

Contour integration, attentional cuing, and conscious awareness: An investigation on the processing of collinear and orthogonal contours

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Previous literature suggests that low-level stimulus properties determine the detection performance of contours and are used to define different contour types. Here we investigated the processing of different types of contours under conscious and unconscious conditions. In Experiment 1, we adopted an inattentional blindness paradigm and showed that collinear contours (i.e., a contour type that is frequently observed in natural images) induced a positive cuing effect in both the conscious and unconscious conditions, whereas orthogonal contours (which are less prevalent in the natural environment) attracted attention only when consciously perceived. In Experiment 2, we showed that collinear contours rendered invisible by continuous flash suppression emerged from suppression more rapidly than a random field, whereas orthogonal contours had no such breaking superiority. These results suggest that collinear but not orthogonal contours can be processed and serve as attentional cues without conscious awareness. Our findings provide further evidence that the relevance of the contours to natural statistics could be a key evolutionary factor that decides whether a contour can be unconsciously processed to increase its detectability in a clutter environment.

Introduction

Conscious perception only processes a small part of the information that is transferred through the sensory

systems of the brain (Baars, 2002; Crick & Koch, 2003); the rest of the information is thought to be received unconsciously. Top-down voluntary attention is the main mechanism that selects the information to be consciously processed (Desimone & Duncan, 1995). However, it is also important for ecologically significant items to emerge into conscious perception automatically for purposes such as foraging and survival (Theeuwes, 1992; Yantis & Egeth, 1999). Therefore, an efficient strategy of information processing in the brain is to implement two mechanisms that are responsible for either hard-wired automatic processing of ecologically relevant information or voluntary processing guided by top-down attention.

Contour integration, the way by which the visual system groups discrete elements across a large space into a whole continuous contour, is a critical early step that bridges primary sensory processing and higher level object-based perception under the natural environment. Based on the findings with a path-detection paradigm, Field, Hayes, and Hess (1993) proposed an influential model of association field that agrees with the edge co-occurrence statistics in the natural environment (Elder & Goldberg, 2002; Geisler, Perry, Super, & Gallogly, 2001; Sigman, Cecchi, Gilbert, & Magnasco, 2001) and the topology of long-range horizontal connections in the primary visual cortex (Bosking, Zhang, Schofield, & Fitzpatrick, 1997). This model is supported by neurophysiological investigations (Kapadia, Ito, Gilbert, & Westheimer, 1995;

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Kapadia, Westheimer, & Gilbert, 2000) and leads to the proposal that the long-range horizontal connections in the primary visual cortex act as the underlying mechanism for contour integration (Hess, Hayes, & Field, 2003; W. Li, Piëch, & Gilbert, 2006; Z. Li, 1998; Piëch, Li, Reeke, & Gilbert, 2013). Furthermore, there is accumulated evidence showing that the feedback connections from the higher visual areas (i.e., V4 and lateral occipital complex) to the primary visual cortex are also involved in contour integration (Chen et al., 2014; Li, Gilbert, & Piëch, 2008; Mijović et al., 2014; Shpaner, Molholm, Forde, & Foxe, 2013).

According to the association field model, neighboring elements are integrated if they satisfy the joint constraints of position and orientation along a smooth contour (Field et al., 1993; Hess et al., 2003). While both position and orientation are important for contour integration (Day & Loffler, 2009; Wang & Hess, 2005), the present study focused on one important feature—that is, the relative orientation of local elements with respect to the underlying contour. The model predicts that the performance of contour detection decreases as the degree of misalignment increases. However, consistent evidence has demonstrated that the function of behavioral performance is a U-shaped curve, with the largest misalignment (i.e., when the orientation of local elements is orthogonal to the underlying contour) showing higher performance than the intermediate degree of misalignment (Bex, Simmers, & Dakin, 2001; Ledgeway, Hess, & Geisler, 2005). This raised the questions of to what extent collinear and orthogonal contours are processed differently and what are the constraints that contribute to the differences.

Here, we propose that the relevance of the contours to the statistical properties of the natural environment plays a key role in determining the processing of collinear and orthogonal contours, especially when the contours are not consciously perceived. Given the predominance of aligned structure in natural environments, it is not surprising that the brain has evolutionarily developed a mechanism that is particularly efficient for coding the prevalent collinear contours, making them better detectable and capturing more attention. However, orthogonal contours are not likely to be required for automatic detection, as the elements oriented perpendicular to the underlying contour are more likely to be indicative of discontinuity rather than contour integration (Elder & Goldberg, 2002; Geisler et al., 2001; Schwarzkopf & Kourtzi, 2008). To test this hypothesis, we conducted two experiments to investigate the processing of collinear and orthogonal circular contours under conscious and unconscious conditions. In agreement with our hypothesis, the results suggest that collinear but not orthogonal circular contours can

be unconsciously processed, leading to a positive attentional cuing effect and better detectability.

Experiment 1

We combined a modified version of inattention blindness (IB) paradigm (Pitts, Martínez, & Hillyard, 2012) and the Posner cuing paradigm (Posner, Snyder, & Davidson, 1980; Zhang, Zhaoping, Zhou, & Fang, 2012) to investigate the level of processing of circular contours under conscious and unconscious conditions.

IB refers to the failure to report visible but unexpected items when attention is engaged by a primary task (e.g., Mack & Rock, 1998; Most, Scholl, Clifford, & Simons, 2005; Simons, 2000). In a typical IB experimental setting, participants perform the primary task for several trials, and an unexpected and task-irrelevant stimulus is presented, generally out of the attentional focus, in a critical trial. Immediately after the critical trial, the participants are asked to answer a surprising question about the presence of the unexpected stimulus. Previous studies showed that most of participants fail to notice the unexpected stimulus and cannot subjectively report its presence. However, this typical paradigm could not meet the requirement of the present study. In order to measure the processing level of contours during IB, the contour needed to be presented multiple times and remain unconsciously perceived. Therefore, we adopted a modified version of the IB paradigm (Pitts et al., 2012) to direct attention away from the contour with a go/no-go task and measured the processing level of the contour with a Posner cuing paradigm (Posner et al., 1980; Zhang et al., 2012). The Posner cuing paradigm is a well-established method to study the effects of covert orienting of attention under different cuing conditions. In the present study, we used a circular contour as the spatial cue and measured the performance of an orientation discrimination task at the cued location. We hypothesized that different levels of processing for collinear and orthogonal contours under the IB paradigm could lead to differential Posner cuing effects.

We used circular contours in the study for the following reasons. We used the Posner cuing effect as an index to investigate the unconscious processing of the contours. The Posner cuing effect is calculated as the performance benefit for the location of valid cue compared to the location of invalid cue. The contours used in Field et al. (1993) extend at least a half of the visual field and are not optimal for directing attention to a specific location where a single Gabor appears in the following orientation discrimination task. An open contour in the optimal size is difficult to identify from

the background due to the small number of elements. On the other hand, there is evidence showing that the global mechanism of closed curvatures do not play a role without awareness (Sweeny, Grabowecky, & Suzuki, 2011), providing us with a foundation for investigating unconscious processing of contour with closed stimuli.

Methods

Participants

Twenty-six naive observers (seven males with a mean age of 21.5 years) with normal or corrected-to-normal vision participated in Experiment 1. All the participants were right-handed and had no known neurological or visual disorders. The study was approved by the local ethics committee.

Stimuli

Stimuli were displayed on the gray uniform background of a CRT monitor (refresh rate: 100 Hz, mean luminance: 24 cd/m²) in the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) programming environment in Matlab (The MathWorks, Inc., Natick, MA). Luminance of the monitor was gamma corrected. Participants viewed images at a distance of 60 cm using a chin and head rest in a dimly lit room.

