paradigm where subjects' attention was divided between two tasks (Noguchi et al., 2011; additional Experiments 2 and 3). Finally, our present results in Experiment 2 showed significant differences in the magnitudes of the illusion among Double, Single, and Uni conditions (Fig. 4). As shown in Figs. 2 and 4B, stimuli in those three conditions differed only in orientations of green bars in the central field, which was outside the scope of spatial or feature-based attention by subjects. The fact that the stimuli totally irrelevant to attentional control settings (the central green bars) greatly modulated the magnitude of misbinding illusion further supports the hypothesis that the illusion did not require attentional analyses. Bottom-up processing appears to be sufficient. In this sense, our present study suggests that the misbinding illusion reflects the active rather than passive filling-in process emerging from neural extrapolation in the lower visual process.

To reiterate a point made at the outset, the misbinding illusion is valuable because it creates illusory conjunctions that can be attended and inspected for extended periods of time. Because physiological limitations make it impossible to correctly resolve the bindings of these crowded peripheral stimuli, we get an unusually clear view of the visual system's efforts to make sense of the soup of basic features. As Prinzmetal and Keysar (1989) proposed, the system does the best it can, using rules of perceptual organization to generate hypotheses about what *might be* present when it is unable to accurately determine what is actually present.

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