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Unconscious Orientation Processing

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Summary

Recent findings have shown that certain attributes of visual stimuli, like orientation, are registered in cortical areas when the stimulus is unresolvable or perceptually invisible; however, there is no evidence to show that complex forms of orientation processing (e.g., modulatory effects of orientation on the processing of other features) could occur in the absence of awareness. To address these questions, different psychophysical paradigms were designed in six experiments to probe unconscious orientation processing. First we demonstrated orientation-selective adaptation and color-contingent orientation adaptation for peripheral unresolvable Gabor patches. The next experiments showed the modulatory effects of perceptually indiscriminable orientations on apparent motion processing and attentional mechanisms. Finally we investigated disappearance patterns of unresolvable Gabor stimuli during motion-induced blindness (MIB). Abrupt changes in local unresolvable orientations truncated MIB; however, orientation-based grouping failed to affect the MIB pattern when the orientations were unresolvable. Overall results revealed that unresolvable orientations substantially influence perception at multiple levels.

Introduction

In peripheral vision, Gabor patches with spatial frequencies beyond the resolution limit cannot be perceptually resolved. In a large range of spatial frequencies, labeled "aliasing range," Gabor patches can be detected but not resolved because of optical blur and neural limitations on visual resolving power (Thibos and Bradley, 1995). He and MacLeod (2001) generated unresolvable Gabor patches in the fovea using a He-Ne laser interferometer and observed that orientation-selective adaptation occurs for high-contrast unresolvable Gabor patches (where the orientation pattern is invisible). They concluded that primary visual cortex (V1) detects invisible patterns of high spatial frequency gratings.

Similarly, some other studies have demonstrated that orientation-selective adaptation occurs when the adapting stimulus is pushed out of the explicit conscious perception using crowding (He et al., 1996) and binocular rivalry (Blake and Fox, 1974) paradigms. These studies suggest that primary visual cortex could be selectively activated in response to perceptually indiscriminable orientation information and thereby area V1 could not be sufficient for generating visual awareness ("V1 hypothesis," Crick and Koch, 1998).

Orientation-selective adaptation is a good psychophysical method to probe orientation processing in unaware conditions; however, it does not show all aspects of orientation processing. In this study we used several psychophysical paradigms to investigate more properties of unconscious orientation processing.

We generated unresolvable Gabor patches in the "periphery" and initially demonstrated orientation-selective adaptation for a single unresolvable oriented item. Since we have used "peripheral" Gabor stimuli in other experiments of this study, orientation-selective adaptation to these stimuli must be initially examined and confirmed. Consistent with classical ideas, unresolvable Gabor patches were able to induce robust orientation-selective adaptation even in the peripheral visual field. The next two experiments provided evidence for higher-order orientation processing in the absence of awareness. One of them indicated color-contingent orientation adaptation for colored unresolvable patterns. The other one showed the priming effects of perceptually invisible orientation on apparent motion direction in a bistable motion display.

In further experiments of this study, we explored some other abilities of the visual system for unconscious orientation processing. The explored phenomena included (1) implicit detection of orientation change in the perceptually invisible condition and (2) covert attentional shift to the location of an unresolvable Gabor patch when it was embedded among (but indistinguishable from) uniform luminance patches. The first and second phenomena could be described as subliminal pop out in temporal and spatial domains, respectively.

Although various paradigms in this study showed a wide range of unconscious orientation processing for a "single Gabor patch," the final experiment demonstrated the absence of contextual orientation interactions ("rivalry" or "cooperation") between two adjacent Gabor patches when the orientation of Gabor stimuli was perceptually invisible.

Results

Experiment 1: Orientation-Selective Adaptation from Unresolvable Gabor Patches

Exposure to a visual pattern (for example, a high-contrast grating) creates aftereffects (adaptation) in perception. A visual discrimination task (for example, orientation discrimination) would be difficult for test patterns that resemble the preexposed pattern (such as gratings of the same orientation), and we require more contrast to discriminate them (Blakemore and Campbell, 1969).

In the first experiment, orientation-selective adaptation was examined for unresolvable Gabor patches. The adapting stimulus was a Gabor patch with high spatial frequency presented for 5 s above the fixation point.