Each stimulus consisted of a square Gabor field (12.79° × 12.79°) centered at the fixation and a ring (radius: 9.05°) comprised eight evenly spaced discs (radius: 0.38°) surrounding the Gabor field (Figure 1). In 90% of the trials, all of the discs were red, whereas in the other 10% of the trials, one of the discs was purple (with the same luminance as the red disc). The square Gabor field consisted of randomly distributed and oriented Gabor elements, within which a circular contour could be embedded. The circular contour was composed of nine Gabor elements aligned along (collinear), perpendicular to (orthogonal), or at a 45° angle (oblique) to an underlying circle (Figure 1A). Oblique contours served as a baseline condition to rule out possible confounding factors such as the differences in density and regularity of the elements between contour and background. The circular contour (radius: 1.13°) was positioned at one of eight candidate positions along an invisible circle (radius: 3.75°).

The algorithm for generating the Gabor fields was adopted from Dakin and Baruch (2009). Stimuli were generated using an iterative procedure to ensure a minimum interelement separation of 0.76°. All elements of the Gabor fields were in cosine phase and had a peak spatial frequency of 2.65 cycles/degree with an envelope

σ of 0.13°. The contrast of the elements was set to 100%.

Procedures

Participants completed three separate phases in Experiment 1: the unconscious condition of an IB dual task (Phase 1), a contour detection task (Phase 2), and the conscious condition of the IB dual task (Phase 3).

In Phase 1, participants were instructed to perform a dual task: a go/no-go task and an orientation discrimination task (Figure 1B). Each trial began with a 500-ms fixation followed by a 50-ms presentation of the Gabor field surrounded by the ring of eight colored discs. After a 100-ms interstimulus interval (ISI), a target Gabor (peak spatial frequency: 1.32 cycles/degree, envelope σ : 0.27°, contrast: 100%) was presented for 50 ms, either at the location of the circular contour (valid cue) or at its contralateral counterpart (invalid cue). The target Gabor was tilted approximately 1.5° clockwise or counterclockwise from the vertical meridian. The background remained gray until a response or 3 s had elapsed. The participants were instructed to press a button as quickly and accurately as possible to indicate the orientation of the target Gabor (i.e., clockwise or counterclockwise) when all discs were red (go trials), and not to press any button when one of discs was purple (no-go trials). The go/no-go task served to direct top-down attention towards the periphery of the stimulus display. The intertrial interval was 1000 ms. No feedback was provided after each trial; however, visual feedback about the overall performance was given after each block. Each participant completed five blocks. Each block consisted of 120 trials, and each combination of contour type (collinear, orthogonal, or oblique) and cue type (valid or invalid) was repeated 20 times. Immediately after the dual task, the participants were asked to fill out a questionnaire (see Appendix) to assess their awareness of the presence of the circular contours (Pitts et al., 2012). In brief, the participants were required to answer whether they had noticed any shape(s) within the Gabor field in Phase 1 and to describe or draw the shape(s) in detail if seen. After answering the questions, six sample shapes, including three circles and three squares, were presented successively to the participants. When the participants were shown the six shapes, we first asked them whether they saw the circle (or square) shown in the screen before they rated their confidence and frequency levels for each shape in the questionnaire. If they could not detect the shape, the experimenter helped the participants by pointing out the shape on the screen. All participants were asked to rate their confidence level and the frequency of seeing each shape on a 5-point scale. The stimuli, procedures,

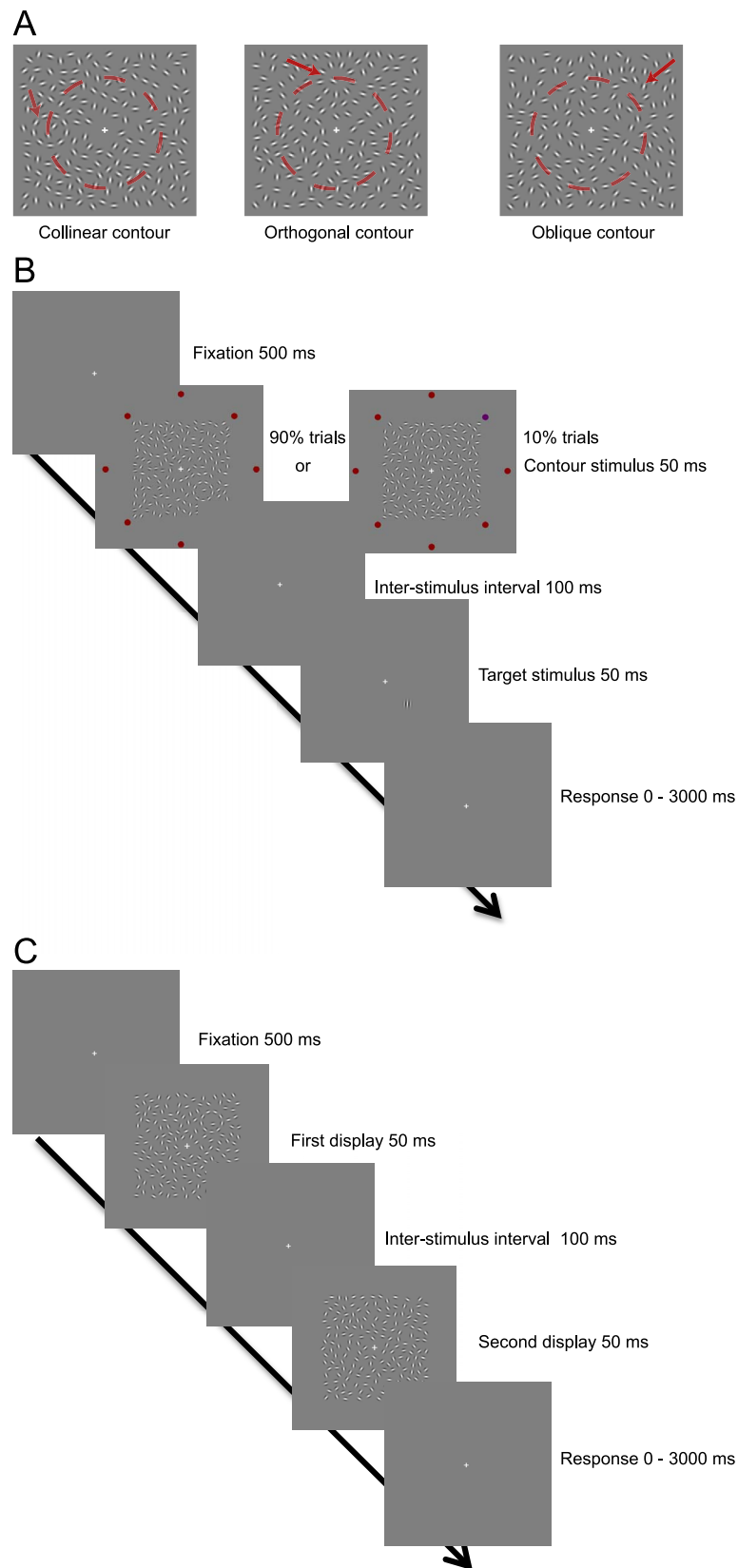


Figure 1. Stimuli and procedures in Experiment 1. (A) Examples of collinear, orthogonal, and oblique circular contours embedded in the background with randomly distributed and orientated Gabor elements. The red dashed lines indicate the invisible circular paths along which the circular contours were positioned. (B) Schematic illustration of the procedure for Phases 1 and 3. Participants were

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instructed to complete a dual task in which a go/no-go task was combined with an orientation discrimination task. The participants were instructed to press a button to indicate the orientation of the target Gabor when all discs were red (go trials), and not to press any buttons when one of the discs was purple (no-go trials). (C) Schematic illustration of the procedure for Phase 2. Participants were instructed to indicate which display contained the circular contour.

and questionnaire in Phase 3 were identical to those used in Phase 1.

