

# Asymmetric visual interactions across the boundary of awareness

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A salient visual object can disappear from conscious perception when surrounded by a moving texture, a phenomenon known as MIB, Motion-Induced Blindness (Bonneh, Cooperman, & Sagi, 2001). Here we tested the information available in the brain from such stimuli that do not access awareness by examining interactions across the boundary of awareness between stimuli that reach awareness and those that do not. Observers performed the MIB task in which a “Cue” was presented next to the “Target” after observers reported the perceptual disappearance of the target (Kawabe, Yamada, & Miura, 2007). Oriented Gabor patches were used as targets and cues; observers reported the target’s reappearance. The results indicated an interaction between the target and the cue, depending on the orientation difference ( $\sim 30^\circ$  bandwidth) and distance ( $\sim 1^\circ$  range), indicating preserved properties of features in the absence of awareness. Object-based representation (binding) of unseen stimuli was tested by examining the interaction between a compound stimulus and its composing features. Here we used vertical and horizontal Gabor patches and their combinations (plaids) as targets and cues. Results indicated asymmetric relations between aware and unaware object representations; a plaid cue was not effective with a component target, but a plaid target efficiently reappeared by its component cues. This result suggests that the unseen, but not the seen plaid, is decomposed into its features. Plaid targets also reappeared with plaid cues, supporting binding without awareness. Our findings suggest preconscious representations of objects and their features, with conscious perception confined to object representations.

## Introduction

“Perceptual disappearance” refers to a group of phenomena in which physically presented visual stimuli are perceived as invisible. This dissociation between the physical world and perceptual experience suggests that visibility is not simply governed by object properties—it can be altered by changes in the internal states of the visual system (Crick & Koch, 2003; Kim & Blake, 2005; Rees, Kreiman, & Koch, 2002).

In the phenomenon of Motion-Induced Blindness (MIB), stationary or slowly moving stimuli disappear and reappear alternately from awareness when surrounded by a high-contrast moving background (Bonneh, Cooperman, & Sagi, 2001). MIB disappearances last for up to several seconds, even with high contrast, relatively large stimuli, and when located near fixation: eccentricity of  $1^\circ$  (Bonneh et al., 2001; Bonneh, Donner, Cooperman, Heeger, & Sagi, 2014). As for Troxler (1804) fading, the mechanisms underlying MIB was suggested to involve low-level processes such as contrast adaptation (Caetta, Gorea, & Bonneh, 2007; Gorea & Caetta, 2009), and filling-in (Hsu, Yeh, & Kramer, 2006), as well as depth ordering and surface completion (Graf, Adams, & Lages, 2002). However, recent findings show additional components in MIB related to the neural competition between the static target and the moving background (Bonneh et al., 2001; Bonneh et al., 2014; Donner, Sagi, Bonneh, & Heeger, 2008).

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Perceptual phenomena such as MIB provide an insight into the visual processes underlying visual perception and the role of awareness in the formation of visual representations (Crick & Koch, 2003; Rees et al., 2002). Current evidence shows that objects rendered invisible by MIB can effectively produce orientation-selective adaptation (Montaser-Kouhsari, Moradi, Zandvakili, & Esteky, 2004), negative after-images (Hofstoetter, Koch, & Kiper, 2004), and still retain grouping relations (Bonne et al., 2001; Mitroff & Scholl, 2005). Here we attempted to specify the information available on perceptually invisible stimuli at the feature and object levels of visual processing. Using a method introduced by Kawabe et al. (2007), we examined the interaction between visible “Cue” and perceptually invisible “Target” stimuli, and determined its effect on the reappearance of the suppressed target. We suggest that the interaction between the target and the cue is governed by their internal representations. Thus, in order for the cue to be effective, some target-related information should be present in the brain to interact with the cue. The implicated representation of the unaware can help in identifying visual processes that do not correlate with stimulus awareness.

## Methods

### Observers

The experiments include 16 naïve observers (four males, 12 females; aged 23–27) with normal or corrected-to-normal vision. Observers gave their written, informed consent approved by the local Institutional Review Board of the Weizmann Institute, and were paid for their participation.