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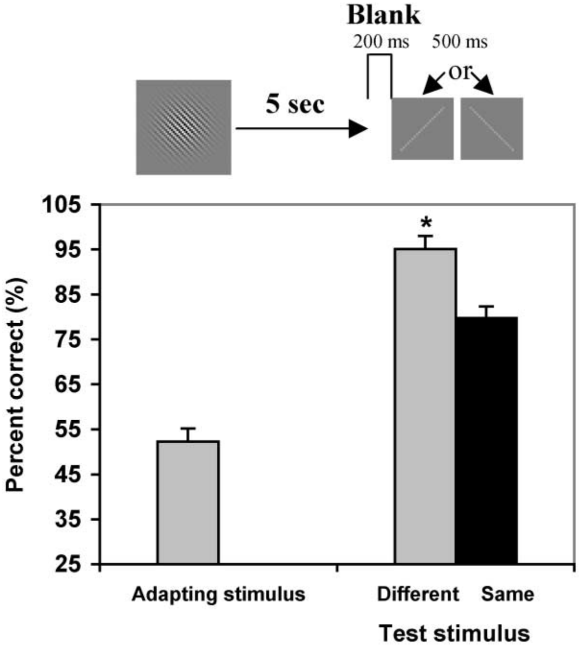

Figure 1. Schematic Diagram of Experiment 1 and Its Results

The adaptation paradigm was designed in this experiment as follows: (1) presentation of adapting stimulus (Gabor patch with high spatial frequency) for 5 s, (2) presentation of the background (blank) during delay (200 s) between adaptation and test periods, (3) presentation of test stimulus (a line with the same orientation as adapting one, "same adapt-test," or perpendicular to the orientation of adapting Gabor patch, "different adapt-test") for 500 ms. The performance of subjects in discriminating the orientation of adapting stimulus was at chance level; however, there was adaptation to such invisible orientation. The difference between percent corrects of different adapt-test and same adapt-test was significant. Significant difference is showed by *. Error bars indicate one SEM.

The adaptation period was followed by 200 ms presentation of the background (blank) and then 500 ms presentation of the test stimulus. Test stimulus was a "low contrast thin line" with either the same ("same adapt-test") or different ("different adapt-test") orientation with respect to the adapting Gabor patch (Figure 1). The test line was a resolvable oriented item presented at the center of adapting stimulus. Subjects were asked to report the orientations of the Gabor patch and the line at the end of trial by pressing down two of four alternative keys on the computer keyboard, the first one for adapting stimulus discrimination (either 45° or 135°) and the second one for test stimulus discrimination.

Results of experiment 1 showed that, although subjects were unable to discriminate the adapting orientation (the performance was at chance level [50% correct] in each subject, $p > 0.05$ using χ^2 test), they discriminated the orientation of different adapt-test more accurately than the orientation of same adapt-test ($p < 0.05$ using two-tailed t test, df = 10) (Figure 1). There was no difference between the adaptation effect of trials in which subjects correctly discriminated the adapting orientation and trials in which the opposite orientation was perceived ($p > 0.05$ using two-tailed t test, df = 10).

Experiment 1 demonstrated orientation-selective adaptation from unresolvable spatial patterns presented in the peripheral visual field.

Experiment 2: Color-Contingent Orientation Adaptation for Unresolvable Gabor Patches

Th McCollough effect is an orientation-contingent color aftereffect in which viewing two colored grids for a few minutes produces negative color aftereffects that are contingent on the orientation of the patterns used to induce it (McCollough, 1965). Held and Shattuck have demonstrated a color-contingent tilt aftereffect, showing that the perceived tilt of a colored grating can be strongly influenced by the color of an adapting grating (Held and Shattuck, 1971). In addition, it has been shown that adaptation to colored gratings produces elevated color contrast thresholds for test gratings that are similar in spatial frequency and orientation to the adapting stimulus (Bradley et al., 1988). These contingent aftereffects can be attributed to the selective adaptation of color-orientation multiplexing cells in V1 and V2 that respond not just to color or to orientation but to combinations of particular color ranges and particular orientation ranges (Leventhal et al., 1995; Friedman et al., 2003). Here we demonstrated that orientation adaptation of colored unresolvable Gabor patches is contingent on the color of adapting stimulus ("color-contingent orientation adaptation").

