

Visible and invisible stimulus parts integrate into global object representations as revealed by combining monocular and binocular rivalry

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Our visual system faces the challenging task to construct integrated visual representations from the visual input projected on our retinæ. Previous research has provided mixed evidence as to whether visual awareness of the stimulus parts is required for such integration to occur. Here, we address this issue by taking a novel approach in which we combine a monocular rivalry stimulus (i.e., a bistable rotating cylinder) with binocular rivalry. The results of Experiment 1 show that in a rivalry condition, where one half of the cylinder is perceptually suppressed, significantly more perceptual switches occur that are consistent with visual integration of the whole cylinder than occur in a control condition, where only half of the cylinder is presented at a time and the presentation of the two images is physically alternated. In Experiment 2, stimulation in the observer's dominant eye was kept dominant by presenting the half cylinder in this eye at higher contrast and by surrounding it with a flickering context. Results show that the strong convexity bias that was found in a control condition, where no stimulus was presented in the suppressed eye, almost completely disappears when the unseen half is presented in the suppressed eye, indicating that both halves visually integrate and, subsequently, compete for convexity. These findings provide evidence that unseen visual information is biased towards a representation

that is congruent with the current visible representation and, hence, that principles of perceptual organization also apply to parts of the visual input that remain unseen by the observer.

Introduction

Our visual system is facing the important but challenging task to translate retinal input into meaningful and coherent representations that it can act upon. Many processes, operating at multiple levels of complexity, are involved in the formation of object representations. Within this process of perceptual organization (Wagemans, 2015) image properties, such as luminance, color, texture, disparity, and motion are detected, while different parts of the visual scene that belong together need to be integrated into a whole (Palmer & Rock, 1994). In normal vision, these processes generally lead to a perceptual outcome that is sharp and unambiguous, which suggests an intimate relationship between perceptual organization and visual awareness. Nevertheless, the relationship be-

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tween perceptual organization and visual awareness still remains very much debated (Lamme, 2014).

Binocular rivalry is arguably the most frequently used perceptual suppression paradigm to study the relationship between perceptual organization and visual awareness. In binocular rivalry, different images presented to the left and right eye compete for visibility, leading to the perceptual suppression of one of the images (Alais & Blake, 2005; Wheatstone, 1838). A specific variant of this paradigm, called continuous flash suppression (CFS; Tsuchiya & Koch, 2005), in which one of the images flashes at a continuous rate of usually 10 Hz, has become a popular method of studying unconscious visual processing, as it effectuates relatively large control over several characteristics of the suppression process, like its onset and its duration. Although there are some inconsistencies in the literature, there is accumulating support for the idea that many relatively basic, low-level visual processes still take place under CFS and binocular rivalry more generally, whereas there is less consistent evidence that this is also the case for higher level visual processing (for recent reviews, see Gayet, Van Der Stigchel, & Paffen, 2014, and Yang, Brascamp, Kang, & Blake, 2014). For instance, it has recently been shown that low-level effects such as collinear facilitation and simultaneous brightness contrast still occur for perceptually suppressed flankers and surfaces, respectively (Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011; Hayashi & Murakami, 2015). In contrast, for a higher level brightness phenomenon like the Craik-O'Brien-Cornsweet effect, awareness of the central luminance edge appears necessary for the effect to occur (Masuda et al., 2011). Furthermore, for cast shadows, the low-level properties are still processed under CFS, as indicated by the motion aftereffect that they generate, but their suppression strongly diminishes illusory motion perception in depth (Khuu, Gordon, Balcomb, & Kim, 2014). Finally, for the classical Kanizsa illusory surface completion conflicting evidence has been reported. Whereas Wang, Weng, and He (2012) showed that Kanizsa pacmen break through suppression faster when they induce an illusory shape compared to when they are oriented randomly, several other studies failed to obtain convincing evidence for the illusory shape to be represented during perceptual suppression (Harris et al., 2011; Moors, Wagemans, van Ee, & de-Wit, 2015; Sobel & Blake, 2003).

The relationship between perceptual organization and visual awareness has generally been studied with paradigms where the effects of perceptual organization solely pertained to the processing of the invisible (i.e., perceptually suppressed) stimulus parts. Although these paradigms have been informative regarding the relationship between perceptual (binocular) suppression and perceptual organization, they are also limited

in what they can teach us on the exact interplay between processes of perceptual organization and visible and invisible input. Indeed, here we asked whether the perceptual representation of a visible object is influenced by the presence of invisible stimulus parts that are congruent with the visible object representation. We used an ambiguous structure from motion stimulus (i.e., a rotating cylinder), which in normal monocular viewing gives the impression of a coherent rotating stimulus (see Figure 1A and also Supplementary Movie 1). Perceptual competition typically takes place at the level of surface representation (Brouwer & van Ee, 2006, 2007) entailing temporal alternation of the perceived rotational motion direction of the front surface. In other words, the perceived motion direction of the front surface of the cylinder is typically ambiguous (indicated in green and red in Figure 1A). Half of the dots are perceived to form a convex surface (i.e., the front surface) while the other half are perceived as a concave surface (i.e., the back surface).