### Apparatus

The experiments were carried out using the MATLAB Psychophysics toolbox (Psychtoolbox-3; www.psychtoolbox.org; Brainard, 1997; Pelli, 1997). Stimuli were displayed on a gamma-corrected 23.6" VIEW-Pixx/3D monitor (1920 × 1080, 10 bit, 120 Hz) viewed at a distance of 100 cm in an otherwise dark room.

### Stimuli

Stimuli included a Target (100% contrast) and a Cue (50% contrast) consisting of Gabor patches ( $\sigma = 0.12^\circ$ ,  $\omega = 5.67\text{cpd}$ ) superimposed onto a rotating mask. The Target was presented in the upper left quadrant at an eccentricity of  $1.5^\circ$  to a central fixation point ( $0.31^\circ$

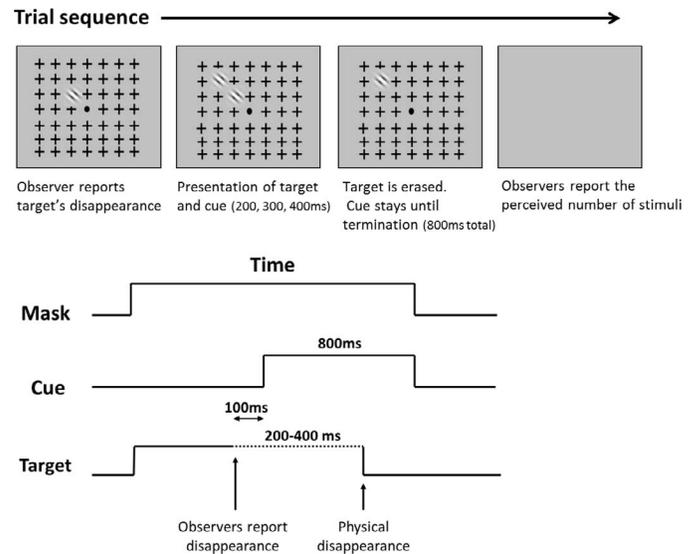


Figure 1. Experimental paradigm; a single trial. Trial began with the presentation of a Gabor target embedded onto rotating mask. The observers instructed to fixate on a central dot and press a button to report the disappearance of the target. A Gabor “Cue” is presented next to the target 100 ms after the observers reported its disappearance. The target and cue were presented concurrently for a limited interval of 200, 300, or 400 ms before the target is physically erased. The Cue is presented until the trial termination (800 ms total). Observers reported the number of Gabor patches they had perceived from the time when the disappearance was reported (i.e., zero, one, or two Gabor patches), wherein two perceived Gabor patches indicate target reappearance induced by the cue.

diameter). The cue was positioned eccentric to the target at a distance of  $4\lambda$  ( $0.7^\circ$  between stimuli’s centers) from the target’s location. The mask was composed of  $10 \times 10$  black “+” patterns ( $0.7^\circ$  width,  $1.4^\circ$  spacing). The complete mask configuration was rotating clockwise, at 2.4 s/cycle, around the central fixation point. Both the Gabor patches and the fixation points were surrounded by a background-colored “protection zone” ( $0.88^\circ$  and  $0.62^\circ$  diameter, respectively) to avoid local interactions with the mask. Stimuli were displayed over a gray background (mean luminance:  $48\text{ cd/m}^2$ ).

### Tasks and procedures

Observers performed the MIB task (Bonne et al., 2001), in which a Cue was presented next to the Target when the observers reported the perceptual disappearance of the Target (Figure 1). Each trial began with the presentation of the MIB display (i.e., target and mask; Figure 1). The observers were instructed to fixate on a central dot and press a button to report the disappearance of the Gabor target. A Gabor “Cue” was presented next to the target 100 ms after the observers

reported its disappearance. The target and cue were presented concurrently for a limited interval of 200, 300, or 400 ms before the target was smoothly erased (logistic decay of 100 ms), permitting us to estimate the time required for perceptual reappearance. The Cue was presented until the trial was terminated (800 ms total). Observers reported the number of Gabor patches they had perceived from the time when the disappearance was reported (i.e., zero, one, or two Gabor patches). Observers' reports of two Gabor patches, following suppression, were used to indicate reappearances of the target induced by the cue. Trials were initiated by the observer pressing a key, freely paced. All cues were presented with equal probability, with presentation randomized within each session (30 trials for each cue  $\times$  time window combination). As a control condition, each experiment included 15%–20% Control trials in which the cue was not presented.