As shown in Figure 2, each trial began with the presentation of a colored Gabor patch (adapting stimulus) above the fixation point (in the same eccentricity as in experiment 1) for 10 s. This constituted the adaptation phase in which the color of the Gabor patch was randomly chosen from among two choices (isoluminant green or red) and the orientation of Gabor patch was randomly chosen from among two choices (45° or 135°). The spatial frequency of adapting stimulus was beyond the perceptual resolution limit. Test stimulus was a low-contrast colored Gabor patch with randomly chosen orientation and color presented in the same location for 500 ms after a 300 ms delay between adaptation and test phases. Spatial frequency of the test stimulus was slightly lower than that of adapting stimulus and its orientation was visible. Color and orientation of adapting and test stimuli could be the same or different. Subjects were asked to report orientations of adapting and test stimuli by pressing two different keys on the computer keyboard. The next trial began after 2 s of intertrial interval.

Results showed that orientation-selective adaptation existed only when the colors of adapting and test stimuli were similar (color-contingent orientation adaptation) (Figure 2). Using a two-way ANOVA, the pure effect of color (same or different adapting and test colors) was not significant [$F(1,5) = 6.43$, $p > 0.05$]. The pure effect of orientation (same or different adapting and test orientations) was also found to be insignificant [$F(1,5) = 5.18$, $p > 0.05$]. However, interaction between color and orientation was significant [$F(1,5) = 14.73$, $p < 0.05$]. Using Scheffe test as a post hoc analysis, difference between percent correct of "same orientation" and "different orientation" groups was significant when colors were the same ($p < 0.05$) but not significant when colors were different ($p > 0.05$).

There was no adaptation effect when the colors of adapting and test patches were different. One may conclude that the "color change" provides a transient signal, which facilitates the test stimulus orientation discrimina-

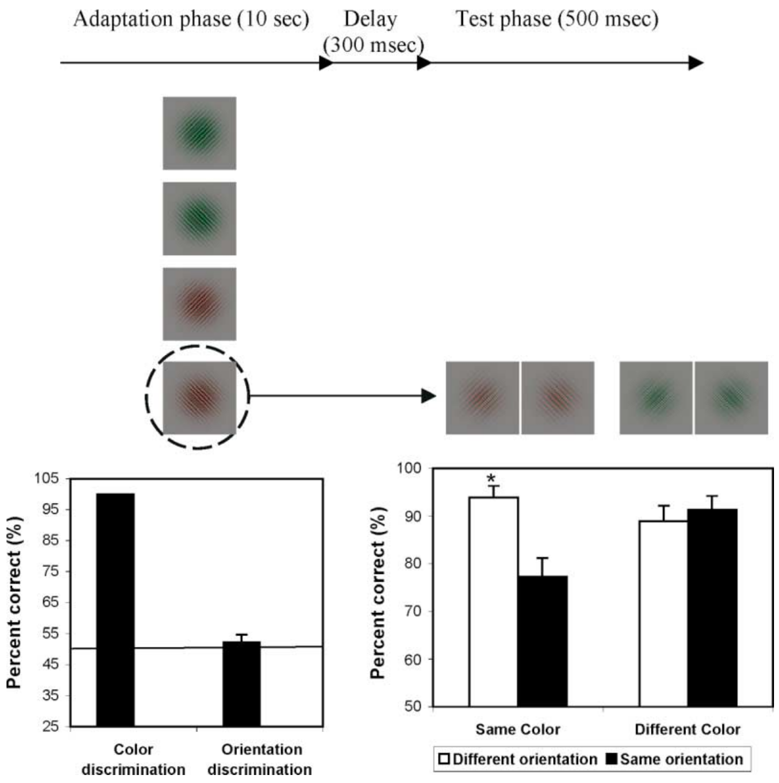

Figure 2. Schematic Diagram of Experiment 2 and Its Results

In the adaptation phase, a colored Gabor patch with high spatial frequency was presented above the fixation point for 10 s. After a 300 ms delay, the test stimulus (a low contrast colored Gabor patch) was presented in the same location as the adapting stimulus for 500 ms. The orientation of the adapting and test stimuli could be either the same or different. Orientation discrimination was at chance level during the adaptation phase; however, subjects could discriminate the color of the adapting stimulus without any error. Orientation-selective adaptation existed only for the test stimulus whose color was the same as the color of the adapting stimulus. In the "same color" condition, the "different orientation" group had significantly better performance than the "same orientation" group. Error bars indicate one SEM.

tion and thereby no adaptation effects are observed. Since the percent correct of the "different color-different orientation" group was a bit lower than that of the "same color-different orientation" group ($p > 0.05$), our adaptation results could not be explained by such transient signal.

