Illusory displacement due to object substitution near the consciousness threshold

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A briefly presented target shape can be made invisible by the subsequent presentation of a mask that replaces the target. While varying the target–mask interval in order to investigate perception near the consciousness threshold, we discovered a novel visual illusion. At some intervals, the target is clearly visible, but its location is misperceived. By manipulating the mask's size and target's position, we demonstrate that the perceived target location is always displaced to the boundary of a virtual surface defined by the mask contours. Thus, mutual exclusion of surfaces appears as a cause of masking.

Keywords: visual illusion, masking, feature inheritance, top-down, surface, gestalt, binding, illusory conjunction, object substitution

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Introduction

Since Helmholtz (1867), many theories of visual perception argue that the construction of the subjective visual percept is not a passive bottom-up process, but rather involves making the best sense of sensory inputs based on a set of hypotheses or constraints derived from prior knowledge and contextual (temporal and spatial) influences (Coppola, Purves, McCoy, & Purves, 1998; Gilbert & Sigman, 2007). Under some circumstances, this process may create a conflict resulting in an illusory or erroneous reconstruction of the visual scene (Howe & Purves, 2005). When two stimuli are presented in short temporal succession, two classes of illusions have been described: *masking* and *feature inheritance*. In masking, one stimulus (the target) is rendered invisible by the presence of another stimulus (the mask) (Bachmann, 1994; Breitmeyer, 1984; Di Lollo, Enns, & Rensink, 2000). For certain masking situations, which cannot be easily explained by low-level competition, it has been proposed (Di Lollo et al., 2000) that masking may be understood in terms of a dynamic competition between bottom-up and re-entrant top-down flows of visual information processing: invisibility would be created when strong bottom-up inputs from the mask override reverberant activity that has been induced by a brief target. Under other circumstances, features of the two different stimuli may be combined or inherited, by the other stimulus, a phenomenon referred as *feature inheritance* or *illusory conjunctions* (Ashby, Prinzmetal, Ivry, & Maddox, 1996; Enns, 2002; Hazeltine, Prinzmetal, & Elliott, 1997; Herzog, Fahle, & Koch, 2001; Herzog & Koch, 2001; Herzog, Koch, & Fahle, 2001; Nisbett & Wilson, 1977; Prinzmetal, 1981; Prinzmetal, Presti, & Posner, 1986; Treisman & Schmidt, 1982; Wolford & Shum, 1980). Masking and feature inheritance may be combined (i.e., the masking element may inherit features

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of the masked object), and a variety of geometric, spatial, and temporal factors may result in shifts between them (Enns, 2002; Herzog & Koch, 2001).

Here we describe a novel visual illusion that shows how our visual system can be correctly informed about target *presence,* yet be misled about its actual *location* by constraints arising from the visual surfaces defined by the mask. It has been postulated that location misattribution may be a source of illusory conjunction (Ashby et al., 1996), and "location illusions" have been measured explicitly (Hazeltine et al., 1997; Maddox, Prinzmetal, Ivry, & Ashby, 1994; Watanabe, Nijhawan, & Shimojo, 2002; Wolford & Shum, 1980). For example, in a briefly presented display of a set of squares, a tick mark in one square may be perceived in adjacent squares (Wolford & Shum, 1980).