In Phase 2, participants were asked to perform a two-alternative forced-choice (2AFC) contour detection task (Figure 1C). Each trial began with a 500-ms fixation. Then, two displays of Gabor fields were presented for 50 ms separated by a 100-ms ISI. One of the Gabor fields was embedded with a circular contour. The background remained gray until either the participant made a response or 3 s had elapsed. Participants were shown the examples of the collinear, orthogonal, and oblique circular contours and instructed to indicate which display contained the circular contour as quickly and accurately as possible, but no feedback was provided. Each participant completed two blocks of the contour detection task. Each block consisted of 144 trials with 48 trials for each contour type (collinear, orthogonal, or oblique). The trials of the three contour types were randomly ordered within a block.

In Phases 1 and 3, we investigated whether collinear and orthogonal contours can induce a positive cuing effect under the unconscious and conscious conditions, respectively. Phase 2 served to confirm that the contour stimuli in our study were comparable to those of previous studies and to assist the participants' successful integration and conscious awareness of circular contours in Phase 3.

Results

Awareness questionnaire

Top-down attention allocated to the contour was reduced by using a peripheral go/no-go task. According to the awareness questionnaire, 18 out of 26 participants were unconscious of all contours in Phase 1. The participants who reported not seeing any shapes to the first question (i.e., whether they had noticed any shape(s) within the Gabor field in Phase 1) and rated

their confidence level in seeing all type of circles as 3 or less were considered to show IB to the circular contours in Phase 1. In addition, four participants reported seeing the collinear and/or orthogonal circles to the first question and rated their confidence in seeing it/them as 4 or 5. Four other participants reported not seeing any shapes, but rated their confidence in seeing the collinear circle as 4 or 5 when being presented with pictures of circles and squares. No participants reported seeing the circle while rating their confidence less than 4. After the dual task in Phase 3, all participants reported seeing the collinear and orthogonal circles to the first question and were confident (rating ≥ 4) that they had seen them. The goal of this study was to investigate the processing of collinear and orthogonal contours under both the conscious and unconscious conditions. Therefore, we only analyzed behavioral data from the 18 participants who were unconscious of the circular contours in Phase 1 and became conscious of them in Phase 3. Participants' average scores on the awareness questionnaire for the circular contours are shown in Table 1.

A two-way repeated-measures ANOVA (awareness [unconscious, conscious] \times contour type [collinear, orthogonal]) for confidence rating revealed a significant awareness main effect, $F(1, 17) = 169.98$, $p < 0.001$, $\eta^2 = 0.91$, and a significant interaction between the two factors, $F(1, 17) = 22.81$, $p < 0.001$, $\eta^2 = 0.57$. Further analysis revealed a significant difference between Phases 1 and 3 for both collinear, $F(1, 17) = 2.86$, $p < 0.001$, $\eta^2 = 0.94$, and orthogonal contours, $F(1, 17) = 63.84$, $p < 0.001$, $\eta^2 = 0.79$. A two-way repeated-measures ANOVA (awareness [unconscious, conscious] \times contour type [collinear, orthogonal]) for frequency rating revealed a significant awareness main effect, $F(1, 17) = 253.24$, $p < 0.001$, $\eta^2 = 0.92$, contour type main effect, $F(1, 17) = 30.60$, $p < 0.001$, $\eta^2 = 0.64$, and interaction between the two factors, $F(1, 17) = 45.33$, $p < 0.001$, $\eta^2 = 0.73$. Further analysis revealed a significant difference between Phases 1 and 3 for both collinear, $F(1, 17) = 2.17$, $p < 0.001$, $\eta^2 = 0.93$, and

Phase	Confidence			Frequency		
	Collinear	Orthogonal	Oblique	Collinear	Orthogonal	Oblique
Phase 1	1.56 (0.62)	2.11 (0.90)	1.67 (0.67)	1.00 (0.00)	1.17 (0.51)	1.00 (0.00)
Phase 3	4.78 (0.43)	4.28 (0.46)	1.00 (0.00)	3.44 (0.70)	2.28 (0.46)	1.00 (0.00)

Table 1. Means and standard deviations (in parentheses) of the rating scores for the circular contours in the 5-point awareness questionnaire. *Notes:* Phase 1 refers to the unconscious phase and Phase 3 refers to the conscious phase. The awareness questionnaire had 5-point scales ranging from 1 (least confidence or frequent) to 5 (most confidence or frequent).

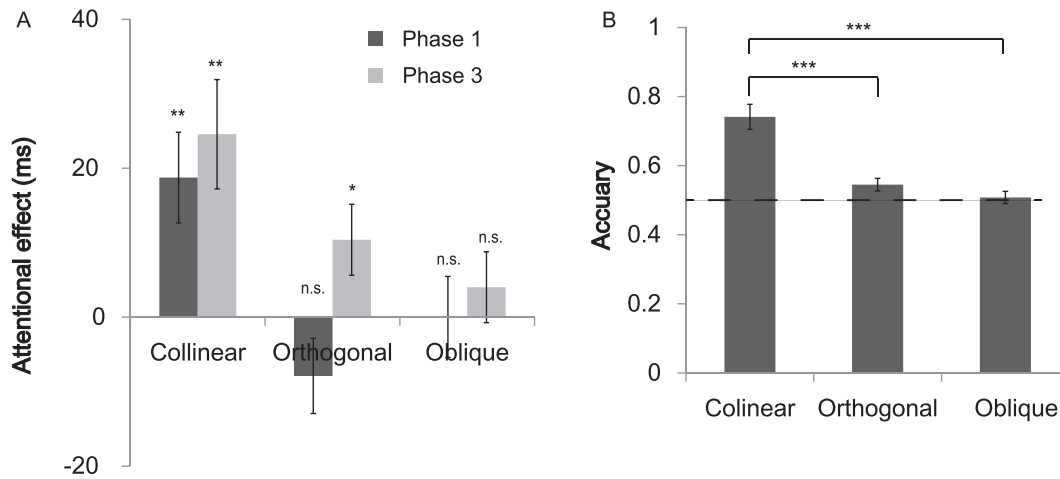


Figure 2. Behavioral results of Experiment 1. (A) Attentional cuing effects (calculated as RT difference between the invalid and valid conditions) are shown for collinear and orthogonal contours in the unconscious (Phase 1) and conscious (Phase 3) conditions. (B) Average accuracy across participants is shown for collinear, orthogonal, and oblique contours in the contour detection task in Phase 2. Error bars denote SEM calculated across participants. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

orthogonal contours, $F(1, 17) = 65.39$, $p < 0.001$, $\eta^2 = 0.79$. These results further confirmed the different awareness states for collinear and orthogonal contours between Phases 1 and 3.

Phases 1 and 3: Go/no-go task

Behavioral performance on the go/no-go task was evaluated in separate ANOVAs for false alarms and miss rates. Miss rates were 3.5% and 3.1% for Phases 1 and 3, respectively. False alarms were 0.2% and 0.2% for Phases 1 and 3, respectively. No significant differences were found for false alarms ($p = 0.51$) or miss rates ($p = 0.48$) between the two phases. These results indicate that top-down attention was well maintained on periphery.