In the analysis of adapting stimulus discrimination, subjects were unable to discriminate the orientation of adapting stimulus, and their performance was not significantly above the chance level (50% correct) ($p > 0.05$ in individual subjects using χ^2 test); however, they could discriminate the color of adapting stimulus without any error (performance = 100%).

This experiment revealed a type of interaction between orientation and color attributes of a colored unresolvable Gabor patch.

Experiment 3: Perceptual Priming by Orientation Information of Unresolvable Gabor Patches

Detection of a target Gabor patch can be facilitated by simultaneous presentation of a similar subthreshold Gabor signal. This priming effect is seen when orientations of the cue and target are similar (Tanaka and Sagi, 1998). Feature-based priming effects by the grating's orientation also occur with moving targets. Francis and Kim (1999) demonstrated that, in a choice between movement along lines drawn parallel or orthogonal to possible motion paths, observers more often see movement along the lines parallel to the motion path. Lines indicating the path of movement can generate the perception of a biased multistable apparent motion direction and disambiguate multistable motion display.

In this experiment we showed that orientation information of Gabor patches (either resolvable or unresolvable) could perceptually prime a specific motion direction in a bistable apparent motion display. Bistable motion display used in this experiment was a motion quartet. Figure 3A schematizes the type of stimuli used in experiment 3. Frame A included two black dots on opposite corners of an imaginary diamond. Frame C included two black dots on the other opposite corners of the imaginary diamond. Dots in frame A alternating with dots in frame C generated a bistable apparent motion either in the 45° or the 135° direction. The direction of such ambiguous motion is determined by the observer's attention (Shioiri et al., 2000), but the direction of perceived motion at the beginning of the frames' alternation ("first perception of motion direction") could be biased by perceptual cues. Cue stimuli were four Gabor patches presented on four sides of the imaginary diamond located in the intervening frames B and D. Four Gabor patches in frames B and D had the same spatial frequency (either low or high) and the same orientation (either 45° or 135°). Low-frequency and high-frequency Gabor patches acted as resolvable and unresolvable cues, respectively. According to the Francis and Kim paradigm (Francis and Kim, 1999), Gabor patches with the orientations of 45° and 135° prime apparent motion directions of 45° and 135°, respectively. In the control trials, simple luminance patches were used instead of Gabor patches. We expected to have no systemic biasing effect in the control trials.

The frames were presented in a loop so that frame A appeared right after frame D. Each frame was presented for approximately 200 ms. The sequence of frames (from A to D) only repeated for two times in order to minimize the interaction of observer's attention for perceiving the