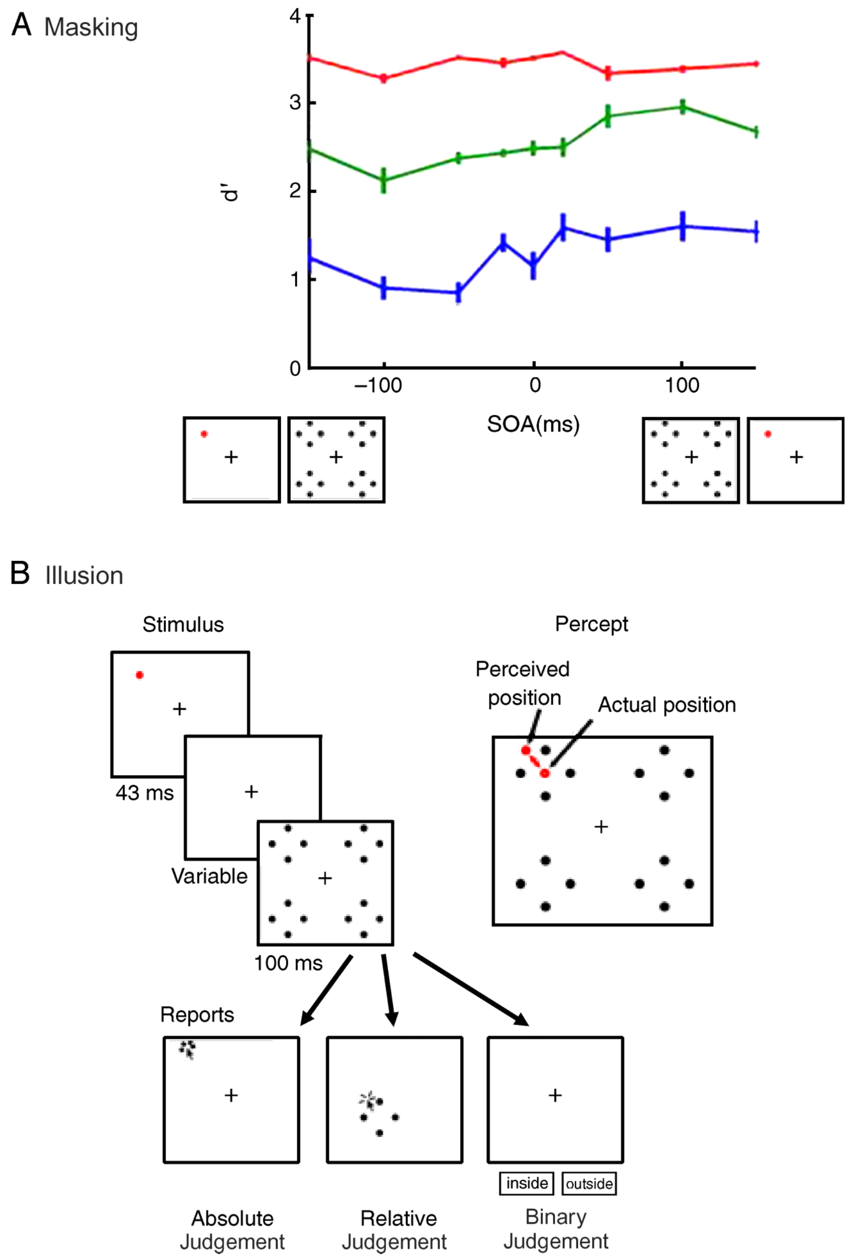

Figure 1. (A) Target visibility can be controlled by target duration (11.76—blue trace, 23.53—green trace, and 35.29 ms—red trace) and stimulus onset asynchrony (SOA) between the target and the mask. Negative SOA values indicate that the target is followed by the mask, which results in significantly more masking than the reverse order. For target durations larger than 35 ms, the target is almost perfectly visible. (B) Description of the displacement illusion and its quantification. Left panel, stimulus sequence resulting in the illusion. Right panel, perceived illusion: Even when the target is presented at the centre of the rhomboid, observers perceive it as appearing outside,

In our experiments, a brief visual target is presented at a short delay before or after a surrounding texture, which we refer to as the mask. The texture is composed of four arrays, one in each visual quadrant, each comprising four stimuli at the vertex of an implicit rhomboid (Figure 1). The target is presented at a spatial location corresponding to the centre of one randomly chosen rhomboid. When the target is presented briefly (less than 20 ms) and the time between the onsets of the target and the mask is short, the target is not seen (Figure 1A). This is consistent with the mechanism of object substitution, which apply to various forms of masking where the target and the mask are nor temporally nor spatially overlapping (Di Lollo et al., 2000) and in which the distribution of attention over the display is crucial to the occurrence of masking. However, when we manipulated target duration and target–mask interval, we discovered that the target was perceived, yet at a subjective location strikingly different from the objective one (the rhomboid centre). Moreover, introspectively, it looked as if the target would be perceived in the border of the implicit surface defined by the mask, suggesting that the mask defines a zone of exclusion, where the target cannot be seen. Several experiments were then conducted to test this hypothesis and understand this effect.

Results

We first performed a control experiment to asses under which parameter conditions the target was either masked or clearly visible. In this experiment, we manipulated the stimulus durations (11.76—blue trace, 23.53—green tarce, and 35.29 ms—red trace) and the stimulus onset asynchrony (SOA) between the target and the mask (Figure 1A). Positive SOA values indicate that the mask precedes the target. We observed that for short stimulus durations the target could be severely masked. At a duration of 35.29 ms the target was highly visible $p(\text{seen}) = 0.97 \pm 0.01$ and target visibility dropped by almost three fold for shorter target durations. For instance, at a target duration of 11.76 ms, $p(\text{seen}) = 0.29 \pm 0.06$. Although false positives were bellow 10% for all subjects and conditions, for statistical purposes, we estimated the sensitivity index d', calculated as conventionally, converting the p-values to z-scores and then estimating $Z(\text{FA}) - Z(\text{Hits})$. The difference in d' for different target durations was highly significant as revealed by a paired t-test ($t = 9.2$, $df = 6$, $p < 0.001$: mean(d') for duration of $35.29 = 3.30 \pm 0.04$, mean(d') for duration of $11.76 = 1.26 \pm 0.12$). For short target durations, there was a significant effect of SOA; visibility was reduced when the mask followed the target. For instance, for the shortest target duration (11.76), d' was 1.03 ± 0.12 for negative SOA values and increased to 1.47 ± 0.12 for positive SOA values. This difference was significant ($t = 3.1$, $df = 6$, $p < 0.01$).

This experiment determined that the target is visible for all SOA values for target durations longer than 35 ms. Thus, for the next experiments—aimed to measure and understand the displacement illusion—we used a target duration of 43 ms, for which the target is clearly visible. We first asked subjects to report whether the target was observed inside or outside one of the rhomboids (binary judgment), as a function of interstimulus interval (ISI) (Figure 1B). Note that in this experiment, we used ISI instead of SOA since we wanted to study experimental displays in which the mask and the target did not overlap in time. The quadrant in which the target was presented was varied randomly. Although the target was always presented at the centre of a rhomboid, for negative ISIs (target presented before the mask) all subjects experienced a powerful illusion of seeing it outside the borders of the rhomboid. When the effect of the illusion (fraction of trials in which subjects reports "outside" when the target was presented in the centre of the rhomboid) was averaged across both negative ISI values, more than 80% of the trails ($81.2 \pm 3.8\%$) corresponded to illusions. The illusion was present in a very small proportion of the trials ($17.3 \pm 4.5\%$) with positive values of ISI (target presented after the mask), which is consistent with the fact that forward masking is much weaker than backward masking, as revealed in our previous experiments (Figure 1A) and as has been reported previously (Breitmeyer, 1984). This effect is highly significant as revealed by a t-test comparing the fraction seen outside for negative ISI vs. fraction seen outside for positive ISI ($t = 13.47$ $df = 9$, $p < 0.001$). We did not see a significant effect of ISI on the fraction of illusory trials for negative ISI (ISI $= -57$, illusion effect $85.1 \pm 3.5\%$ and ISI $= -28$, illusion effect $= 77.1 \pm 4.7\%$). A paired t-test comparing these two conditions was not significant ($t = 2.1$ $df = 9$, $p > 0.05$).