Phases 1 and 3: Orientation discrimination task

Correct trials with reaction times (RTs) beyond 2 SDs from the mean RTs of these trials were regarded as outliers and removed from the analysis for each participant. Fewer than 5% of the trials were removed from the analysis. Cuing effects were indexed by the RT difference between the invalid cue and valid cue conditions (Figure 2A). Attentional cuing effects were observed in both unconscious, 19 ± 6 ms, $t(17) = 3.08$, $p < 0.01$, and conscious conditions, 25 ± 7 ms, $t(17) = 3.34$, $p < 0.01$, for collinear contours. However, for orthogonal contours, we found a cuing effect in the conscious, 10 ± 5 ms, $t(17) = 2.18$, $p < 0.05$, but not unconscious condition, -8 ± 5 ms, $t(17) = -1.56$, $p = 0.14$. There were also no cuing effects in both phases (Phase 1: 0 ± 5 ms, $t[17] = 0.01$, $p = 1.0$; Phase 3: 4 ± 5 ms, $t[17] = 0.84$, $p = 0.41$) for oblique contours. A two-

way repeated-measures ANOVA (awareness [unconscious, conscious] \times contour type [collinear, orthogonal, oblique]) revealed a larger cuing effect in the conscious condition than in the unconscious condition, $F(1, 17) = 8.47$, $p = 0.01$, $\eta^2 = 0.33$, and a significant contour type main effect, $F(2, 34) = 5.60$, $p < 0.01$, $\eta^2 = 0.25$. Pairwise comparisons revealed a larger cuing effect for collinear contours than for orthogonal ($p < 0.01$) and oblique contours ($p = 0.059$), but no significant interaction was observed, $F(2, 34) = 1.05$, $p = 0.36$, $\eta^2 = 0.06$. In sum, these results suggest that collinear contours can be processed unconsciously, whereas orthogonal contours only capture attention in the conscious condition when they are successfully integrated.

A repeated-measures ANOVA (awareness \times contour type) of accuracy revealed only a trend of larger cuing effects in the conscious condition than in the unconscious condition, $F(1, 17) = 3.42$, $p = 0.08$, $\eta^2 = 0.17$, without a significant main effect of the contour type, $F(2, 34) = 1.11$, $p = 0.34$, $\eta^2 = 0.06$, or a significant interaction, $F(2, 34) = 0.74$, $p = 0.49$, $\eta^2 = 0.04$. Furthermore, a one-sample t test compared with 0 showed that there were no significant cuing effects in any condition (all $ps > 0.1$), although there was a negative trend toward a cuing effect for the oblique condition in the conscious condition (2.5%, $t[17] = 2.04$, $p = 0.06$). These results indicate that there was no trade-off between RT and accuracy.

Phase 2: Contour detection task

For the contour detection task in Phase 2, a one-sample t test compared with 50% performance level revealed that accuracy for collinear (74%, $t[17] = 6.65$, p

< 0.001) and orthogonal (55%, $t[17] = 2.47$, $p < 0.05$) contours, but not for the oblique contour (51%, $t[17] = 0.44$, $p = 0.67$), was significantly higher than chance level (Figure 2B). A one-way repeated-measures ANOVA revealed a significant main effect of contour type, $F(2, 34) = 31.74$, $p < 0.001$, $\eta^2 = 0.65$. Pair-wise comparisons revealed that accuracy was higher for collinear contours than orthogonal (mean difference: 20%, $p < 0.001$) and oblique (mean difference: 23%, $p < 0.001$) contours. These results were consistent with previous findings that the detection performance of collinear contours was better than that of orthogonal and oblique contours (Bex et al., 2001; Field et al., 1993; Hess, Ledgeway, & Dakin, 2000; Ledgeway et al., 2005; May & Hess, 2008). Furthermore, the chance level performance in Phase 2 and the absence of attentional cuing effect in Phases 1 and 3 for oblique contours confirmed that the results of collinear and orthogonal contours cannot be explained by the differences in density or regularity of the elements between contour location (valid cue) and its contralateral counterpart (invalid cue). Taken together, these results suggest that collinear but not orthogonal contours can be processed without conscious awareness. However, the evidence was obtained in terms of the attentional cuing effect, which is an indirect measurement of perceptual processing of contours. To further validate this conclusion, we used the breaking-continuous flash suppression (b-CFS) paradigm (Jiang, Costello, & He, 2007) in Experiment 2 to investigate the unconscious processing of the contours with a sensitive index by estimating the duration of a stimulus emerging from interocular suppression. The b-CFS paradigm has been successfully applied to render the contour stimuli invisible with CFS (Fang & He, 2005; Tsuchiya & Koch, 2005) and measure the unconscious processing of various visual stimuli (Jiang, Costello, Fang, Huang, & He, 2006; Mudrik, Breska, Lamy, & Deouell, 2011; Sklar et al., 2012; Yang, Zald, & Blake, 2007), including the unconscious processing of the higher level visual features that cannot be detected with other paradigms (e.g., emotional expression; Stein, Seymour, Hebart, & Sterzer, 2014; Yang, Hong, & Blake, 2010).

Experiment 2

This experiment investigated whether collinear and orthogonal circular contours presented under CFS have prioritized access to conscious awareness relative to the Gabor field without an embedded contour (random field). Superiority in breaking time between the presence and absence of the contour could be interpreted as an indicator of contour processing without conscious awareness.

Methods

Participants

Eighteen naive observers with normal or corrected-to-normal vision participated in Experiment 2. None of the participants in Experiment 2 had participated in Experiment 1. The participants (nine males with a mean age of 23.5 years) had no known neurological or visual disorders. The study was approved by the local ethics committee.

Stimuli

Stimuli were displayed on the gray uniform background of a CRT monitor (refresh rate: 100 Hz, mean luminance: 24 cd/m²) in the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) programming environment in Matlab (The Math-Works, Inc., Natick, MA). Luminance of the monitor was gamma corrected. Participants viewed dichoptic images through a four-mirror stereoscope (mean luminance: 18 cd/m²) mounted on a chin and head rest from a distance of 72 cm in a dimly lit room. The mirror stereoscope was adjusted for each participant to ensure stable binocular fusion.

Stimuli were square Gabor fields ($6.10^\circ \times 6.10^\circ$) that contained on average 100 randomly distributed and oriented Gabor elements and were presented in one of four quadrants (Figure 3). Gabor fields were generated by the same algorithm as used in Experiment 1. All elements of the Gabor fields were in cosine phase and had a peak spatial frequency of 4.54 cycles/degree with an envelope σ of 0.08° . The contrast of the elements was set to 100%. A circular contour could be embedded in the Gabor field. The circular contour was composed of 19 Gabor elements aligned either along (collinear) or perpendicular (orthogonal) to an underlying circle. The separation of the contour elements was 0.45° . The center of the circular contours (radius: 1.38°) was located randomly at 3.15° – 4.5° from the fixation point. The random Gabor field without an embedded circular contour served as the baseline condition.

The Mondrian-like CFS mask ($6.27^\circ \times 6.27^\circ$) consisted of randomly arranged grayscale ellipses. Two black frames ($12.54^\circ \times 12.54^\circ$) with four bars that extended beyond the outer border of the frame and a red central fixation cross ($0.66^\circ \times 0.66^\circ$) were always presented to enhance binocular fusion.

Procedures

In the CFS condition of the b-CFS task, each trial started with the presentation of four dynamic Mondrian patterns at four separate quadrants on the right half of the monitor at full contrast. A test Gabor field with or without an embedded contour (collinear or



Figure 3. Stimuli and procedures in Experiment 2. (A) In the CFS condition, a Gabor field was gradually displayed to the left eye at one quadrant at a jittered onset time, while four dynamic Mondrian patterns were presented at 10 Hz to the right eye. The participants were instructed to press a key when they saw any part of the Gabor field. (B) In the control condition, the Mondrian patterns and the Gabor field were both presented binocularly, and the Gabor field was added on top of the Mondrian patterns transparently from 100% to 0% within 8.5 s. The onset of the appearance of the Gabor field was jittered. Participants were instructed to press one of four keys when they saw any part of the Gabor field.

orthogonal) was then gradually presented to the other eye in one quadrant on the left half of the monitor at a jittered onset time (100, 200, 300, 400, or 500 ms from the beginning of the trial). The contrast of the test Gabor field was increased linearly from 0% to 100% within a period of 1 s and remained constant until a response was made.