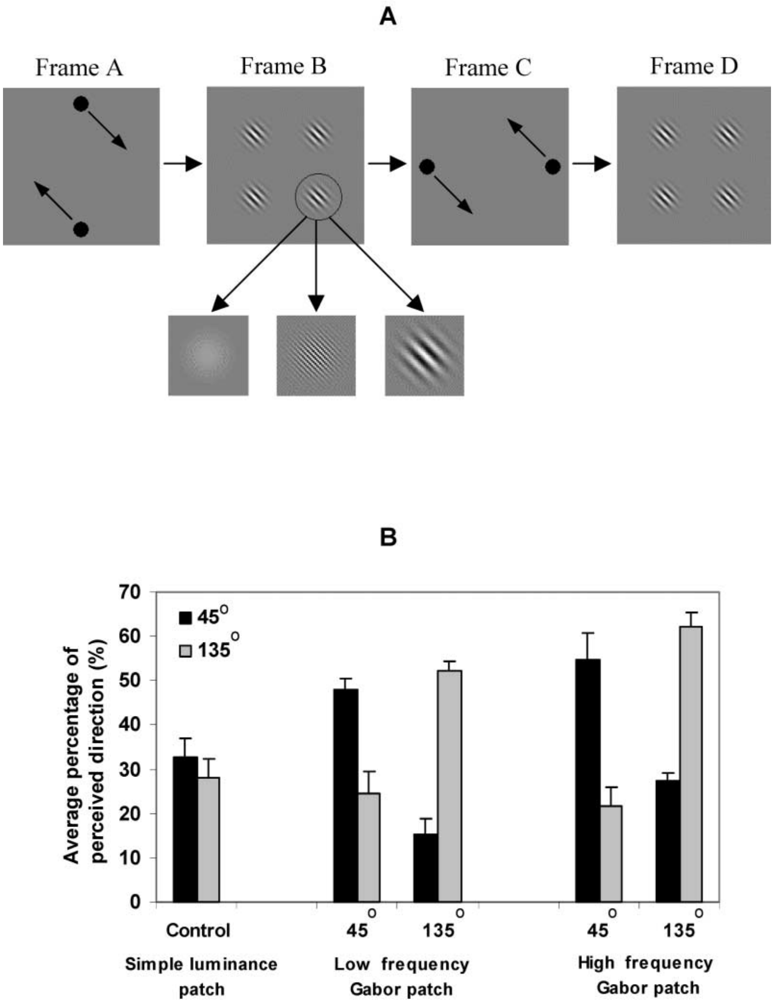

Figure 3. Priming Experiment with Resolvable and Unresolvable Cues

(A) Frames A, B, C, and D were presented sequentially. Frame A was presented again after frame D. In each trial, the presentation of the frames' sequence was repeated only two times. The presentation time of each frame was 200 ms. Dots in frame A in alternation with dots in frame C produced a bistable apparent motion either in the 45° or the 135° direction. The orientation of Gabor patches (either resolvable or unresolvable) located between dots induced apparent motion in the 135° direction (as an example in this figure). Arrows in frames A and C represent the preferred direction of movement for dots in parallel to the orientation of Gabor patches (arrows are only for illustration purpose).

(B) Subjects perceived 45° and 135° directions of motion when the orientation of the cue (either resolvable or unresolvable) was 45° and 135°, respectively. In the control condition with simple luminance patches, there was no priming effect. Error bars indicate one SEM.

direction of apparent motion. Frames were located above the fixation point. Distance of the fixation point from Gabor patches located in the lower part of the frames was equal to the eccentricity of the Gabor patches in the previous experiments.

At the end of each trial, subjects were required to report perceived direction of apparent motion by pressing one of three adjacent keys on the computer keyboard (labeled as "45°," "135°," and "no specific direction") and then report the orientation of stimulus patches (45° or 135°) by pressing either one of another set of two-alternative keys on the computer keyboard.

Results showed that the "expected" direction of motion primed by the Gabor patches was consistent with the "perceived" motion direction (Figure 3B). These priming effects were seen with high spatial frequency Gabor patches as well as with low ones ($p < 0.05$ using two-tailed t test, df = 10). In the control condition, there was no priming effect (the average percentages of perceived 45° and 135° directions were statistically equal [$p > 0.05$ using two-tailed t test, df = 10]).

We also observed a robust priming effect when we analyzed trials where the cue was a high-frequency Gabor patch and the reported orientation for Gabor patches in those trials was wrong ($p < 0.05$ using two-tailed t test, df = 10). The magnitude of the priming effect in these trials was as high as the magnitude for trials where the cue was a high-frequency Gabor patch and the reported orientation for Gabor patches was correct ($p > 0.05$ using two-tailed t test, df = 10). The magnitude of the priming effect was defined as the difference between the percentage of perceived motion direction parallel to the cue's orientation and the percentage of perceived motion direction orthogonal to the cue's orientation.

The performance of subjects in reporting the orientation of the high-frequency Gabor patch was at chance level (50% correct) ($p > 0.05$ in individual subjects using χ^2 test). Subjects had minimal error in discriminating the orientation of low-frequency Gabor patches (percentage of correct responses was almost 100%). Reported orientation for simple luminance patches was shared equally between 45° and 135° orientations ($p > 0.05$ in individual subjects using χ^2 test). Further analysis for the control trials showed no systemic relationship between reported direction for motion and reported orientation for luminance patches. Percentages of reported 45° and 135° orientations were statistically equal when the perceived direction of motion was 45° or 135° ($p > 0.05$ in individual subjects using χ^2 test). It means that subjects had no bias in reporting the orientation of stimulus patches on the basis of perceived direction of motion.

Attending to the overall higher portions of the display and to the motion display might have caused the increased upward fixation drifts. One may conclude that upward fixation drifts might have made high-frequency Gabor patches visible in some trials, and these trials are responsible for the priming effects observed with high-frequency Gabor patches. But this seems to be an unlikely explanation since we showed that orientation discrimination of high-frequency Gabor stimuli was seriously impaired even when subjects reported the orientation of Gabor patches and direction of motion in the same experiment. Furthermore, the priming effect was greatly robust in trials where the orientation of cue has been reported incorrectly. In these trials, Gabor patches were undoubtedly unresolvable.