## Data analyses

The percentage of target reappearances induced by the cue were calculated for each observer as  $100 \times$  number of trials in which two Gabor patches were perceived divided by the total number of trials. Repeated-measures ANOVAs were used to test the differences in the percentage of reappearances across conditions. Sphericity violations were corrected by the Greenhouse-Geisser method. Paired-samples  $t$  tests, corrected by the Bonferroni method, were used for comparing the differences between two data points.

## Results

### Features representation of a subconscious stimulus

Reappearances of the suppressed target were tested as a function of orientation similarity between the target and the cue ( $N = 7$  observers). The orientation of the Gabor target was fixed during all trials ( $-45^\circ$ ), whereas the cue was tilted  $0^\circ$ ,  $30^\circ$ ,  $45^\circ$ , or  $90^\circ$  relative to the target's orientation. Figure 2a illustrates the percentages of reappearances as a function of the cue-target orientation-difference. The percentages of reappearances markedly decreased as the target-cue orientation differences increased,  $F(4, 24) = 12.92$ ,  $p = 0.002$ . Complementary post-hoc analyses indicated that a collinear cue was most effective in bringing back the suppressed target ( $p < 0.011$ ). Interestingly, no significant difference was found between orthogonal cues and no cue conditions,  $t(6) = 1.61$ , n.s. Analysis of

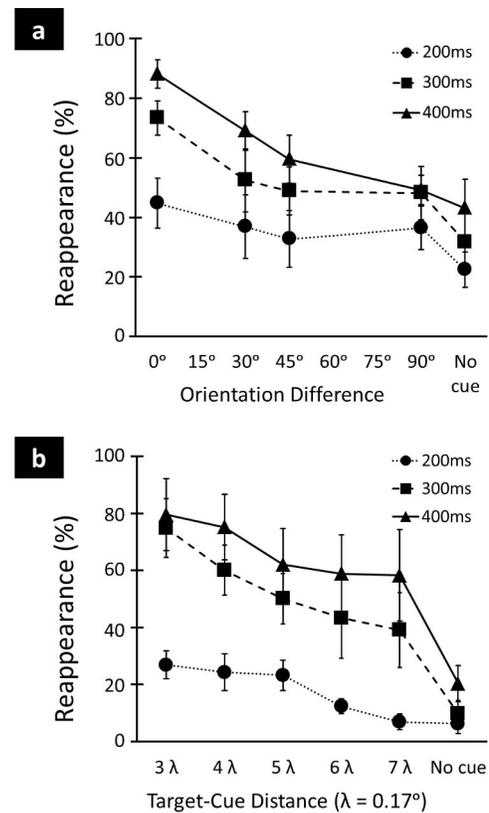


Figure 2. Dependence of the target's reappearance on the target-cue orientation difference (a), and distance (b). Data points represent means across observers (a:  $N = 7$ ; b:  $N = 6$  observers), with error bars representing the standard error of the mean.

the time window revealed increased percentages of reappearances over time,  $F(2, 12) = 32.41$ ,  $p = 0.000$ . The percentages of reappearances were higher at the 400 ms time window than at the 300 ms or 200 ms time windows,  $t(6) = 4.19$ ,  $p = 0.006$  and  $t(6) = 6.51$ ,  $p = 0.001$ , respectively.