In the two experiments presented here, the two halves of the cylinder (i.e., leftward and rightward moving dots, respectively) were separated and presented at overlapping retinal regions, one half to each eye. This procedure resulted in binocular rivalry where only one of the halves was visible at a time, while the other half was perceptually suppressed. We were interested in how the presence of the invisible half of the cylinder affects the perceptual appearance of the visible half. That is, if processes of perceptual organization (i.e., integration of both ambiguous stimulus halves into one coherent stimulus) require conscious perception of the presented stimulus, then we expected the perceptual dynamics (i.e., the perceived convexity/concavity of the surface, as well as its perceived motion direction) of the visible part of the ambiguous stimulus to be similar, regardless of whether the unseen part of the stimulus is presented or not. If, however, processes of perceptual organization do *not* require awareness of the full stimulus (i.e., if visible and invisible stimulus parts can be perceptually organized into a single, coherent whole), then we expected the perceptual dynamics to be influenced by the presence of invisible stimulus parts.

Experiment 1: Serial dependence

The first experiment tested whether the presence of invisible parts of the above described ambiguous rotating cylinder influences the perceptual dynamics of the visible parts of the stimulus. The temporal dynamics in perceptual dominance (i.e., perceived front vs. back surface and perceived leftward vs. rightward

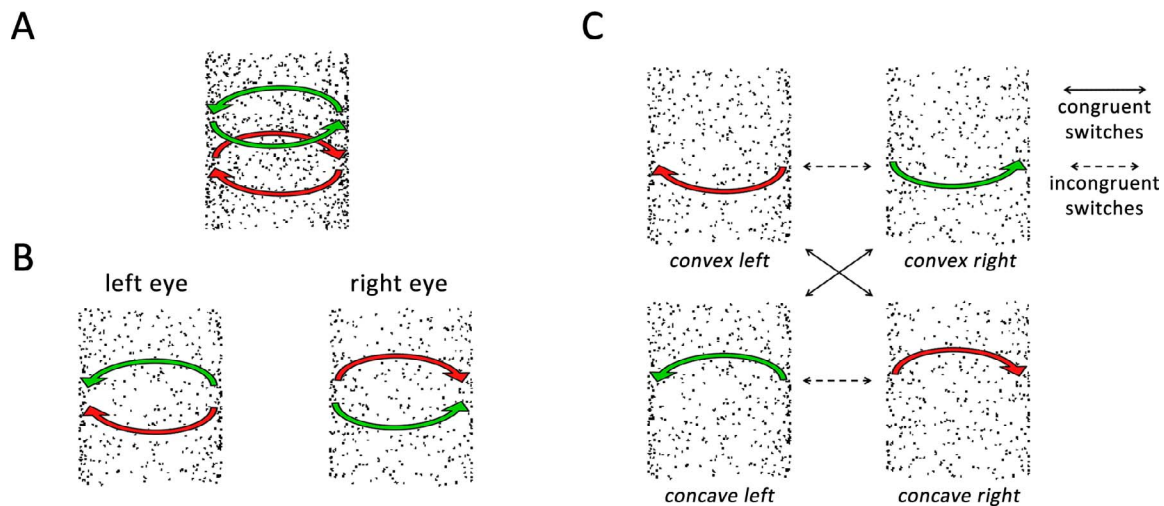


Figure 1. The binocular cylinder. (A) The original version of a rotating cylinder can be perceived with its front surface rotating either leftwards or rightwards (as indicated with the red and green arrows, respectively). The perceived rotational motion direction usually alternates over time. (B) In Experiment 1, dots were presented in the left eye when they were moving leftwards and in the right eye when they were moving rightwards on the screen, at the same retinal region. As a result, the left and right eye stimuli competed for visual awareness. (C) The stimulus and its four possible percepts: (a) a convex shell consisting of leftward moving dots, (b) a concave shell consisting of leftward moving dots, (c) a convex shell consisting of rightward moving dots, and (d) a concave shell consisting of rightward moving dots.

moving dots, as well as their interaction) provide us with a tool to investigate visual integration of seen and unseen elements into congruent object representations. If such integration would occur, then the unseen stimulus half would be represented in a way that is congruent with the current representation of the visible half. For instance, if the visible half consisting of dots moving to the right is perceived as convex, then the unseen half (consisting of dots moving to the left) should be represented as concave, which would be congruent with the representation of the seen half. We predicted that in such a case, these congruent representations should be reflected in a higher percentage of congruent switches in eye dominance (i.e., from a convex shell moving rightward towards a convex shell moving leftward) compared to when the invisible half is not presented.

Method

Observers

Ten healthy observers (three males, seven females) participated in the experiment (mean age 19.5 years old, $SD = 2.8$). The participants were compensated for their participation with course credits and gave their informed consent preceding the experiment.