Judging whether the target falls inside or outside of the mask collapses a continuous percept in two categories, thus loosing very valuable information on the precise distribution of perceived positions. To provide a more detailed description, subjects were asked to place a cursor at the position where they had seen the target, by moving the computer mouse on a blank screen following the target and mask (absolute judgment). This measure yielded two clearly distinct distributions of responses: For positive ISIs—red (ISI = 57) and magenta (ISI = 28) traces—subjective responses were scattered around the centre of the rhomboid (objective location in which the target was presented). Note that the distributions in Figure 2A correspond to distances and thus are defined positive: the shift from zero thus reflects the dispersion of this measure. For negative ISI—blue (ISI $= -57$) and cyan (ISI $= -28$) traces—the distribution was shifted away from the centre of fixation. Responses were scattered close to the border of the rhomboid (Figure 2A, the vertical black line indicates the distance to the nearest edge), suggesting that the surface implicitly defined by the rhomboid establishes a zone of exclusion where the target cannot be seen.

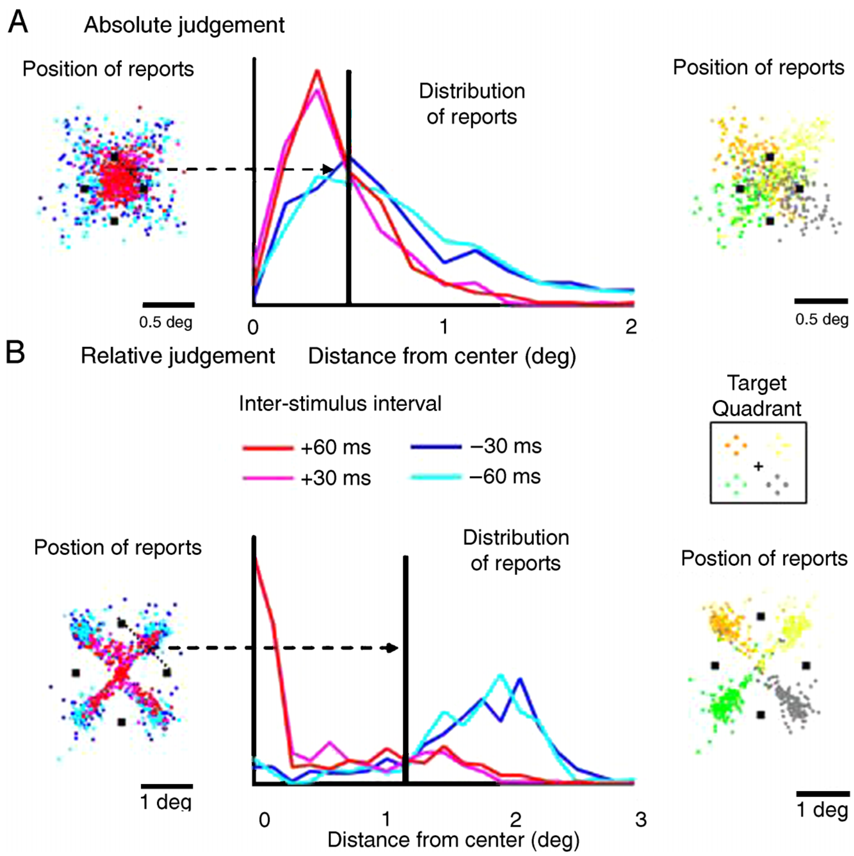

Figure 2. Distribution and positions of the reports of perceived position for absolute judgment (top panels) and relative judgment (bottom panels), in an experiment where target–mask interstimulus interval (ISI) was varied. Negative ISIs (target before mask)—blue (ISI = −57) and cyan (ISI = −28) traces—result in reports scattered outside the implicit surface defined by the rhomboid. Positive ISIs (mask before target)—red (ISI = 57) and magenta (ISI = 28) traces—result in reports typically confined to the centre of the rhomboid (no illusion). Note that the distributions in Figure 2A correspond to distances and thus are defined positive. Although both report types give similar results, position information (left column) is more precise for relative than for absolute location judgments. The distribution of reports (central column) shows that percepts lie almost entirely outside of the implicit surface (the border is indicated by the black line superposed in the distribution). A quadrant by quadrant analysis (right column) (color code: yellow—top right, grey—bottom right, green—bottom left, orange—top right) indicates that responses are typically displaced towards the periphery.

To provide a more reliable measure, in a different setup (relative judgment), we asked subjects to use the computer mouse to report the position where they had seen the object relative to a single rhomboid (similar to the rhomboids of the mask), which appeared at a random position on the screen. For positive ISIs, where no illusion is seen—red (ISI = 57) and magenta (ISI = 28) traces—we observed an extremely sharp spike of responding at the objective location of the target, thus establishing the reliability of this measurement. For negative ISIs—blue (ISI = −57) and cyan (ISI = −28) traces—very few responses fell within the implicit rhomboid surface. The vast majority were scattered around its boundary, mostly extending out of it in the radial direction. The distribution of responses starts ramping at the border of the surface (Figure 2B), further suggesting that the effect is not merely a shift in the perceived position but rather an exclusion produced by the surface defined by the mask.