Next, we tested whether the reappearance of the target depends on the target-to-cue distance ( $N = 6$  observers). A collinear Gabor cue was presented at distances of  $3\lambda$ ,  $4\lambda$ ,  $5\lambda$ ,  $6\lambda$ , and  $7\lambda$  relative to the target location ( $\lambda = 0.17^\circ$ ). Reappearances markedly decreased as a function of target-cue distance,  $F(5, 25) = 9.52$ ,  $p = 0.000$  (Figure 2b). Post-hoc analysis showed higher percentages of target reappearance in the presence of a proximal cue ( $3\lambda$ ) than a more distant cue ( $7\lambda$ ),  $t(5) = 3.27$ ,  $p = 0.02$ , or no cue condition,  $t(5) = 4.22$ ,  $p = 0.008$ . Trials with no cue were not significantly different from relatively distant cues,  $t(5) = 2.46$ , n.s. and  $t(5) = 2.02$ , n.s., for  $6\lambda$  and  $7\lambda$ , respectively. In line with the above results, higher percentages of reappearance were observed over time,  $F(2, 10) = 18.19$ ,  $p = 0.006$ .

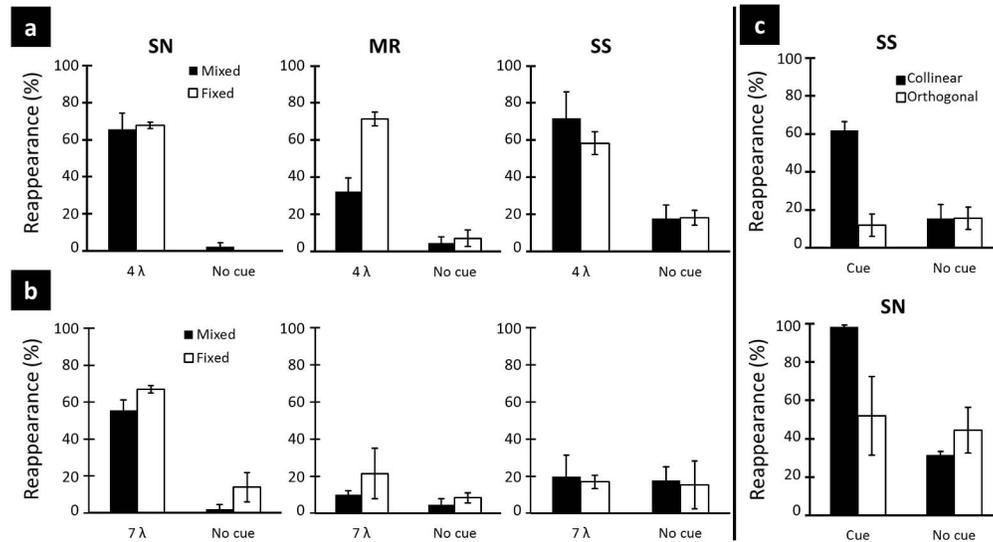


Figure 3. Individual data from three observers, showing the percentages of reappearances in high-uncertainty contexts (i.e., mixed conditions) and low-uncertainty contexts (i.e., fixed conditions) at a target-to-cue distance of  $4\lambda$  (a) and  $7\lambda$  (b). Figure 3c illustrates reappearances with and without a cue, for collinear and orthogonal Gabor patches.

## Stimulus predictability

To test the robustness of the current results, we examined whether the reappearances were affected by the statistics of the stimuli. The percentages of reappearances were tested as a function of the uncertainty level (Figure 3a and b). In the low-uncertainty condition, the cue was presented at a fixed distance relative to the target, either  $4\lambda$  or  $7\lambda$  in different blocks of trials (i.e., “Fixed condition”), whereas in the high-uncertainty condition, the distance between the target and the cue was randomized as in the main experiment (i.e., “Mixed condition”:  $3\lambda$ ,  $4\lambda$ ,  $5\lambda$ ,  $6\lambda$ , and  $7\lambda$ ). Figures 3a and b present individual data of three observers by comparing the percentages of reappearance under the Fixed and the Mixed conditions, with and without a cue. There were no observed differences between the Fixed and the Mixed conditions with or without a cue, at  $4\lambda$  (Figure 3a) as well as at  $7\lambda$  (Figure 3b) distances. Furthermore, when comparing the  $4\lambda$  and the  $7\lambda$  distances, there were no observed differences in the percentages of reappearances without a cue (false alarms). This lack of difference under the Fixed condition indicates a similar criterion for reappearances for the  $4\lambda$  and the  $7\lambda$  distances. Therefore, our findings suggest that reappearances in the presence of a cue is governed by the target-cue distance. A similar criterion for reappearances in the absence of a cue was also found for collinear and orthogonal Gabor patches.