Apparatus

Stimuli were displayed on a 22-inch Dell LCD screen (1920×1080 pixels at 60 Hz) driven by a DELL

Optiplex 755 computer with an Intel Core 2 Duo E4500 Processor (2200 MHz) running on Windows 7. A four-mirror stereo setup achieved binocular presentation. The left eye and right eye image were presented on the left and right side of the screen, respectively. A vertically oriented black cardboard septum was positioned between the horizontal center of the monitor and the stereo setup to avoid parts of the images being visible to the contralateral eye. A head-and-chin rest positioned at 4 cm from the mirrors was used to stabilize head position and orientation. The effective viewing distance was 180 cm. Stimulus presentation, timing and keyboard responses were controlled with custom software programmed in Python 2.7 using the PsychoPy library (Peirce, 2007, 2009).¹

Stimuli

Stable vergence was established by presenting four static lines with a length of 0.51 arcdeg, one on each side of the stimulus (i.e., vertical lines above and below, and horizontal lines left and right of the stimulus), at the same relative retinal location to each eye. The distance from the center of each vergence line to the center of the cylinder was 1.18 arcdeg. The cylinder consisted of 800 dots, moving horizontally about a vertical axis in a sinusoidal pattern of 0.50 arcdeg amplitude which caused the overall impression of the rotating cylinder. The high dot density of the cylinder was chosen to establish stable rivalry between the left and right eye image. The dots were white (74 cd/m^2)

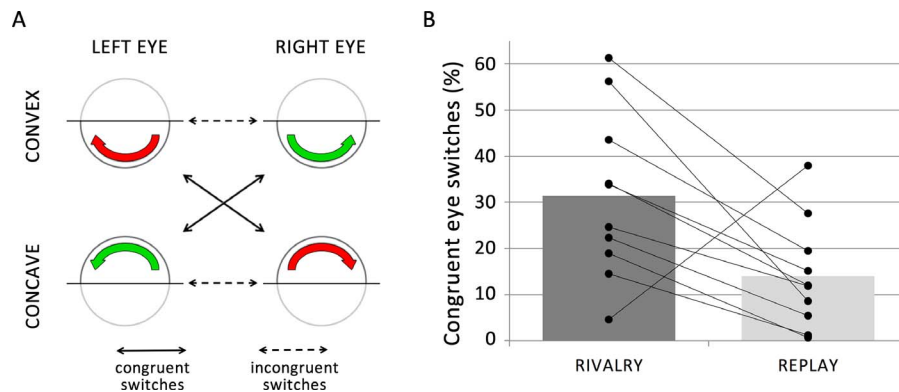


Figure 2. Results of Experiment 1. (A) Illustration of how the proportions of congruent perceptual switches are defined. Convex, leftward motion and concave, rightward motion (indicated with red arrows) both support clockwise rotation of the cylinder. Similarly, concave, leftward motion and convex, rightward motion (indicated with green arrows) both support counterclockwise rotation of the cylinder. Solid arrows represent switches in eye dominance that are perceptually congruent in terms of global, holistic integration, whereas dashed arrows show incongruent perceptual switches. (B) Mean percentages of perceptual eye switches supporting the same rotational motion for both the Rivalry and the Replay condition. Connected dots represent data points of individual observers.

with a diameter of 1.01 arcmin, presented on a black background. The dots moved at a speed of 0.095 cycles/s. The vertical starting position of each dot was chosen randomly within a visual angle of 1.26 arcdeg while horizontally the dot was placed at a random phase of the sinusoidal cycle that defined the motion path. A mirror stereo setup was used to achieve binocular presentation. Leftward moving dots were presented to the left eye, and rightward moving dots were presented to the right eye (see Figure 1B; see also Supplementary Movie 2). All observers confirmed during debriefing that binocular rivalry was achieved, so that either the leftward moving dots or the rightward moving dots were visible, but never both at the same time. In addition, the visible dots could be perceived to form a convex shield or a concave shield. Hence, in total four different global percepts could be dominant (see Figure 1C): (a) a convex surface consisting of rightward moving dots, (b) a concave surface consisting of rightward moving dots, (c) a convex surface consisting of leftward moving dots, and (d) a concave surface consisting of leftward moving dots. In other words, the possible percepts reflect both binocular rivalry (i.e., between leftward and rightward moving surfaces) and monocular rivalry (i.e., between surfaces either perceived as convex or as concave). The different possible percepts alternated over time, as is typically the case both in binocular rivalry and for ambiguous stimuli like the rotating cylinder.

Procedure and design

In each *Rivalry* trial, the two halves of the rotating cylinder were presented continuously, for 120 s, one half in each eye, respectively. The observers' task was to report perceptual switches with a single keyboard

press immediately after each perceptual switch. Four different responses were possible, corresponding with the four possible percepts as described above. Responses and dominance durations were both collected. Each *Rivalry* trial was followed by a so-called *Replay* trial. In these trials, only one half of the cylinder was presented at each point in time. Which half was presented was determined by the eye dominance durations reported in the preceding *Rivalry* trial. In other words, each *Replay* trial replayed the eye dominance durations of the preceding *Rivalry* trial, regardless of perceived convexity or concavity. The task of the observers was the same, to indicate their current percept with single key presses after every perceptual switch. A total of 20 trials, 10 *Rivalry* and 10 *Replay* trials, were presented in alternating order for each observer. Observers were instructed to press the "spacebar" to continue with the next trial.