In the control condition, the stimuli and procedures were identical to those used in the CFS condition with the following exceptions. The Mondrian patterns and the Gabor field in the control condition were presented binocularly. The test Gabor field was gradually blended into the Mondrian masks at a jittered onset time by reducing their transparency linearly from 100% to 0% within a period of 8.5 s. The transparency of the test Gabor field was increased from 0% to 100% over the same time period. The participants were asked to fixate on the central cross throughout each trial and press one of four keys on the keyboard to indicate as quickly and accurately as possible when they saw any part of the Gabor field. They were not told about the specific content of the stimuli, and auditory feedback was given on incorrect responses. The control viewing condition was used to control possible confounding effects that the RT difference between different contours in the CFS viewing condition might not only come from perceptual difference but also postperception difference such as different response criteria between contour present and absent conditions. The possible con-

founding effects among the three contour conditions were most likely to be the same within a participant. If there is no difference between collinear and orthogonal contours in the control condition, then it is reasonable to infer that the effect in the CFS condition is due to the processing difference under unconscious state.

After the b-CFS task, a contour detection task was conducted. Four Gabor fields were presented binocularly in four quadrants. One of the Gabor fields was embedded with a collinear or orthogonal circular contour and the other three Gabor fields did not contain contours. The stimuli were presented for 400 ms followed by a 500-ms ISI. A gray background was presented until a response or 3 s had elapsed. Four-alternative forced choice (4AFC) was required to indicate the quadrant in which the circle was located as quickly and accurately as possible. No feedback was provided.

There were six blocks for both the b-CFS and control tasks, and each block consisted of 48 trials with 16 trials for each stimuli condition (collinear, orthogonal, or random). The b-CFS and control tasks were conducted separately. Participants performed at least 12 practice trials before beginning the experiment. In the contour detection task, there were four blocks, and each block consisted of 96 trials. Each block had 24 trials for each combination of contour type (collinear, orthogonal) and retinal eccentricity (3.15° , 4.5°). The

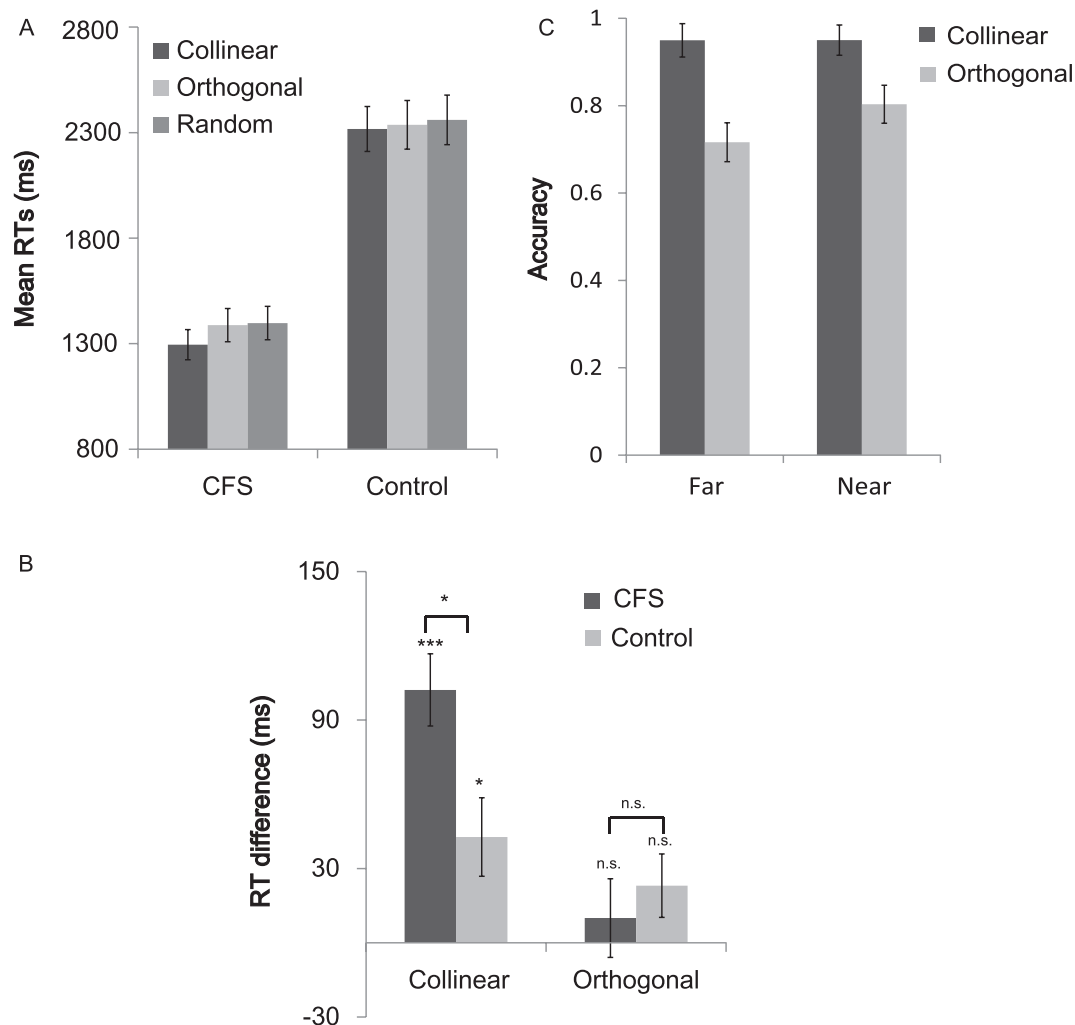


Figure 4. Behavioral results of Experiment 2. (A) Average RTs across participants for collinear, orthogonal, and random Gabor fields in the CFS and control conditions. (B) Difference in average RTs between contours present and absent across participants for collinear and orthogonal contours in the CFS and control conditions. (C) Average accuracy across participants for collinear and orthogonal contours located in the near and far retinal eccentricities in the contour detection task. Error bars denote *SEM* calculated across participants. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

circle was presented the same amount of times in each quadrant for each combination.

Results

Breaking-CFS task

The mean accuracy of the b-CFS task was 99.6%. There were no significant differences between any conditions ($ps > 0.2$), as revealed by an ANOVA, suggesting that there was no trade-off between RT and accuracy. RTs were measured as the breaking duration of the Gabor field from suppression. Mean RTs were calculated for correct trials within the range between 0.5 and 5 s, resulting in 1.15% of the trial being rejected. A repeated-measures ANOVA of RT (contour type [collinear, orthogonal, random] \times viewing condition

[CFS, control]) revealed significant main effects for the contour type, $F(2, 34) = 21.08$, $p < 0.001$, $\eta^2 = 0.56$, and the viewing condition, $F(1, 17) = 118.54$, $p < 0.001$, $\eta^2 = 0.88$, which were qualified by a significant interaction between the two factors, $F(2, 34) = 5.01$, $p < 0.05$, $\eta^2 = 0.23$ (Figure 4A). To explain the interaction effect, superiority-breaking effects (random – collinear and random – orthogonal) were examined using repeated-measures ANOVA (Figure 4B). There was a significant main effect of contour type, $F(1, 17) = 19.81$, $p < 0.001$, $\eta^2 = 0.54$, but no significant main effect of viewing condition, $F(1, 17) = 2.40$, $p = 0.14$, $\eta^2 = 0.12$. There was a significant interaction, $F(1, 17) = 5.87$, $p < 0.05$, $\eta^2 = 0.26$, indicating a larger superiority effect of collinear contours in the CFS than in the control condition, 59 ± 23 ms, $F(1, 17) = 6.86$, $p < 0.05$, $\eta^2 = 0.29$. No significant difference was observed between the CFS

and control conditions for orthogonal contours, -13 ± 19 ms, $F(1, 17) = 0.45$, $p = 0.51$, $\eta^2 = 0.03$. Furthermore, the suppression duration was shorter for collinear contours than for the random field, both in the CFS (102 ± 15 ms, $t[17] = 6.82$, $p < 0.001$) and control (43 ± 17 ms, $t[17] = 2.52$, $p < 0.05$) conditions. However, there were no significant superiority effects in either the CFS (10 ± 16 ms, $t[17] = 0.61$, $p = 0.55$) or control (23 ± 13 ms, $t[17] = 1.75$, $p = 0.10$) condition for orthogonal contours. These results suggest that collinear contours had an advantage to access awareness, while orthogonal contours had no such superiority.