To directly test this exclusion hypothesis, we reasoned that if the perceived illusion is determined by the border of the surface then: (1) The illusion should scale with the rhomboid size; and moreover, (2) the perceived position should be insensitive to the actual position of the target within the implicit rhomboid. In a subsequent experiment, we thus varied the size of the four rhomboids, while presenting targets at a fixed location at rhomboid centre (Figure 3A). In another, we presented the target at three eccentricities within fixed-size rhomboids (Figure 3B). As predicted, the results showed that the critical feature to determine the perceived position of the mask is the position of the rhomboids' external border. In the first experiment, as the mask size varied, the distributions of perceived targets positions were shifted towards the periphery by an amount equal to the displacement of the rhomboid's border (see Figure 3A and Supplementary Figure 2A). An ANOVA revealed a significant effect of

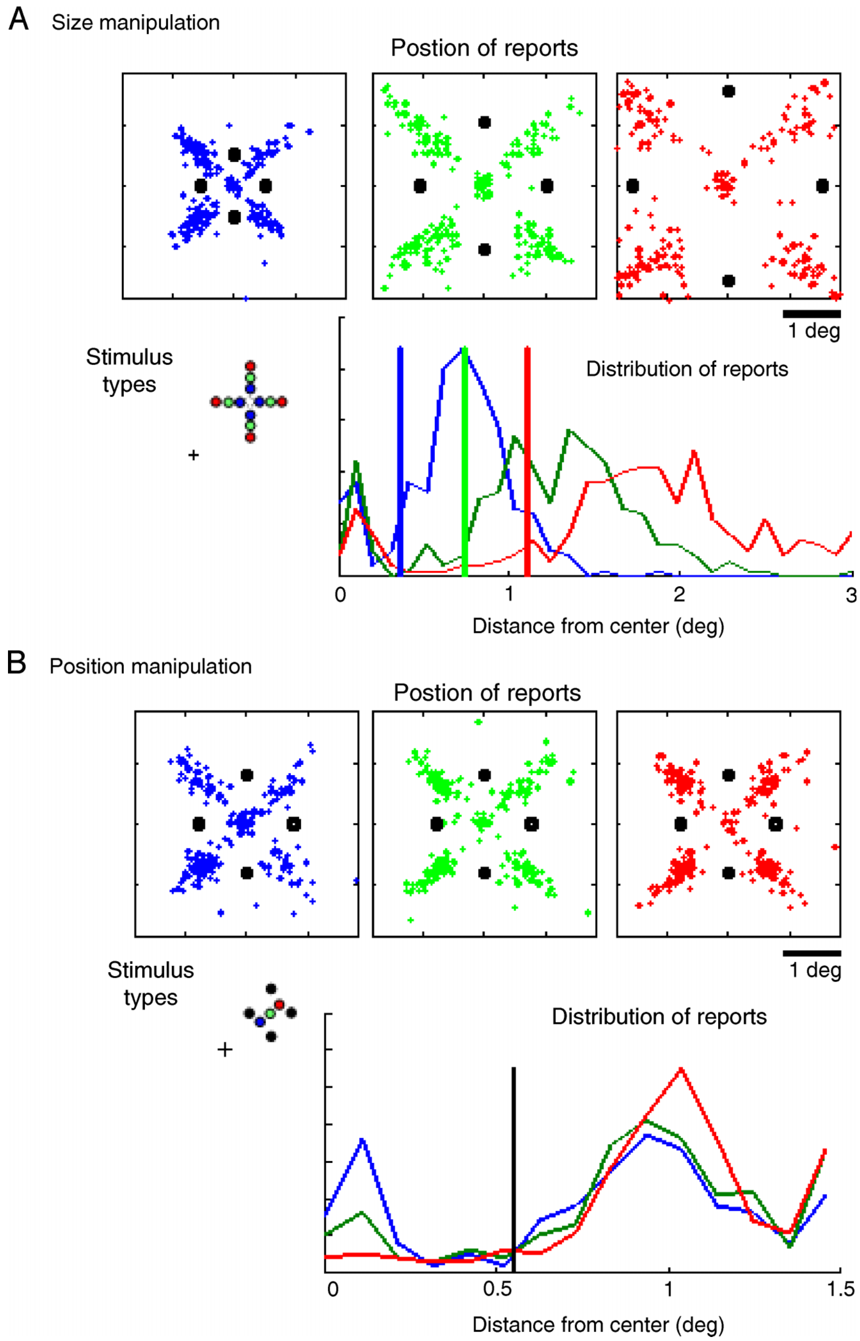

Figure 3. Manipulations of the rhomboid size and of the position of the target within the rhomboid indicate that the illusion does not result from a fixed spatial shift but rather that the target is seen systematically in the boundary of the implicit surface. (A) When manipulating rhomboid size, the amount of illusory displacement increased, following tightly the displacement of the boundary as seen in the position and distribution of reports. The different sizes correspond to 0.52 (blue), 1.04 (green), and 1.56 (red) in visual angle. (B) Manipulating the objective position of the target relative to rhomboid centre did not result in a shift of the distribution of perceived locations. Target positions were 0.3 degrees closer to the fovea in the radial direction from the centre of the rhomboid (blue), at the centre of the rhomboid (green), or at 0.3 degrees away from the fovea (red) as indicated in the stimulus types. While the position of the maximum of the distribution was unaffected, the number of trials in which subjects saw the illusion was affected by the position of the target within the rhomboid (for a more quantitative analysis, see Supplementary Figure 2).