Results and discussion

For our analysis we were interested in perceived rotation at the moment of perceptual eye switches (see Figure 2A). Perception after an eye switch either supported the same rotational motion pattern as before the eye switch (i.e., congruent switches), or it supported rotational motion in the opposite direction (i.e., incongruent switches). In other words, congruent perceptual switches involve switches from the left to the right eye (or vice versa) that are accompanied by a switch from a convex to a concave percept (or vice versa). For all observers, the proportions of these congruent perceptual switches during eye switches were calculated as a fraction of total eye switches, both for *Rivalry* trials and for *Replay* trials (*Rivalry*: $M = 0.31$,

$SD = 0.06$ vs. Replay: $M = 0.14$, $SD = 0.04$; see Figure 2B).²

Because the switch rate in dominance between both eyes varied considerably across observers, we used a logistic mixed effects regression model to take into account the uncertainty associated with the percentage of congruent switches for each observer. In the Rivalry condition there were significantly more congruent eye-dominance switches of the so-called rotating cylinders than in the Replay condition ($z = 4.13$, $\beta = 1.42$, $SD = 0.34$, $p < 0.001$). In other words, when the two halves of the rotating cylinder were presented at the same time, which was the case in the Rivalry condition, there were more reversals from convexity to concavity and vice versa during perceptual eye switches, compared to the Replay condition, where only half of the stimulus was presented at a time. This result is in line with the hypothesis that the visual system represents unseen stimulus parts in a way that is congruent with the currently active visible object representation. According to this hypothesis, if the visible half of the cylinder is represented as convex, then the invisible half should be represented as concave, and vice versa, to support the same rotational motion. This leads to the prediction that during a switch in eye-dominance, the previously suppressed half of the cylinder becomes visible in the state at which it was already represented (either convex or concave), which, following our hypothesis, is the opposed representational state compared to the previously visible half of the cylinder. This prediction is reflected in the data by significantly more perceptual switches from convex to concave (or vice versa) during eye switches in the Rivalry condition compared to the Replay condition, where the unseen half was not represented at all. Note that in both conditions the percentage of congruent switches is still relatively low, which is most likely due to the strong convexity bias that is often reported in the literature (Bertamini & Wagemans, 2013). Indeed, the overall percentage of convex percepts is much higher than the percentage of concave percepts (71.3% vs. 28.7%; $t_9 = 7.623$, $p < 0.0001$). This convexity bias is much smaller for the Rivalry condition, compared to the Replay condition (58.2% vs. 86.1 % of convex percepts; $t_9 = 3.73$, $p < 0.005$), indicating that indeed the presence of visible and invisible halves influence each other's visual representation in terms of convexity and concavity.

Although these data support the hypothesis that invisible and visible stimulus parts can be integrated into coherent, three-dimensional visual representations, the continuous switching in eye dominance complicates the interpretation of these data in terms of the perceptual dynamics between visible and invisible stimulus parts. For instance, it is difficult to rule out the influence of stimulus integration processes occurring *during* perceptual eye switches, where in some instances

piecemeal percepts combining the stimuli of both eyes may have occurred. We cannot fully rule out the possibility that dynamics during such piecemeal percepts could have biased the results towards the observed effect, although observers did report that perceptual switches were generally fast, without clear piecemeal percepts. In addition, the perceptual eye switches in the Rivalry condition were mimicked in the Control condition by means of a sudden stimulus offset in one eye, and a simultaneous sudden stimulus onset in the other eye. It cannot be ruled out that these visual transients might have had an influence on the perceptual dynamics in terms of perceived convexity and concavity, although there is no clear indication that this was the case. A second experiment was conducted that used a different experimental approach to test the hypothesis of perceptual organization between visible and invisible stimulus halves, which did not require, nor allowed perceptual eye switching, hence preventing integration processes during eye switches to bias the results in any way.

Experiment 2: Suppressed convexity

In Experiment 1, we found that sequential dominance states are influenced by the presentation of invisible stimulus parts, congruent with the visible global representation. We interpreted this finding as support for the idea that invisible stimulus parts can be integrated with a visible representation, in the sense that these invisible parts are represented congruently with the visible representation. Whereas Experiment 1 focused on sequential dominance states, here we tested how the presence of a perceptually suppressed half of a rotating cylinder influences the perception of the visible half. As argued above, it is possible that a phase of perceptual uncertainty that generally accompanies perceptual switches in bistable perception (Knapen, Brascamp, Pearson, van Ee, & Blake, 2011) could contribute to the effect observed in Experiment 1, rather than solely the integration between visible and suppressed stimulus parts. Therefore, in Experiment 2 we took an approach that rules out the dynamics during perceptual eye switches as a possible confounding factor.