The results of experiment 3 showed that even an unresolvable Gabor patch could induce the perceptual preference of motion direction parallel to its own orientation.

Experiment 4: Orientation-Dependent Spatial Cueing by Unresolvable Gabor Patches

An unresolvable Gabor stimulus is seen as a uniform patch lighter (desaturated) relative to the background (Shady and MacLeod, 2002). "Perceptually uniform" patches (i.e., unresolvable Gabor patches) are indistinguishable from "physically uniform" ones (i.e., simple luminance patches). In this experiment we addressed the question of whether an unresolvable Gabor patch can attract attention when it is located in an array of luminance patches.

To test this idea, a "stimulus array" consisting of physically uniform patches was constructed (Figure 4A). Each stimulus array had 16 items arranged on an imaginary circle. The eccentricity of each item was the same as the Gabor patches of experiments 1 and 2. In a subset of trials (two-thirds of the trials), one item was an unresolvable Gabor patch (perceptually uniform stimulus). An unresolvable Gabor patch was "visually" salient in the array ("singleton") because the orientation feature existed only in one item. The location of the unique item was selected randomly across trials. The stimulus array was presented for 250 ms following a blank display presented for 800 ms. Display time was 250 ms in order to prevent any possible eye movements toward items of the display (Wolfe and Gancarz, 1996). To measure whether an "oddball item" (unresolvable Gabor patch) can induce the covert shift of attention to the visually conspicuous location, a serial search array (conjunction search display) was presented 200 ms after the disappearance of the stimulus array (the time of 200 ms is the optimal interval for spatial cueing [Nakayama and Mackeben, 1989]). If the oddball item acts as an exogenous cue for target present trials of serial search array then the target will be found rapidly with less error rate during the search time (Joseph and Optican, 1996). The serial search array containing Ts or inverted Ts with either blue or yellow hues (located on an imaginary circle) was presented briefly for 50 ms (see Figure 4A). The target was a "blue invert T" (conjunction of two features), and subjects were asked to fixate on the fixation point, maintain their fixation through the trial, and report as fast as possible if the target existed in the serial search array. There were three conditions, which we called cue-valid (target presented at the location of the oddball item), cue-invalid (target presented at the opposite location of the oddball item), and neutral (the stimulus array had no oddball item). Reaction time and percentage of correct target detection were measured in the three conditions.

To confirm that physically and perceptually uniform patches were perceptually indistinguishable, the stimulus array was presented per se in a separate experiment,

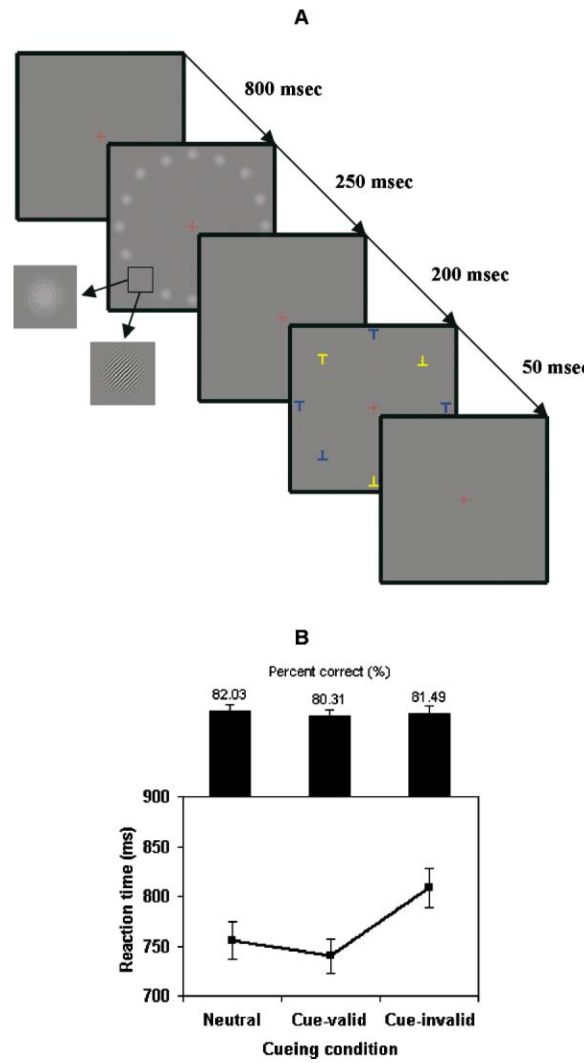

Figure 4. Schematic Diagram Demonstrating the Temporal Succession of Visual Stimuli in a Typical Trial of Experiment 4 and Results of This Experiment