rhomboid size on the modal distance at which the illusory percept was reported ($p < 0.01$, $F(2,9) = 46$)—contrary to what was to be expected if the illusion was due to a fixed spatial shift. In the second experiment, when the objective eccentricity of the target was varied, most subjective responses still lied just outside of the rhomboid surface (see Figure 3B and Supplementary Figure 2B), and an ANOVA indicated that the modal illusory displacement was not significantly affected by the objective target location (p = 0.69, $F(2,9)$ = 0.37). Interestingly, we did observe that the *proportion* of displaced targets varied with objective target location, reflecting an *all or none* character of the illusion (see Supplementary Figure 2B; ANOVA measuring the proportion of reports within the implicit rhomboid surface, $p < 0.05$, $F = 3.96$, $df = 1$). In other words, the real location of the target affects the probability of generating an illusion, but if there is an illusion, the magnitude of the displacement is insensitive to the actual stimulus position.

To further address whether the spatial overlapping between the stimulus and the surface defined by the mask constitutes the critical aspect of the illusion, we examined its robustness to different feature (form, color) modifications (see Figure 1). The illusion was not affected by any the modifications we explored. We observed a very strong illusion regardless of whether the stimulus and mask where of the same or different color, whether they were made of symbolic or non-symbolic elements, or whether rhomboid size changed.

Finally, since saccades or saccade preparations have also been shown to yield illusory distortions of spatial and temporal maps (Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 2005; Ross, Morrone, Goldberg, & Burr, 2001), it seemed possible that our observed illusion may result from a differential saccade. Even though our observation that the spatial shift in the perceived position was directed to the border of the implicit surface made this hypothesis unlikely, we performed two experiments to understand whether the illusion was related to saccade preparation or execution. First, to avoid a specific quadrant bias which may induce a saccade in that direction, we presented the target in two diametrically opposed locations, and subjects were asked *a posteriori* to report the position of only one of them. While significantly weaker, the illusion was still very strong in this situation (illusion effect = 74.4%, $p < 0.001$, $n = 8$). Indeed subjects reported that they saw both targets outside of their respective rhomboids. In another control experiment, we explicitly ruled out the possibility that saccades could be involved by measuring eye movements during stimulus presentation. We found the illusion in complete absence of saccades (ISI = −57 ms, illusion effect = 71%, $p < 0.013$, $df = 2$, $n = 3$, CI = [30.4, 113.3]), and moreover, we did not see any bias for saccades towards the quadrant in which the target was presented (see Supplementary Figure 3).

Discussion

Our observations reveal that changing the strength of bottom-up information (the duration of the target and ISI) may result in a shift from a masking to a surface exclusion illusion. A unitary feature of both phenomena seems to be the fact that the visual system does not integrate the two stimuli, but on the contrary places them in competition (Di Lollo et al., 2000). Previous experiments and theoretical models have also postulated a recursive interaction between top-down mechanisms and bottom-up information and which results, under conflictive circumstances, either in masking or in illusory conjunctions in which features of a stimulus are inherited by another stimulus (Ashby et al., 1996; Enns, 2002; Gilbert & Sigman, 2007; Hazeltine et al., 1997; Herzog, Fahle, et al., 2001; Herzog & Koch, 2001; Herzog, Koch, et al., 2001; Nisbett & Wilson, 1977; Prinzmetal, 1981, 1995; Prinzmetal et al., 1986; Treisman & Schmidt, 1982; Wolford & Shum, 1980). There is however an important difference; in all these prior experiments, illusory conjunctions result from merging properties from two presented stimulus. For example, in Wolford and Shum (1980), the location of the mark is inherited by adjacent squares in the lattice. Similarly, in (Prinzmetal, 1981) the presentation of an array circle containing a vertical and a horizontal segment in distinct circles is often seen as a plus sign suggesting that one of the segments inherits the location of the other, where the plus sign is perceived. In our experiment, the perceived position of the target is in strict relation with the implicit surface defined by the mask. Beyond the implicit character of the masking element—not so surprising since implicit surfaces have been often shown to behave as real surfaces (Shimojo, Kamitani, & Nishida, 2001)—the most striking difference is that the mask *does not* define a location that the target can inherit but rather a precluded region where it cannot be seen. This can be understood in terms of feature integration mechanism according to which it is not likely to bridge conjunctions between different perceptual groups in consistency with the laws of perceptual organization as described by Gestalt psychologists (Gilbert, Sigman, & Crist, 2001; Hazeltine et al., 1997; Prinzmetal, 1995; Sigman & Gilbert, 2000; Sigman, Cecchi, Gilbert, & Magnasco, 2001; Sigman et al., 2005; Wertheimer, 1938).