We tested whether a continuously suppressed stimulus half can influence the percept of the continuously visible stimulus. A similar structure-from-motion stimulus was used as in Experiment 1, with several parametrical changes to facilitate the continuous perceptual suppression of the stimulus half presented to one eye (i.e., the observer's nondominant eye) throughout the experiment. We hypothesized that if the integration of the invisible and visible parts pertains to

one whole, coherent object representation, as suggested by the results of Experiment 1, presenting the unseen half of the cylinder or not, could differentially influence the way the visible part of the stimulus will be perceived. According to this hypothesis, when half of the cylinder is present in the suppressed eye, this could lead to “competition for convexity” between both halves, because only one half of the cylinder can be represented as convex (as is the case for a conventional, fully visible ambiguous rotating cylinder). This hypothesis leads to the prediction that the convexity bias for the seen half would be reduced in the rivalry condition, compared with a condition where the unseen half is not presented to the observer.

Method

Observers

The participants were six observers (mean age 20.5 years old, $SD = 2.6$; one male, five females) who met our strict inclusion criterion of exclusive perceptual dominance of the dominant eye throughout the full experiment. All observers were paid or compensated with credits for their participation and gave their informed consent preceding the experiment.

Apparatus

The apparatus was the same as described in Experiment 1.

Stimuli

In Experiment 2, we again made use of the ambiguous rotating cylinder. For the purpose of this experiment, several changes were made regarding the presentation of the moving dots. The cylinder consisted of 300 dots, again moving horizontally around a vertical axis in a sinusoidal pattern of 0.50 arcdeg amplitude with a speed of 0.191 cycles/s. The start position of each dot was chosen randomly within an angle of 1.26 arcdeg while horizontally the dot was placed at a random phase of the sinusoidal cycle. Each dot had a diameter of 4.04 arcmin. In the Rivalry condition, both halves of the rotating cylinder were presented, one half to each eye. The dots presented in the observer's dominant eye were presented at a high luminance (106.0 cd/m^2) while the dots in the observer's nondominant eye were presented at a much lower luminance (5.21 cd/m^2), and both were presented on a black background. The aim of the large difference in luminance was to increase perceptual dominance of the stimulus presented in the dominant eye. For the same purpose, the stimulus in the observer's dominant eye was surrounded by a dynamic-noise pattern, which

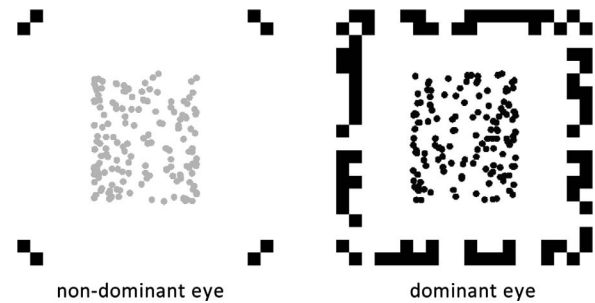


Figure 3. Stimulus as used in Experiment 2. Presentation of suppressed and visible stimuli with their surroundings, respectively.

increased the saliency of the dominant eye presentation (see Figure 3 and also Supplementary Movie 2). The dynamic-noise pattern consisted of 2×16 squares of 8.422 arcmin length \times width on each side (up, right, left, and below the stimulus). Each square alternated in black and white at 10 Hz to create a flickering percept. Each corner of the frame consisted of a 2×2 static black and white checkerboard. The same static checkerboards were presented in the observers' non-dominant eye to stabilize vergence.

Design and procedure

Before the experiment started, the observers' dominant eye was determined by means of a simple binocular grating rivalry task with the eye that showed the longest cumulative dominance duration over a 120 s viewing period taken as the observers' dominant eye. In this eye, the high contrast stimulus was presented during the main experiment. In the *Rivalry* condition, both stimulus halves as described above were presented, one half to each eye. As in Experiment 1, observers were asked to indicate their current percept with a single keyboard press after each perceptual switch. Response options were (a) a concave shell consisting of rightward moving dots, (b) a convex shell consisting of rightward moving dots, or (c) some leftward moving dots are visible. Observers were instructed to use the third response option even if only some of the leftward moving dots were visible. Trials in which such responses were given were later excluded from the analysis. In the *Control* condition only the dots presented to the observer's dominant eye were present. The other half of the dots (i.e., the dots that were presented in the suppressed eye in the Rivalry condition) were not presented at all. The presentation of the dots in the dominant eye was the same in both conditions. The experiment consisted of 10 Rivalry and 10 Control trials of 120 s each. Rivalry trials and Control trials alternated. Observers were instructed to press the “spacebar” to continue with the next trial.