Two observers completed an additional experiment in which the target orientation was either  $-45^\circ$  or  $+45^\circ$  (with equal probability), whereas the orientation of the cue was fixed for all trials ( $-45^\circ$ ). Since the target

orientation was presented before its disappearance, during the initial MIB display, the observers could predict the collinearity or orthogonality of the target and the cue. The target-to-cue distance was set to  $4\lambda$ . In line with the above findings, reappearances induced by a cue were more frequent for collinear Gabor patches than for orthogonal Gabor patches (Figure 3c). However, in the absence of a cue, although collinearity could be predicted, no observed difference in reappearances (false alarms) was evident. Appropriately, our findings indicate the reappearances of the invisible target as a function of orientation-similarity between the target and the cue.

## Object representation of a subconscious stimulus

Here we tested whether a visible object can induce the reappearances of an invisible target consisting of its features. The target was a horizontal Gabor patch. The cues were Gabor patches same as the target, orthogonal to it, or a plaid pattern consisting of horizontal and vertical Gabor patches. The cues were presented with one of three contrast levels, 25%, 35%, and 50% (for a plaid cue, the contrast refers to the underlying Gabor components).

Different cue contrasts were tested to examine possible contrast-effects of the plaid relative to its local features ( $N = 6$ ). Results show no difference in reappearances between the different contrast levels: horizontal target,  $F(2, 10) = 1.15$ , n.s.; plaid target,  $F(2, 10) = 1.24$ , n.s. (Figure 4). For further analyses, the percentages of reappearances were averaged across the

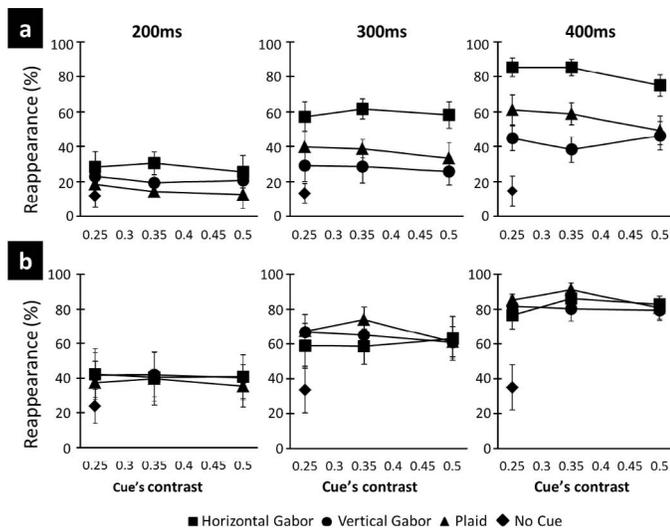


Figure 4. The percentages of reappearances as a function of cue type and contrast for horizontal Gabor target (a) and plaid target (b). Data points are means across observers ( $N = 6$ ), with error bars representing the standard error of the mean.

three possible cue contrasts. These results rule out effects due to differences in perceived contrast between plaids (having larger RMS contrast) and component Gabor patches (Tiippana, Näsänen, & Rovamo, 1994) or due to cross-orientation suppression (Priebe & Ferster, 2006).