Thus, the finding that the exclusion area is precisely marked by the borders of the implicit surface defined by the mask, argues that the simultaneous percept is not possible because it is not consistent with an adequate surface reconstruction of the scene (Bakin, Nakayama, & Gilbert, 2000; Gilbert et al., 2001; Nakayama & Shimojo, 1990, 1992), which also argues in favor of an implicit filling in of the surface defined by the mask (Shimojo et al., 2001). Early accounts of masking appealed to on-line interactions and lateral inhibition between the target and the mask (Bridgeman, 1971; Ganz, 1975). However, these models would not explain our surface exclusion illusion. More recent models (Bachmann, 1994; Di Lollo et al., 2000) postulate a dynamic reconstruction of the target–mask sequence whereby the perceptual hypotheses about the target are revised after the presentation of the mask. This revision process may lead to what has been referred in the literature as *object substitution,* i.e., visual replacement of the target by the mask. This theory may be extended to explain the present illusion. At the shortest target durations and ISI, the occurrence of the mask interrupts recurrent feed-back loops so strongly that it prevents all target features from accessing consciousness (masking). At slightly longer values of these parameters, however, the temporal and spatial features of the target may be processed independently of its identification (Mewhort, Huntley, & Duff-Fraser, 1993). Thus, the identification of the stimulus becomes possible, while its spatial localization is still submitted to competition by the mask. If the mask outlines a well-defined surface, as was the case here, a *surface exclusion* illusion occurs whereby target location is erroneously displaced.

An intriguing question is why, for the most part, the target appears displaced to the periphery of the visual field and not in other possible directions. A possible explanation arises from the fact that in a crowded field visibility decreases with eccentricity (Toet & Levi, 1992; Tripathy & Cavanagh, 2002) and with the radial arrangement of items in the scene (He, Cavanagh, & Intriligator, 1996). The external border of the rhomboids thus corresponds to the portion of the visual field where actual information is least accurate. It appears as if the visual system, acting according to Bayesian principles, attributes seeing the target to the location where there is minimal sensory evidence to the contrary. In the same line of reasoning, it is also possible, that the four rhomboids define a second order surface of exclusion, covering the central portion of the display.

Another possible explanation for the systematic displacement of targets to the periphery is related to the course of the deployment of spatial attention during this task. First, it has been shown that a briefly presented probe is perceived as displaced away from the focus of attention (Suzuki & Cavanagh, 1997). In our setup, this would requires a more complicated interpretation since it is the same stimulus (the target), which attracts attention and also the displaced probe. The attentional repulsion interpretation is possibly related to the eye movements distortion of perceived space maps, as discussed previously (Lappe et al., 2000; Morrone et al., 2005; Ross et al., 2001) since, similar to what happens during covert directing of attention, spatial attention allocation leads to an activation of oculomotor circuits, in spite of eye immobility (Sheliga, Riggio, & Rizzolatti, 1994, 1995; Sheliga, Riggio, Craighero, & Rizzolatti, 1995). Thus, despite the fact that eye movements have been controlled, it is possible that the activation (and inhibition) of these circuits may result in similar phenomenon. While the distortion of visual space resulting from attention may be related to these findings, it is unlikely that this can be the determinant of our observations. The fact that varying the rhomboid size results in a comparable amount of the displacement illusion is very difficult to reconcile with a pure mechanism of contraction or dilatation of visual space due to the target orienting of attention. The two plausible explanations described here, attentional distortion and a scene reconstruction mechanism, which makes the most likely interpretation in the context of crowding may be non-independent, given the links between attention and crowding. (He et al., 1996; Jehee, Roelfsema, Deco, Murre, & Lamme, 2007; Motter, 1993).

Our work shows that imperfect masking can lead to a reconstructed percept in which the spatial attribute of the target is subjectively shifted by the appearance of the mask. This is in line with the idea that the attribution of a position to visual stimuli may be affected in a dynamic fashion by other contextual sources such as high-level motion (Maddox et al., 1994; Watanabe et al., 2002). In the temporal domain, a similar subjective shift has been reported (Didner & Sperling, 1980): during metacontrast masking, while reaction time to the target is unaffected by the mask, its perceived onset time appeared delayed. More importantly in the context of the present work, Suzuki and Cavanagh (1998) have referred to a labile stage of visual processing in which the contours of a shape can be perceived clearly, with sharply defined contours (contrary to what happens for shorter stimulus presentations in which the stimulus is either invisible or looks fuzzy), but yet, its apparent perceived shape is very labile. More specifically, it is found that in this "labile" regime, a prime has a repulsion effect, i.e., the target is perceived as more dissimilar to the prime, a phenomenon referred as shape–contrast effect. Thus, the surface exclusion illusion observed in this experiment may more generally be interpreted in terms of competitions of representations, which may result in different experimental setups, in shape, or in position misattributions of well-identified visual stimuli. All these phenomena can be understood in terms of separable processes of identification and of ascription of spatial, temporal, and object identity parameters, which are submitted to constraint satisfaction mechanisms ensuring the subjective reconstruction of the most likely scene compatible with the sensory data.

Methods

Twenty-five naive participants performed the three experiments reported in this study. Targets (unless indicated explicitly for certain control experiments) were red dots (extending 0.15° of visual angle); masks were composed of 16 random black dots of the same size, forming four rhomboids, each of them positioned precisely around one of the possible target location (Figure 1). Target eccentricity was 3.1° at 75 cm viewing distance.

Seven participants performed a *first experiment* to determine the stimulus conditions values that yielded masking (Figure 1A). To explore the masking regime, target durations and the stimulus onset asynchrony between target and masked were varied (Figure 1A). Experiments were performed using a 17-in. CRT monitor (85 Hz refresh). Target durations were of 1, 2, or 3 frames, which corresponded, respectively, to 11.76, 23.53, and 35.29 ms. SOA values were sampled in nine different values: (-150, -100, -50, -20, 0, 20, 50, 100, 150) ms. In this experiment, after each stimulus presentation subjects indicated with the mouse whether they had seen the target or not (right button click to indicate the target was present and left button click to indicate it was absent). To measure false positives, in 14.29% of the trials, the target was not presented. False positives were bellow 10% for all subjects. For statistical purposes, we estimated d' by calculating Z(false alarms) $-$ Z(hits), where Z results from the conversion of the obtained probabilities to the z-score given by the normal distribution with mean zero and SD of 1. Positive values indicate that the mask precedes the target (see Figure 1A). In this experiment, each subject performed a total of 378 trials (108 for each stimulus duration and 54 trials in which the target was absent). Once we determined that for stimulus durations greater than 30 ms, the target was visible, we conducted a second experiment to measure the displacement illusion.