Contour detection task

In the contour detection task, mean accuracy in all conditions was higher than chance level ($ps < 0.001$). A two-way ANOVA of accuracy revealed a significant interaction between contour type and retinal eccentricity, $F(1, 17) = 6.62$, $p < 0.05$, $\eta^2 = 0.28$. As shown in Figure 4C, accuracy was higher in the collinear than orthogonal condition, both at the near location, $F(1, 17) = 20.70$, $p < 0.001$, $\eta^2 = 0.55$, and far location, $F(1, 17) = 48.38$, $p < 0.001$, $\eta^2 = 0.74$. There were also significant main effects of contour type, $F(1, 17) = 44.99$, $p < 0.001$, $\eta^2 = 0.73$, and retinal eccentricity, $F(1, 17) = 6.13$, $p < 0.05$, $\eta^2 = 0.27$. These results demonstrate that the contours were super-threshold at both retinal eccentricity locations.

Discussion

Previous studies have shown that collinear contours can be better detected than orthogonal contours (Bex et al., 2001; Field et al., 1993; Ledgeway et al., 2005; May & Hess, 2007, 2008; Robol & Dakin, 2012). It has been shown that local features, such as element scale and phase (Hansen & Hess, 2006; May & Hess, 2008), spatial separation between elements (Ledgeway et al., 2005), and context around the contour (Dakin & Baruch, 2009) differentially influence the processing of collinear and orthogonal contours. Our results suggest that collinear but not orthogonal contours can be unconsciously processed (see also Schwarzkopf & Rees, 2011) and have the advantage to reach consciousness under suppression.

However, the stimuli in our study were closed contours and raised the possibility that global form processing played a significant role in the observed behavioral effects. Previous literature suggests that the processing of closed contours may reflect a combination of contour integration and shape coding (Hess, May, & Dumoulin, 2013). Kovács and Julesz (1993) found that the detection threshold is lower for closed or

roughly closed collinear contours than open control contours. This conclusion was supported by other investigations (Gerhardstein, Tse, Dickerson, Hipp, & Moser, 2012; Mathes & Fahle, 2007) and it was argued that the integration of closed collinear contours may involve specialized global mechanism in extrastriate cortex (Dumoulin & Hess, 2007). However, other researchers have argued that the probability summation rather than closure mechanism contributes to the small “closure” facilitation effect (Braun, 1999; Tversky, Geisler, & Perry, 2004). It remains an open question as to whether the integration of closed collinear contour involved higher level shape processing. Importantly, despite the evidence of global mechanism beyond contour integration for the closed contours, it does not necessarily mean the processing of closed contour is bound to the global mechanism. Sweeny et al. (2011) found that the curvature aftereffect is preserved for the open curve but eliminated for the closed curve when the stimulus is presented under CFS condition. Their findings suggest that the global processing of closed curvatures require conscious awareness. Therefore, the observed effect for the collinear circular contour under unconscious level in our study unlikely benefits from the higher level form processing.

Furthermore, it is well known that the task and expectation have great influence on visual processing (Gilbert & Li, 2013; W. Li, Piëch, & Gilbert, 2004; Mcmanus, Li, & Gilbert, 2011; Vancleef & Wagemans, 2013). In our study, the form of the stimulus was task-irrelevant and rendered invisible. It was inefficient for the brain to process the extra global form information if it was not required by the task. Nevertheless, we are not against the higher level global mechanism for the integration of closed contour. The inconsistency between the results in the conscious and task-relevant condition (e.g., contour detection paradigm) and unconscious condition (e.g., CFS paradigm) remains an interesting issue for further investigation. For the conscious condition (Phase 3) in our Experiment 1, the collinear and orthogonal contours were both successfully integrated, and it is difficult to determine whether the global mechanism was involved. Further brain imaging experiments are required to address this issue.

The accumulated evidence have shown that stimulus can be processed along feedforward sweep and has an impact on perception even if it is not consciously perceived (Lamme & Roelfsema, 2000; Moore & Egeth, 1997). Brain imaging studies with IB paradigm have demonstrated that the unexpected stimuli can be processed in ventral visual pathway beyond V1 (Lamme, 2006; Pitts et al., 2012), and have evoked recurrent processing in early visual cortex (Scholte, Witteveen, Spekreijse, & Lamme, 2006). Particularly, Pitts et al. (2012) used a modified IB paradigm similar

to our study to investigate the processing of collinear square contour pattern under unconscious and conscious conditions. They found a contour integration–related negativity at occipital area between 220 and 260 ms after stimulus onset both in the unconscious and conscious conditions, suggesting that the unnoticed collinear contour can be processed when it is not consciously perceived. Furthermore, physiological and imaging studies in monkeys have shown that contours can be integrated even if they are task-irrelevant and cannot be subjectively reported (Gilad, Meirovithz, & Slovin, 2013; W. Li et al., 2008; W. Li et al., 2006). W. Li et al. (2006) recorded the activation of V1 neurons when monkeys performed a collinear contour detection task. The results showed that the encoding ability of single V1 neurons about the contours can be as reliable as monkeys' behavioral response. Moreover, although being lower in the missed trials as compared to the hit trials, the activation of the single V1 neurons could discriminate whether the contour was present or absent even if the monkey could not report it. Furthermore, the contour-related activation in V1 neurons was still present when monkeys performed a dimming task and the collinear contours was task-irrelevant (W. Li et al., 2008). These studies provide us with a solid foundation for measuring the processing of contours even when contours are task-irrelevant and not consciously perceived. In our Experiment 1, when the top-down attention was engaged by a periphery go/no-go task, most of the subjects did not notice the unexpected circular contour in Phase 1. However, the collinear but not orthogonal contours induced a positive cuing effect in this unconscious condition. In Experiment 2, we adopted a sensitive index with the b-CFS paradigm to investigate the unconscious processing of the collinear and orthogonal contours (for review, Stein & Sterzer, 2014; Yang, Brascamp, Kang, & Blake, 2014). We found the significantly superior breaking effect only for the collinear but not orthogonal contours. The converging results from the different measuring techniques suggest that collinear but not orthogonal contours can be processed without being consciously perceived, leading to a positive attentional cuing effect and better detectability.

A possible interpretation for the integration of collinear contours in the unconscious condition is V1 saliency model (Z. Li, 1998, 2002; Zhaoping & May, 2007). This is an implementation of the association field model, which regards contour integration as an example of a more general process of computing bottom-up saliency based on a fragment of the collinear contour. According to this model, collinear facilitation between V1 neurons causes collinear contour to attract attention and predict positive cuing effect. Similarly, orthogonal contour could induce attentional suppression due to iso-orientation suppres-

sion between its parallel elements and could predict a negative cuing effect. However, the orthogonal contour neither induced facilitation nor suppression effect in our study. Further investigation with specific stimuli and design is required to test this interesting issue. Another class of model of contour integration, the filter-overlap model, developed by Hess and Dakin (1997) and extended by May and Hess (2008), incorporates two filtering stages with a nonlinear threshold in between. Specifically, collinear and orthogonal contours are encoded by parallelizing and orthogonalizing the second-order filters with respect to the first-order filters, respectively. This model predicts that both collinear and orthogonal contours generate higher response than the background elements. In our study, the results that collinear contours can be integrated in both unconscious and conscious conditions agree with the prediction by the filter-overlap model. The result of orthogonal contours in the unconscious condition remains an issue for further investigation.