We tested whether an invisible object can be brought into awareness by its features. The target was a plaid pattern (50% contrast of the components), whereas the cues were the same as in the previous experiment (horizontal or vertical Gabor patches, or a plaid pattern consisting of horizontal and vertical Gabor patches). Cues assumed one of the three contrast levels of 25%, 35%, and 50%. Horizontal and plaid targets reappeared as a function of the presented cue,  $F(3, 15) = 10.63$ ,  $p = 0.014$  and  $F(3, 15) = 10.52$ ,  $p = 0.015$ , for horizontal and plaid targets respectively (Figure 5). For a horizontal Gabor target, the percentages of reappearances were higher in the presence of a horizontal Gabor cue than a plaid cue,  $t(5) = 6.31$ ,  $p = 0.001$ , a vertical Gabor cue,  $t(5) = 9.93$ ,  $p = 0.000$ , or no cue condition,  $t(5) = 4.47$ ,  $p = 0.007$ . There were no additional differences between cues. As for plaid targets, post-hoc analyses revealed no significant differences between cues.

## Discussion

In the current work we attempted to specify the information available on visual stimuli during perceptual suppression. Our results provide evidences for preserved representation of the unaware at the features

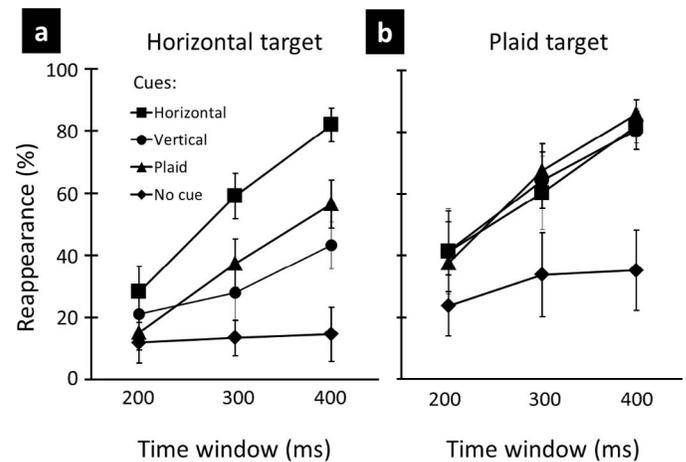


Figure 5. The percentages of reappearances for a horizontal Gabor target (a) and a plaid target (b) at three different time windows. Data points are means across observers ( $N = 6$ ), with error bars representing the standard error of the mean.

as well as the object level of visual processing. Using the MIB paradigm, we examined the interactions between visible and perceptually invisible stimuli. Kawabe et al. (2007) previously showed that the abrupt onset of a visible cue next to a perceptually suppressed target revived visual awareness of the unaware. The authors proposed that the cue draws attention towards the target location, inducing its reappearances. In this work we suggest that the interaction between the target and the cue is a selective process governed by stimulus representations. Our results indicate a clear dependence of target reappearances on the target-cue orientation's similarity and distance. The frequencies of reappearances were highest in the presence of a collinear Gabor cue and with a proximal cue, thus demonstrating narrow tuning of orientation ( $<30^\circ$ ) and distance ( $<1^\circ$ ). First, our results indicated an interaction between a visible cue and a perceptually invisible target. This interaction between two distinct awareness states implies that some visual processes operate across the boundary of awareness. Second, our findings indicate that this interaction, between the perceived and the unperceived, involves a feature-specific component. A visible stimulus selectively facilitates the reappearances of the suppressed object as a function of features similarity. As with any other study involving visual awareness, our conclusions depend on the authenticity of subjective report of disappearance (see below) but do not require the transitions between awareness states to be awareness dependent (Dieter, Tadin, & Pearson, 2015).

Studies of visual awareness have attempted to assess the involvement of conscious awareness in the early stages of visual processing (He & MacLeod, 2001; Kim & Blake, 2005; Rees et al., 2002; Tong, 2003). Our findings show similarity-based reappearances of the

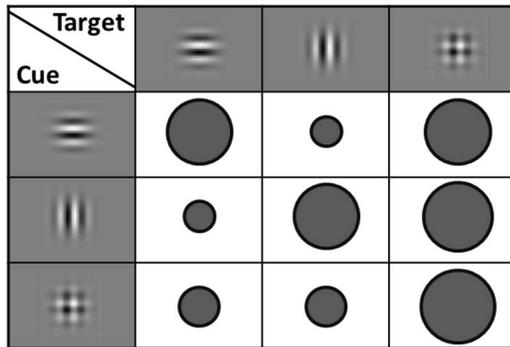


Figure 6. Relative frequency of reappearances depending on target and cue type. Data are represented by the size of a circle patch, with larger circles representing more reappearances.