Ten participants performed a *second experiment* to measure and characterize the displacement illusion (Figures 1B and 2). Stimulus display for this experiment was identical and only parameter values (duration of the stimuli) and the response modality were changed. Experiments were performed using a 17-in. CRT monitor (70 Hz refresh). Each trial began by a fixation cross at the centre of the screen (700 ms), then either the mask (129 ms) or the target (43 ms) was presented followed by the other after a variable (28 or 57 ms) interstimulus interval (ISI). Targets could appear at any of the four corners of an imaginary square centered on fixation. Target eccentricity was 3.1° at 75 cm viewing distance. Note that in this experiment, we used ISI instead of SOA since we wanted to study experimental displays in which the mask and the target did not overlap in time.

Order of stimuli (target or mask first), quadrant of target presentation, and duration of ISI were randomized within each block. Subjects made their response immediately after stimuli presentation, using the computer mouse. In this experiment, subjects performed different blocks with three different response modalities (binary, absolute, and relative judgments).

In the binary response mode, subjects had to indicate whether they had seen the target inside or outside the rhomboid. They were instructed to report "outside" in case they had seen the target lying within the imaginary line between two dots of a rhomboid, i.e., when they had seen it precisely in the border of the implicit rhomboid. Subjects responded with the mouse, clicking the right button to indicate "outside" and the left button to indicate "inside." As sketched in Figure 1, in the "absolute judgment," after stimulus presentation subjects saw a display that contained exclusively the fixation cross. They moved the mouse until the arrow of the mouse was placed in the position where they thought the target appeared. No spatial references were provided (except the fixation point) for this response modality. In the "relative judgment," subjects indicated the location in which they had seen the target relative to the rhomboid of the quadrant in which it had been seen. A rhomboid identical to the one defined by the mask (in each quadrant) was presented in a random location of the screen. Subjects responded, clicking with the mouse, the position in which they had seen the target relative to this rhomboid location. In each experiment, subjects performed two blocks corresponding to each response modality, each block contained 64 trials. Thus, in one experiment, subjects performed 384 trials. Block order was randomized across subjects.

Eight naive participants performed a third experiment (Figure 3, Supplementary Figure 1 and 2) in which different aspects of the stimuli were varied to understand the robustness and specificity of the illusion (for a display of all tested conditions, see Supplementary Figure 1). In this experiment, subjects performed a total of six different blocks in which different aspects of the stimuli were varied. Timing and spatial location of the stimuli were identical to the previous experiment.

Block one was merely a repetition of our previous experiment. In *block two,* the target consisted of a red digit (always number 5) and the mask consisted of letters which were varied randomly (Supplementary Figure 1). The letters and the digit extended 0.3° of visual angle. In *block three,* target and mask were as in experiment two (dots). In this experiment, the color of the target was black, identical to the color of the mask. In *block four,* two targets were presented simultaneously (on diametrically opposed quadrants, i.e., top-right and bottom-left or top-left and bottom-right). Since the aim of the experiments explored in blocks 1–4 was merely to see if the displacement illusion persisted under this different displays, in these blocks subjects made binary responses, indicating, in each trial, whether the target was "inside" or "outside" using the mouse, as in experiment two. In block four (two-target condition), 700 ms after the mask, an arrow in the centre of the visual screen, indicated on which target (left or right visual hemifield) the subject had to base his report ("inside" or "outside").

In *block five* (Figure 3A), target was a red dot and the mask was composed of black dots, which defined rhomboids of three different sizes which were randomly varied: 0.52, 1.04, 1.56 visual angle from target. In *block six* (Figure 3A), the target was a red dot and the mask was composed of black dots (as in experiment two). In this block, the position of the target was varied inside the rhomboid: It was either at the center or at 0.3° of visual angle of the center in the radial direction. In blocks 5–6, subjects responded in the relative judgment condition to provide a quantitative measure of their perceived stimulus spatial location. All blocks were randomly varied and each block contained 60 trials. Subjects repeated twice each block, yielding a total of 720 trials.

Finally three participants performed an experiment to control for eye movements (including one of the authors, J.S.). Stimulus display was as in experiment two, with only the ±57-ms ISI conditions. Participants performed binary responses. Eye movements were monitored by an Eyelink II (SR Research, Osgoode, Ontario, Canada) and scanned at 500 Hz. Observers were given 400 trials, half of which were mask first, the other half target first.

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References

Ashby, F. G., Prinzmetal, W., Ivry, R., & Maddox, W. T. (1996). A formal theory of feature binding in object perception. *Psychological Review, 103,* 165–192. [PubMed]

Bachmann, T. (1994). *Psychophysiology of visual masking: The fine structure of conscious experience*. Commack, NY: Nova Science.

Bakin, J. S., Nakayama, K., & Gilbert, C. D. (2000). Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *Journal of Neuroscience, 20,* 8188–8198. [PubMed] [Article]

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. New York: Oxford University Press.