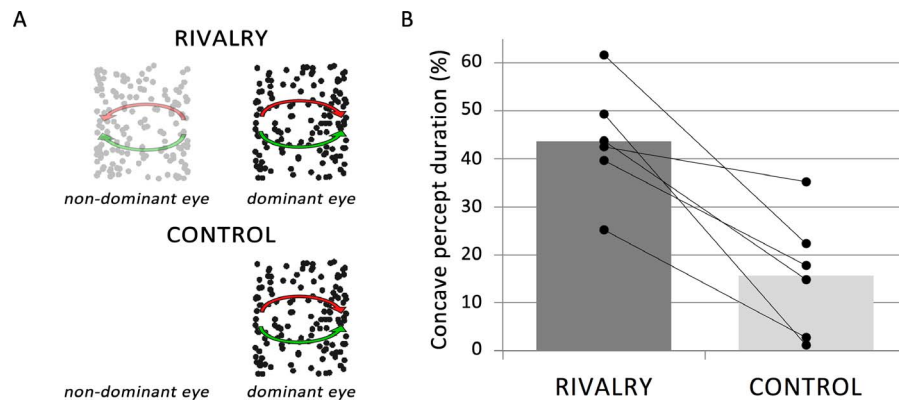


Figure 4. Results of Experiment 2. (A) In the Rivalry condition, both the rightward moving half and the leftward moving half can either be represented as convex (as indicated in green) or as concave (as indicated in red). If both halves are visually integrated into one coherent object, only one half can be represented as convex, while the other half is represented as concave. In the Control condition, only half of the stimulus is presented, which is represented as either convex or concave. Since in this condition no dots are presented to the nondominant eye, there will be no competition for convexity here. (B) Dominance duration of concave percepts, as a percentage of the summed dominance duration of convex and concave percepts, per condition, calculated for the Rivalry and Control condition, separately. Connected dots represent data points of individual observers.

Results and discussion

Out of a total of 26 observers that started the experiment, 20 observers reported seeing (parts of) the stimulus presented to their nondominant eye at any point during the experiment, or during verbal debriefing. Considering the importance of continuous suppression of the observers' nondominant eye for our research question, we opted to use a strict, conservative inclusion criterion and to exclude all observers from the analysis who did not experience exclusive perceptual dominance of the stimulus presented to their dominant eye throughout the experiment. For the remaining six observers, the ratio of concave dominance was calculated as the total concave dominance time per condition divided by the total response duration of both percepts per condition (see Figure 4).

A paired samples t test revealed that the ratio of concave percept dominance durations was significantly higher for the Rivalry condition than for the Control condition ($t_5 = 4.77$, $p < 0.01$), indicating that the presence of the suppressed half of the rotating cylinder influenced the perception of the dominant stimuli in such a way that the number of concave perceptions increased. An additional analysis was performed in which all observers were included for which at least in one Rivalry trial the image presented to the nondominant eye did not break through into perception (12 out of 26). For all these observers, only those Rivalry trials were included for which no breakthrough of the nondominant eye image had occurred. Again a paired samples t test compared the ratio of concave percept dominance durations of the Rivalry and the Control conditions, yielding similar

results as the original analysis did ($t_{11} = 3.01$, $p < 0.05$). We argue that these findings support our hypothesis that the visible and suppressed halves are integrated into one coherent visual object representation of a rotating cylinder. Although half of the cylinder is not represented³ consciously, both halves do compete for convexity, as is the case in a conventional structure-from-motion rotating cylinder. As a result, the visible half of the cylinder is perceived as convex much less often than is the case in the Control condition. In the Control condition, competition for convexity does not occur, causing the general convexity bias to maintain a deterministic influence on perception of the visible half cylinder. We would like to stress that these data cannot fully rule out alternative explanations that to a lesser extent rely on the visual integration of seen and unseen parts of the cylinder. For instance, one could argue that the mere presentation of the unseen half could bias the perceived velocity or depth of the visible half and that these features could have affected the observers' response behavior. However, we consider such an alternative account unlikely, partially based on personal observation and also because none of the observers reported any qualitative differences between the percepts in the Rivalry and in the Condition during debriefing.

General discussion

We have reported two experiments that investigate the interaction between visible and invisible stimulus parts of a structure from motion stimulus. The main

objective of these experiments was to test if both parts can be integrated into one coherent visual object representation. Taken together, the two experiments in this study provide evidence that such integration between visible and invisible stimulus parts can indeed occur when both parts are congruent with the same representation, as was the case in the manipulations applied here (Experiment 1). In addition, the presence of the suppressed half can influence the perceptual state of the visible half of the ambiguous stimulus, as its strong convexity bias is altered towards almost complete ambiguity between convexity and concavity (Experiment 2).

Previous research related to this topic has primarily focused on the interaction between visible and invisible stimuli as a function of their low-level feature similarity (Alais & Blake, 1999; Stuit, Paffen, van der Smagt, & Verstraten, 2011; van Lier & de Weert, 2003; Vergeer & van Lier, 2010). For instance, the presence of a visible stimulus speeds up the perceptual appearance of perceptually suppressed stimuli with the same color (van Lier & de Weert, 2003) and orientation (Vergeer & van Lier, 2010), whereas the presence of a perceptually suppressed stimulus delays the perceptual appearance of perceptually suppressed stimuli with the same color and orientation (Vergeer & van Lier, 2010). In addition, it has been shown that the visibility of a probe differs as a function of its feature similarity with a suppressed stimulus, in terms of orientation of motion direction (Stuit et al., 2011). Studies that focused more directly on global stimulus integration have predominantly shown that stronger Gestalts give larger dominance durations than less strong Gestalts (de Weert, Snoeren, & Koning, 2005; Suzuki & Grabowecky, 2002), rather than looking at global integration between visible and invisible stimuli. To our knowledge, the current study is the first to demonstrate global, holistic visual integration between visible and invisible stimulus parts. In addition, our results show that the perceptual properties of the visible stimulus parts can be altered significantly by the presence of invisible stimulus parts.