unperceived, indicating that some target-related information is represented in the system to interact with the cue. These preserved visual representations out of awareness suggest that some processes, sensitive to analysis of features, do not correlate with stimulus awareness. Specifically, we showed a dissociation between early visual processes and the perceptual experience. The current findings converge with previous studies, showing adaptation after-effects induced by perceptually invisible features (Montaser-Kouhsari et al., 2004; O'Shea & Crassini, 1981; Wade, 1980; Wade & Wenderoth, 1978). However, it was shown that the strength of these after-effects is not affected by the stimulus strength within a range of contrast levels, thus allowing for preserved after-effects with reduced effective contrast of the suppressed object (Blake, Tadin, Sobel, Raissian, & Chong, 2006). Critically, the existence of local after-effects does not necessarily imply an accessible representation of what is perceptually unseen. Thus, to test for available stimulus representations in the absence of stimulus awareness, the current study tested for interactions between visible and invisible stimuli by examining the effects of visible stimuli on the reappearance of invisible stimuli.

Object-based representation of the subconscious was demonstrated here by examining the interaction between a compound stimulus and its composing features. Figure 6 depicts the resulting interaction matrix. Overall, the results indicate that an invisible object has more than one dominant representation: A suppressed plaid object is represented at the features level of visual processing as well as at the object level of visual processing. This is supported by results showing that the reappearance of a horizontal Gabor target was more effective in the presence of a horizontal cue than in the presence of a plaid cue, the latter exhibiting behavior that was not significantly different than that of an orthogonal cue. These findings suggest that a visible object is represented globally (possibly as a conjunction of features) without a specific reference to

its features, therefore showing no feature-similarity based reappearances. On the other hand, for an invisible plaid target, all cues, Gabors and plaid, were equally effective, indicating that out of awareness a plaid is represented at multiple levels of abstraction, including both feature and object representations. This pattern of interactions reflects asymmetric relations between aware and unaware object representations: A visible object cue was not effective in bringing back its invisible component; however, an invisible object target was efficiently induced to reappear by its visible component cues. In terms of similarity-based reappearances, as found with orientation, an invisible plaid target is decomposed into its features, thereby is similar to its visible feature cues, whereas a visible object has a holistic representation which is not simply the sum of its features. Taken together, our results indicate that the representation of objects depends on the awareness state: Perceptually visible as well as invisible objects are represented by combinations of features, possibly at the object level of processing. However, the perceptually invisible, but not the visible object is decomposed into its features.

There is an open question regarding the relationship between attention and awareness (Koch & Tsuchiya, 2007; Lamme, 2003; Posner, 1994). To the extent that attention is required for object binding (e.g., Julesz, 1987, 1993; Treisman & Gelade, 1980), our results indicating object representations with and without visual awareness, support a dissociation between attention and awareness.

Reappearance of the suppressed object was found to be relatively slow and required the target to appear for 300–400 ms after cue presentation. These results are consistent with reports suggesting that the transition between awareness states is not immediate, but rather, requires the representations to be integrated within a continuous time window (Mitroff & Scholl, 2004). We also considered the possible effects of eye movements. Similar to Troxler, MIB reappearance is highly sensitive to small fixational eye movements (i.e., microsaccades) (Bonne et al., 2010, 2014). However, whereas stimulus driven microsaccades are influenced by the likelihood of the stimulus appearance (Bonne, Adini, Sagi, Tsodyks, Fried, & Arieli, 2013; Valsecchi, Betta, & Turatto, 2007), our findings show no effect of the uncertainty level on the reappearances of the invisible. To test directly for the possible effect of microsaccades, we carried out a supplementary experiment in which we monitored eye movements (four observers). In this experiment (see Figure 7), the stimuli consisted of collinear and orthogonal cues ( $4\lambda$  separation), with time windows of 400, 600, and 1000 ms. As in the main experiments, the reported reappearance was affected by the spatial relations (Figure 7a). However, very few microsaccades preceded the reappearance:

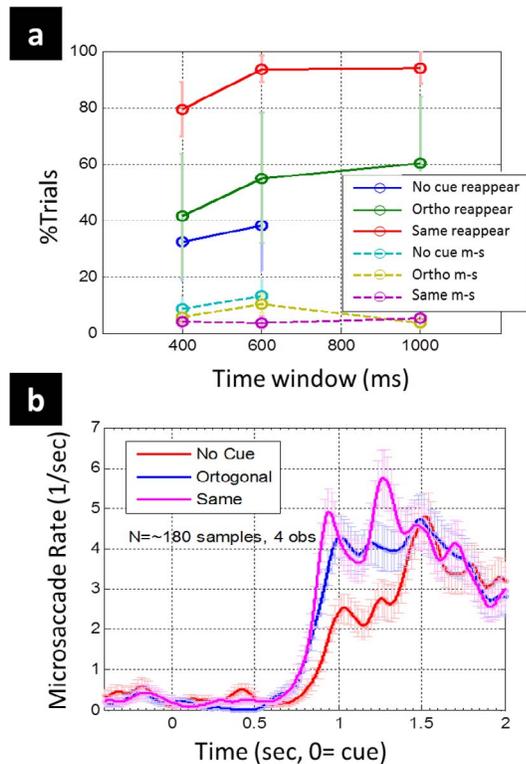


Figure 7. Microsaccades and reappearance. Observers ( $N = 4$ ) performed a subset of the cue paradigm while their eyes were tracked, in order to check if reappearance could be caused by microsaccades (i.e., small and rapid fixational eye-movement occurring involuntarily). The cues consisted of collinear (“Same”) and orthogonal Gabor patches ( $4\lambda$  separation), using time windows of 400, 600, and 1000 ms, with an additional No Cue condition. Microsaccades were analyzed and two measures were computed: (a) the percentage of microsaccades (dashed lines) to be compared with the percentage of reappearances (solid lines) in the relevant time window, and (b) the rate modulation. Detailed methods can be found in Bonne et al. (2010) and Bonne, Adini, & Polat (2015). The results indicate that microsaccades were rare, and appeared (one or more) in fewer than 10% of trials (Figure 7a; dashed lines). For the same (collinear) trials, perceptual reappearance was reported for  $\sim 90\%$  (Figure 7a; red line). Moreover, the percentage of trials with microsaccades did not vary as function of the cue type, unlike the percentage of reappearance. A similar conclusion could be derived from the rate modulation functions (b), where throughout the reappearance window (of 600 ms) microsaccades were tightly inhibited with all cues. Taken together, these analyses show that microsaccades could not explain differences in reappearance in the cuing paradigm.

One or more microsaccades were found in less than 10% of the trials, in a window of 0–600 ms, in which reappearance rate was above 90% (Figure 7a, compare “same” to “same m-s,” see also Figure 7b). These results rule out any role for microsaccades in the interactions reported here.

Our study shows preserved representation of the perceptually invisible targets. To measure visibility we use subjective report and hypothesize the existence of a sharp boundary between the visible and the invisible (a hypothesis strongly supported by introspection, when watching a MIB demo or our experimental trials). Such a boundary may correspond in the brain to a threshold-like mechanism or to a decision boundary (“criterion” in Signal Detection Theory). The latter can account for other cases of nontrivial invisibility, such as visual extinction and blindsight, by considering constraints on criterion setting (Gorea & Sagi, 2001, 2002). The results presented here indicate interactions across this boundary, between the visible and invisible targets, as a function of similarity at the features level as well as at the object level of representation. These selective interactions indicate that some properties of the perceptually invisible target are preserved to interact with the cue during visual suppression.

*Keywords: Motion Induced Blindness (MIB), visual awareness, visual suppression*

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