Taken with the proposal that top-down information is critical for conscious awareness (Lamme & Roelfsema, 2000), we conclude that top-down information plays different roles in the processing of the two contour types. This conclusion is in agreement with the varied requirement of top-down attention for processing different types of local information in the natural environment (e.g., grouping aligned elements vs. segregating disconnected elements). The different results of collinear and orthogonal contours suggest that collinear contours are mediated by a different mechanism than orthogonal contours at the unconscious level. A possible mechanism to account for this differential processing is incremental grouping theory, which proposes two processes in neurophysiological level (Roelfsema, 2006; Roelfsema & Houtkamp, 2011). The theory suggests a parallel base grouping that relies on activation of neurons tuned for feature conjunction and a sequential incremental grouping that is based on spread of neural activity along attended object. We suggest that collinear contours that induce attentional cuing effect without conscious awareness could be processed through parallel base grouping, while orthogonal contours that exert the similar cuing effect under conscious condition might be processed through sequential incremental grouping with the help of top-down facilitation.

Conclusions

Our results suggest that collinear but not orthogonal contours can be processed without being consciously perceived, making them better detectable in a clutter

environment. These findings provide further evidence that the relevance of the contours to natural statistics could play an important role in implementing a dual process mechanism, including an automatic unconscious process and a controlled process with the involvement of top-down attention, at an early stage of sensory processing.

Keywords: contour, attention, conscious awareness, natural statistics, continuous flash suppression, inattention blindness

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References

- Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, 6(1), 47–52.
- Bex, P. J., Simmers, A. J., & Dakin, S. C. (2001). Snakes and ladders: The role of temporal modulation in visual contour integration. *Vision Research*, 41(27), 3775–3782.
- Bosking, W. H., Zhang, Y., Schofield, B., & Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *Journal of Neuroscience*, 17(6), 2112–2127.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436.
- Braun, J. (1999). On the detection of salient contours. *Spatial Vision*, 12(2), 211–225.
- Chen, M., Yan, Y., Gong, X., Gilbert, C. D., Liang, H., & Li, W. (2014). Incremental integration of global contours through interplay between visual cortical areas. *Neuron*, 82(3), 682–694.
- Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6(2), 119–126.
- Dakin, S. C., & Baruch, N. J. (2009). Context influences contour integration. *Journal of Vision*, 9(2):13, 1–13, doi:10.1167/9.2.13. [PubMed] [Article]
- Day, M., & Loffler, G. (2009). The role of orientation and position in shape perception. *Journal of Vision*, 9(10):14, 1–17, doi:10.1167/9.10.14. [PubMed] [Article]
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Dumoulin, S. O., & Hess, R. F. (2007). Cortical specialization for concentric shape processing. *Vision Research*, 47(12), 1608–1613.
- Elder, J. H., & Goldberg, R. M. (2002). Ecological statistics of Gestalt laws for the perceptual organization of contours. *Journal of Vision*, 2(4):5, 324–353, doi:10.1167/2.4.5. [PubMed] [Article]
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8(10), 1380–1385.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local “association field.” *Vision Research*, 33, 173–193.
- Geisler, W. S., Perry, J. S., Super, B. J., & Gallogly, D. P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, 41(6), 711–724.
- Gerhardstein, P., Tse, J., Dickerson, K., Hipp, D., & Moser, A. (2012). The human visual system uses a global closure mechanism. *Vision Research*, 71, 18–27.
- Gilad, A., Meirovithz, E., & Slovin, H. (2013). Population responses to contour integration: Early encoding of discrete elements and late perceptual grouping. *Neuron*, 78(2), 389–402.
- Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, 14(5), 350–363.
- Hansen, B. C., & Hess, R. F. (2006). The role of spatial phase in texture segmentation and contour integration. *Journal of Vision*, 6(5):5, 594–615, doi:10.1167/6.5.5. [PubMed] [Article]
- Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. *Nature*, 390(6660), 602–604.
- Hess, R. F., Hayes, A., & Field, D. J. (2003). Contour integration and cortical processing. *Journal of Physiology, Paris*, 97(2–3), 105–119.

- Hess, R. F., Ledgeway, T., & Dakin, S. (2000). Impoverished second-order input to global linking in human vision. *Vision Research*, 40(24), 3309–3318.
- Hess, R. F., May, K. A., & Dumoulin, S. O. (2015). Contour integration: Psychophysical, neurophysiological and computational perspectives. In J. Wagemans (Ed.), *Oxford handbook of perceptual organization*. Oxford, UK: Oxford University Press.
- Jiang, Y., Costello, P., Fang, F., Huang, M., & He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proceedings of the National Academy of Sciences, USA*, 103(45), 17048–17052.
- Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science*, 18(4), 349–355.
- Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys. *Neuron*, 15, 843–856.
- Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (2000). Spatial distribution of contextual interactions in primary visual cortex and in visual perception. *Journal of Neurophysiology*, 84, 2048–2062.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3? *Perception*, 36(14), 1.
- Kovács, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences*, 90(16), 7495–7497.
- Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, 10(11), 494–501.
- Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23(11), 571–579.
- Ledgeway, T., Hess, R. F., & Geisler, W. S. (2005). Grouping local orientation and direction signals to extract spatial contours: Empirical tests of “association field” models of contour integration. *Vision Research*, 45(19), 2511–2522.
- Li, W., Gilbert, C. D., & Piëch, V. (2008). Learning to link visual contours. *Neuron*, 57, 442–451.
- Li, W., Piëch, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651–657.
- Li, W., Piëch, V., & Gilbert, C. D. (2006). Contour saliency in primary visual cortex. *Neuron*, 50, 951–962.
- Li, Z. (1998). A neural model of contour integration in the primary. *Neural Computation*, 10, 903–940.
- Li, Z. (2002). A saliency map in primary visual cortex. *Trends in Cognitive Sciences*, 6(1), 9–16.
- Mack, A., & Rock, I. (1998). *Inattention blindness* (p. 288). Cambridge, MA: MIT Press.
- Mathes, B., & Fahle, M. (2007). Closure facilitates contour integration. *Vision Research*, 47(6), 818–827.
- May, K. A., & Hess, R. F. (2007). Dynamics of snakes and ladders. *Journal of Vision*, 7(12):13, 1–9, doi:10.1167/7.12.13. [PubMed] [Article]
- May, K. A., & Hess, R. F. (2008). Effects of element separation and carrier wavelength on detection of snakes and ladders: Implications for models of contour integration. *Journal of Vision*, 8(13):4, 1–23, doi:10.1167/8.13.4. [PubMed] [Article]
- Mcmanus, J. N. J., Li, W., & Gilbert, C. D. (2011). Adaptive shape processing in primary visual cortex. *Proceedings of the National Academy of Sciences, USA*, 108, 9739–9746.
- Mijovi, B., de Vos, M., Vanderperren, K., Machilsen, B., Sunaert, S., Huffel, S., & Wagemans, J. (2014). The dynamics of contour integration: A simultaneous EEG-fMRI study. *NeuroImage*, 88, 10–21.
- Moore, C. M., & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention to shape constancy. *Journal of Experimental Psychology, Human Perception, & Performance*, 23(2), 339–352.
- Most, S. B., Scholl, B. J., Clifford, E. R., & Simons, D. J. (2005). What you see is what you set: Sustained inattention blindness and the capture of awareness. *Psychological Review*, 112(1), 217–242.
- Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration without awareness: Expanding the limits of unconscious processing. *Psychological Science*, 22(6), 764–770.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Piëch, V., Li, W., Reeke, G. N., & Gilbert, C. D. (2013). Network model of top-down influences on local gain and contextual interactions in visual cortex. *Proceedings of the National Academy of Sciences, USA*, 110, E4108–E4117.
- Pitts, M. A., Martínez, A., & Hillyard, S. A. (2012).