Bridgeman, B. (1971). Metacontrast and lateral inhibition. *Psychological Review, 78,* 528–539. [PubMed]

Coppola, D. M., Purves, H. R., McCoy, A. N., & Purves, D. (1998). The distribution of oriented contours in the real world. *Proceedings of the National Academy of Sciences of the United States of America, 95,* 4002–4006. [PubMed] [Article]

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General, 129,* 481–507. [PubMed]

Didner, R., & Sperling, G. (1980). Perceptual delay: A consequence of metacontrast and apparent motion. *Journal of Experimental Psychology: Human Perception and Performance, 6,* 235–243. [PubMed]

Enns, J. T. (2002). Visual binding in the standing wave illusion. *Psychonomic Bulletin & Review, 9,* 489–496. [PubMed]

Ganz, L. (1975). Temporal factors in visual perception. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception* (pp. 169–231). New York: Academic Press.

Gilbert, C. D., & Sigman, M. (2007). Brain states: Top-down influences in sensory processing. *Neuron, 54,* 677–696. [PubMed]

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron, 31,* 681–697. [PubMed] [Article]

Hazeltine, R. E., Prinzmetal, W., & Elliott, W. (1997). If it's not there, where is it? Locating illusory conjunctions. *Journal of Experimental Psychology: Human Perception and Performance, 23,* 263–277. [PubMed]

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383,* 334–337. [PubMed]

Helmholtz, H. V., (1867). *Handbuch der physiologischen Optik*. Leipzig: Leopold Voss.

Herzog, M. H., Fahle, M., & Koch, C. (2001). Spatial aspects of object formation revealed by a new illusion, shine-through. *Vision Research, 41,* 2325–2335. [PubMed]

Herzog, M. H., & Koch, C. (2001). Seeing properties of an invisible object: Feature inheritance and shine-through. *Proceedings of the National Academy of Sciences of the United States of America, 98,* 4271–4275. [PubMed] [Article]

Herzog, M. H., Koch, C., & Fahle, M. (2001). Shine-through: Temporal aspects. *Vision Research, 41,* 2337–2346. [PubMed]

Howe, C., & Purves, D. (2005). *Perceiving geometry: Geometrical illusions explained in terms of natural scene statistics*. New York: Springer.

Jehee, J. F., Roelfsema, P. R., Deco, G., Murre, J. M., & Lamme, V. A. (2007). Interactions between higher and lower visual areas improve shape selectivity of higher level neurons-explaining crowding phenomena. *Brain Research, 1157,* 167–176. [PubMed]

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403,* 892–895. [PubMed]

Maddox, W. T., Prinzmetal, W., Ivry, R. B., & Ashby, F. G. (1994). A probabilistic multidimensional model of location information. *Psychological Research, 56,* 66–77. [PubMed]

Mewhort, D. J., Huntley, M. F., & Duff-Fraser, H. (1993). Masking disrupts recovery of location information. *Perception & Psychophysics, 54,* 759–762. [PubMed]

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience, 8,* 950–954. [PubMed]

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology, 70,* 909–919. [PubMed]

Nakayama, K., & Shimojo, S. (1990). Towards a neural understanding of visual surface representation. *Cold Spring Harbor Symposia on Quantitative Biology, 55,* 911–924.

Nakayama, K., & Shimojo, S. (1992). Experiencing and perceiving visual surfaces. *Science, 257,* 1357–1363. [PubMed]

Nisbett, R., & Wilson, T. (1977). Telling more than we can know: Verbal reports on mental processes. *Psychological Review, 84,* 231–259.

Prinzmetal, W. (1981). Principles of feature integration in visual perception. *Perception & Psychophysics, 30,* 330–340. [PubMed]

Prinzmetal, W. (1995). Visual feature integration in a world of objects. *Current Directions in Psychological Science, 4,* 90–94.

Prinzmetal, W., Presti, D. E., & Posner, M. I. (1986). Does attention affect visual feature integration? *Journal of Experimental Psychology: Human Perception and Performance, 12,* 361–369. [PubMed]

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences, 24,* 113–121. [PubMed]

Sheliga, B. M., Riggio, L., Craighero, L., & Rizzolatti, G. (1995). Spatial attention-determined modifications in saccade trajectories. *Neuroreport, 6,* 585–588. [PubMed]

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research, 98,* 507–522. [PubMed]

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research, 105,* 261–275. [PubMed]

Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science, 293,* 1677–1680. [PubMed]

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 of Academy of Sciences of the United States on America, 98,* 1935–1940. [PubMed] [Article]

Sigman, M., & Gilbert, C. D. (2000). Learning to find a shape. *Nature Neuroscience, 3,* 264–269. [PubMed]

Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D., & Gilbert, C. D. (2005). Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron, 46,* 823–835. [PubMed] [Article]

Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: An attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance, 23,* 443–463. [PubMed]

Suzuki, S., & Cavanagh, P. (1998). A shape–contrast effect for briefly presented stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 1315–1341. [PubMed]

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32,* 1349–1357. [PubMed]

Treisman, A., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology, 14,* 107–141. [PubMed]

Tripathy, S. P., & Cavanagh, P. (2002). The extent of crowding in peripheral vision does not scale with target size. *Vision Research, 42,* 2357–2369. [PubMed]

Watanabe, K., Nijhawan, R., & Shimojo, S. (2002). Shifts in perceived position of flashed stimuli by illusory object motion. *Vision Research, 42,* 2645–2650. [PubMed]

Wertheimer, M. (1938). *Laws of organization in perceptual forms.* London: Harcourt, Brace & Jovanovitch.

Wolford, G., & Shum, K. H. (1980). Evidence for feature perturbations. *Perception & Psychophysics, 27,* 409–420. [PubMed]