One could argue that the findings reported here are somewhat inconsistent with the literature on perceptual organization and continuous flash suppression/binocular rivalry, in which there seems to be no convincing evidence for more complex, Gestalt-like organization under perceptual suppression. Indeed, these latter findings are consistent with predictions derived from currently dominant theories and models on how binocular rivalry is resolved. To a large extent, these rely on reciprocal inhibitory networks operating at early visual processing stages (Blake, 1989; Noest, van Ee, Nijs, & van Wezel, 2007; Tong, Meng, & Blake, 2006; Wilson, 2003), occurring

presumably before more complex object integration is completed. However, previous studies on perceptual integration for invisible stimuli often explicitly focused on how the invisible stimulus is represented during perceptual suppression. Nearly always, this involved presenting a suppressor that was irrelevant to the perceptually suppressed stimulus. In contrast, the stimulus paradigm applied here involves a visible stimulus that is directly relevant to the suppressed stimulus. In other words, here, access to the invisible input is not required for completing the formation of the global representation (i.e., of a rotating cylinder), as also without the presentation of the invisible stimulus half, one already has the impression of a rotating cylinder. Thus, it may be the case that holistic object representations cannot be established “from scratch” (i.e., purely bottom-up driven) under binocular suppression, but, speculatively, once a global representation has been established, recurrent connectivity may influence the processing of its components at lower processing stages, and also for components that are not consciously represented. This idea is in line with the current dominant theories on binocular rivalry and also with accumulating evidence suggesting that bottom-up sensory processing and top-down influences can interact in determining the perceptual outcome of bistable stimulation (e.g., de Jong, Brascamp, Kemner, van Ee, & Verstraten, 2014; Klink et al., 2008; Lupyan & Ward, 2013). Hence, although the bottom-up processing of suppressed visual stimuli may not be strong enough to establish a global, holistic representation in itself, this suppressed information may still be represented in a way congruent with the currently visible representation (as indicated by the results of Experiment 1) and, in addition, alter its perceptual appearance (as indicated by the results of Experiment 2).

By combining an ambiguous structure-from-motion stimulus with a binocular rivalry paradigm, the two experiments reported here show that perceptually suppressed visual information can still be represented by the visual system in a way congruent with an already established visible holistic representation. Moreover, the representation of perceptually suppressed stimulus parts can alter the visual appearance of the already established representation. These findings provide evidence that unseen visual information is biased towards a representation that is congruent with the current visible representation and, hence, that principles of perceptual organization also apply to parts of the visual input that remain unseen by the observer.

Keywords: perceptual organization, visual awareness, bistability, structure-from-motion, binocular rivalry

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Footnotes

¹ PsychoPy scripts of both experiments are available upon request.

² Raw data of both experiments are available unconditionally upon request.

³ As the image presented to the nondominant eye is continuously suppressed perceptually, we avoid using the word “perceived” when referring to the stimulus presented to the eye that is currently suppressed. Throughout the manuscript, we use the term “representation” instead to indicate that, although this stimulus half is not perceived consciously, it may still be represented by the visual system internally in either a convex or concave state.

References

- Alais, D., & Blake, R. (1999). Grouping visual features during binocular rivalry. *Vision Research*, 39(26), 4341–4353.
- Alais, D., & Blake, R. (2005). *Binocular rivalry*. Cambridge, MA: MIT Press.
- Bertamini, M., & Wagemans, J. (2013). Processing convexity and concavity along a 2D contour: Figure-ground, structural shape, and attention. *Psychonomic Bulletin & Review*, 20(2), 191–207.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167.
- Brouwer, G. J., & van Ee, R. (2006). Endogenous influences on perceptual bistability depend on exogenous stimulus characteristics. *Vision Research*, 46(20), 3393–3402, doi.org/10.1016/j.visres.2006.03.016.
- Brouwer, G. J., & van Ee, R. (2007). Visual cortex allows prediction of perceptual states during ambiguous structure-from-motion. *The Journal of Neuroscience*, 27(5), 1015–1023, doi.org/10.1523/JNEUROSCI.4593-06.2007.
- de Jong, M. C., Brascamp, J. W., Kemner, C., van Ee, R., & Verstraten, F. A. J. (2014). Implicit perceptual memory modulates early visual processing of ambiguous images. *The Journal of Neuroscience*, 34(30), 9970–9981, doi.org/10.1523/JNEUROSCI.2413-13.2014.
- de Weert, C. M. M., Snoeren, P. R., & Koning, A. (2005). Interactions between binocular rivalry and Gestalt formation. *Vision Research*, 45(19), 2571–2579, doi.org/10.1016/j.visres.2005.04.005.
- Gayet, S., Van Der Stigchel, S., & Paffen, C. (2014). Breaking continuous flash suppression: Competing for consciousness on the pre-semantic battlefield. *Frontiers in Psychology*, 5, 460, doi.org/10.3389/fpsyg.2014.00460.
- Harris, J. J., Schwarzkopf, D. S., Song, C., Bahrami, B., & Rees, G. (2011). Contextual illusions reveal the limit of unconscious visual processing. *Psychological Science*, 22(3), 399–405, doi.org/10.1177/0956797611399293.
- Hayashi, D., & Murakami, I. (2015). Facilitation of contrast detection by flankers without perceived orientation. *Journal of Vision*, 15(15):15, 1–16, doi:10.1167/15.15.15. [PubMed] [Article]
- Khuu, S. K., Gordon, J., Balcomb, K., & Kim, J. (2014). The perception of three-dimensional cast-shadow structure is dependent on visual awareness. *Journal of Vision*, 14(3):25, 1–16, doi:10.1167/14.3.25. [PubMed] [Article]
- Klink, P. C., van Ee, R., Nijs, M. M., Brouwer, G. J., Noest, A. J., & Van Wezel, R. J. A. (2008). Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision. *Journal of Vision*, 8(5):16, 1–18, doi:10.1167/8.5.16. [PubMed] [Article]
- Knapen, T., Brascamp, J., Pearson, J., van Ee, R., & Blake, R. (2011). The role of frontal and parietal brain areas in bistable perception. *The Journal of Neuroscience*, 31(28), 10293–10301, doi.org/10.1523/JNEUROSCI.1727-11.2011.
- Lamme, V. (2014). *The crack of dawn: Perceptual functions and neural mechanisms that mark the transition from unconscious processing to conscious vision*. Open MIND. Frankfurt am Main, Germany: MIND Group. Retrieved from <http://open-mind.net/papers/the-crack-of-dawn-perceptual-functions-and-neural-mechanisms-that-mark-the->