- Visual processing of contour patterns under conditions of inattention blindness. *Journal of Cognitive Neuroscience*, 24(2), 287–303.
- Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology, General*, 109(2), 160–174.
- Robol, V., & Dakin, S. C. (2012). The role of crowding in contextual influences on contour integration. *Journal of Vision*, 12(7):3, 1–18, doi:10.1167/12.7.3. [PubMed] [Article]
- Roelfsema, P. R. (2006). Cortical algorithms for perceptual grouping. *Annual Review of Neuroscience*, 29, 203–227.
- Roelfsema, P. R., & Houtkamp, R. (2011). Incremental grouping of image elements in vision. *Attention, Perception, & Psychophysics*, 73(8), 2542–2572.
- Scholte, H. S., Witteveen, S. C., Spekreijse, H., & Lamme, V. A. F. (2006). The influence of inattention on the neural correlates of scene segmentation. *Brain Research*, 1076(1), 106–115.
- Schwarzkopf, D. S., & Kourtzi, Z. (2008). Experience shapes the utility of natural statistics for perceptual contour integration. *Current Biology*, 18(15), 1162–1167.
- Schwarzkopf, D. S., & Rees, G. (2011). Interpreting local visual features as a global shape requires awareness. *Proceedings of the Royal Society: Biological Science*, 278(1715), 2207–15.
- Shpaner, M., Molholm, S., Forde, E., & Foxe, J. J. (2013). Disambiguating the roles of area V1 and the lateral occipital complex (LOC) in contour integration. *NeuroImage*, 69, 146–156.
- Sigman, M., Cecchi, G. A., Gilbert, C. D., & Magnasco, M. O. (2001). On a common circle: Natural scenes and Gestalt rules. *Proceedings of the National Academy of Sciences, USA*, 98(4), 1935–1940.
- Simons, D. J. (2000). Attentional capture and inattention blindness. *Trends in Cognitive Sciences*, 4(4), 1452–1456.
- Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., & Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proceedings of the National Academy of Sciences, USA*, 109(48), 19614–19619.
- Stein, T., Seymour, K., Hebart, M. N., & Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychological Science*, 25(2), 566–574.
- Stein, T., & Sterzer, P. (2014). Unconscious processing under interocular suppression: Getting the right measure. *Frontiers in Psychology*, 5(387), 1–5.
- Sweeny, T. D., Grabowecky, M., & Suzuki, S. (2011). Awareness becomes necessary between adaptive pattern coding of open and closed curvatures. *Psychological Science*, 22(7), 943–950.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, 51(6), 599–606.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096–101.
- Tversky, T., Geisler, W. S., & Perry, J. S. (2004). Contour grouping: Closure effects are explained by good continuation and proximity. *Vision Research*, 44, 2769–2777.
- Vancleef, K., & Wagemans, J. (2013). Component processes in contour integration: A direct comparison between snakes and ladders in a detection and a shape discrimination task. *Vision Research*, 92, 39–46.
- Wang, Y. Z., & Hess, R. F. (2005). Contributions of local orientation and position features to shape integration. *Vision Research*, 45(11), 1375–1383.
- Yang, E., Brascamp, J., Kang, M.-S., & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in Psychology*, 5(724), 1–17.
- Yang, E., Hong, S., & Blake, R. (2010). Adaptation aftereffects to facial expressions suppressed from visual awareness. *Journal of Vision*, 10(12):2, 1–13, doi:10.1167/10.12.2. [PubMed] [Article]
- Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*, 7(4), 882–886.
- Yantis, S., & Egeth, H. E. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 25(3), 661–676.
- Zhang, X., Zhaoping, L., Zhou, T., & Fang, F. (2012). Neural activities in V1 create a bottom-up saliency map. *Neuron*, 73(1), 183–192.
- Zhaoping, L., & May, K. A. (2007). psychophysical tests of the hypothesis of a bottom-up saliency map in primary visual cortex. *PLoS Computational Biology*, 3(4), 616–633.

Appendix

Awareness questionnaire

Phase:

Subject:

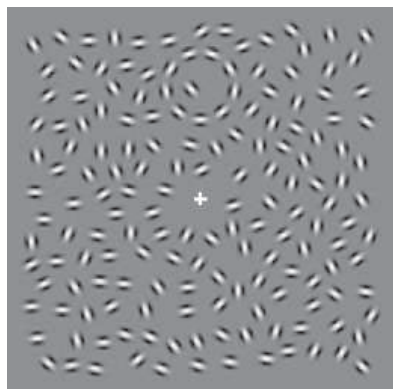
1. Did you notice any shape(s) within the field during the experiment?
2. If you see any shape, please describe or draw it (them) with as much details as possible.
3. How confident are you that you saw the shape shown in the screen?

Shape number	Very confident I didn't see it	Confident I didn't see it	Uncertain	Confident I saw it	Very confident I saw it
1	1	2	3	4	5
2	1	2	3	4	5
3	1	2	3	4	5
4	1	2	3	4	5
5	1	2	3	4	5
6	1	2	3	4	5

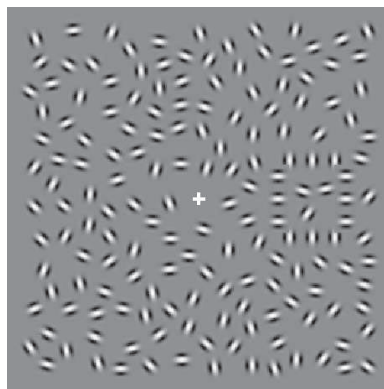
4. How often did you see the shape shown in the screen?

Shape number	Never	Rarely (less than 10 times)	Infrequently (10–50 times)	Frequently (50–100 times)	Very frequently (more than 100 times)
1	1	2	3	4	5
2	1	2	3	4	5
3	1	2	3	4	5
4	1	2	3	4	5
5	1	2	3	4	5
6	1	2	3	4	5

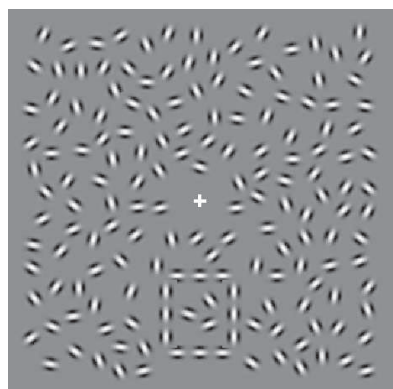
Sample shapes shown in the awareness questionnaire.



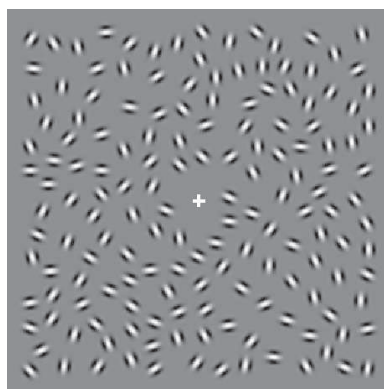
1



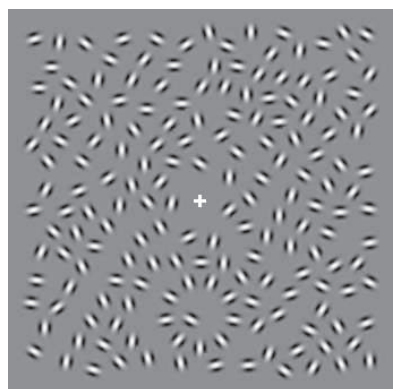
4



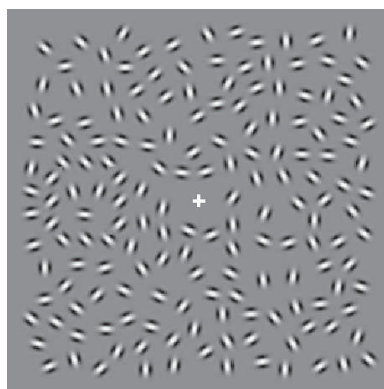
2



5



3



6