transition-from-unconscious-processing-to-conscious-vision/getAbstract

- Lupyan, G., & Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proceedings of the National Academy of Sciences, USA*, 110(35), 14196–14201, doi.org/10.1073/pnas.1303312110.
- Masuda, A., Watanabe, J., Terao, M., Watanabe, M., Yagi, A., & Maruya, K. (2011). Awareness of central luminance edge is crucial for the Craik-O'Brien-Cornsweet effect. *Frontiers in Human Neuroscience*, 5(125), 128–135, doi.org/10.3389/fnhum.2011.00125.
- Moors, P., Wagemans, J., van Ee, R., & de-Wit, L. (2015). No evidence for surface organization in Kanizsa configurations during continuous flash suppression. *Attention, Perception & Psychophysics*, 78(3), 902–914, doi.org/10.3758/s13414-015-1043-x.
- Noest, A. J., van Ee, R., Nijs, M. M., & van Wezel, R. J. A. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision*, 7(8):10, 1–14, doi:10.1167/7.8.10. [PubMed] [Article]
- Palmer, S. E., & Rock, I. (1994). Rethinking perceptual organization: The role of uniform connectedness. *Psychonomic Bulletin & Review*, 1(1), 29–55, doi.org/10.3758/BF03200760.
- Peirce, J. W. (2007). PsychoPy—Psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1–2), 8–13, doi.org/10.1016/j.jneumeth.2006.11.017.
- Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2, 10, doi.org/10.3389/neuro.11.010.2008.
- Sobel, K. V., & Blake, R. (2003). Subjective contours and binocular rivalry suppression. *Vision Research*, 43(14), 1533–1540.
- Stuit, S. M., Paffen, C. L. E., van der Smagt, M. J., & Verstraten, F. A. J. (2011). Suppressed images selectively affect the dominant percept during binocular rivalry. *Journal of Vision*, 11(10):7, 1–11, doi:10.1167/11.10.7. [PubMed] [Article]
- Suzuki, S., & Grabowecky, M. (2002). Evidence for perceptual “trapping” and adaptation in multi-stable binocular rivalry. *Neuron*, 36(1), 143–157.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, 10(11), 502–511, doi.org/10.1016/j.tics.2006.09.003.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096–1101, doi.org/10.1038/nn1500.
- van Lier, R., & de Weert, C. M. M. (2003). Intra- and interocular colour-specific activation during dichoptic suppression. *Vision Research*, 43(10), 1111–1116, doi.org/10.1016/S0042-6989(03)00075-0.
- Vergeer, M., & van Lier, R. (2010). Feature-based activation and suppression during binocular rivalry. *Vision Research*, 50(8), 743–749, doi.org/10.1016/j.visres.2010.01.011.
- Wagemans, J. (2015). *The Oxford Handbook of Perceptual Organization*. New York: Oxford University Press.
- Wang, L., Weng, X., & He, S. (2012). Perceptual grouping without awareness: Superiority of Kanizsa triangle in breaking interocular suppression. *PLoS ONE*, 7(6), e40106, doi.org/10.1371/journal.pone.0040106.
- Wheatstone, C. (1838). Contributions to the physiology of vision. Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 128(0), 371–394, doi.org/10.1098/rstl.1838.0019.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences, USA*, 100(24), 14499–14503, doi.org/10.1073/pnas.2333622100.
- 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, doi.org/10.3389/fpsyg.2014.00724.