(A) Each trial began with a small cross appearing at the fixation point for 800 ms, followed by a 250 ms interval in which the "stimulus array" was presented. The trial continued with a 200 ms blank interval, followed by a serial search array presented for 50 ms. The trial ended with a blank display presented for 2000 ms as the intertrial interval. The stimulus array consisted of physically uniform patches arranged on an imaginary circle. In some trials, one item was an unresolvable Gabor patch (perceptually uniform stimulus), which was valid or invalid for target letter of serial search array. The neutral condition occurred when the oddball item (unresolvable Gabor patch) was absent.

(B) The percent correct of serial search task was approximately similar among cue-valid, cue-invalid, and neutral conditions; however cue-valid condition resulted in significant improvement of reaction time compared to cue-invalid condition. Error bars indicate one SEM.

and subjects were asked to report whether a unique item was present in the array or not.

We analyzed the trials where the target of the serial search array was present (note that the reaction time was analyzed only for target-present trials where subjects could detect the target correctly). The percent correct of the serial search task was approximately similar among cue-valid, cue-invalid, and neutral conditions ($p > 0.05$ using Bonferroni t test, Statistical Power = 0.90); however, the cue-valid condition resulted in significant improvement of reaction time compared to the cue-invalid condition ($p < 0.05$ using Bonferroni t test) (Figure 4B). This effect is also observed in classic spatial cueing paradigms (e.g., Posner et al., 1978).

Further analysis confirmed that subjects were at chance level (50% correct) in detecting the unique item in the stimulus array ($p > 0.05$ in individual subjects using χ^2 test), thus, the visually salient item (unresolvable Gabor patch) was not perceptually distinguishable from distractors (simple luminance patches).

Results showed that the orientation of a single unresolvable stimulus embedded among luminance patches was detected by the visual system and caused subliminal involuntary shifts of visual attention.

Experiment 5: Implicit Detection of Change in the Orientation of Unresolvable Gabor Patches

One of the circumstances in which "visual pop out" occurs is when an abrupt change in the attributes of a stimulus is made (Theeuwes, 1995). Fernandez-Duque and Thornton (2000) have demonstrated that change detection can be performed implicitly without awareness. In this experiment the existence of visual pop out was examined in the cases of abrupt change in the orientation of resolvable and unresolvable Gabor patches during motion-induced blindness (MIB). MIB is observed with normal-sighted observers under normal conditions. When a global moving pattern (moving mask) is superimposed on a high-contrast stationary or slowly moving object, the latter disappears and reappears alternatively for periods of several seconds (Bonneh et al., 2001). Bonneh et al. have shown that large and abrupt transients tend to bring the disappeared patterns in the MIB back to awareness, but small and regular changes (like flickering of the target) do not disrupt disappearance. The abrupt transients pop out in the MIB paradigm.

The MIB paradigm was designed by using a global moving pattern superimposed on a Gabor patch (either resolvable or unresolvable). The Gabor patch served as a target and was presented in the periphery in the same eccentricity as Gabor patches of the previous experiments (Figure 5A). In each trial, subjects were asked to report the invisibility pattern of the target during 1 min exposure time. They were required to press a key on the computer keyboard and hold the key down during each invisibility period. Each time the key was pressed (the beginning of blindness), the orientation of the target was suddenly changed to its orthogonal orientation (e.g., 45° to 135°) or remained unchanged. Had the orientation changed, it occurred right at the time of the key press. These two conditions pseudorandomly repeated during each trial. At the time of reappearance of the target, subjects released the key and then reported with another key whether there was a change in orientation or not. The time interval between pressing and releasing the key was considered as a "single" blindness period. The Gabor patches with either low spatial frequency (resolvable) or high spatial frequency (unresolvable) were presented in the random trials. The mean duration of single blindness periods was compared between "changed" and "unchanged" conditions (separately for targets with low and high spatial frequency).

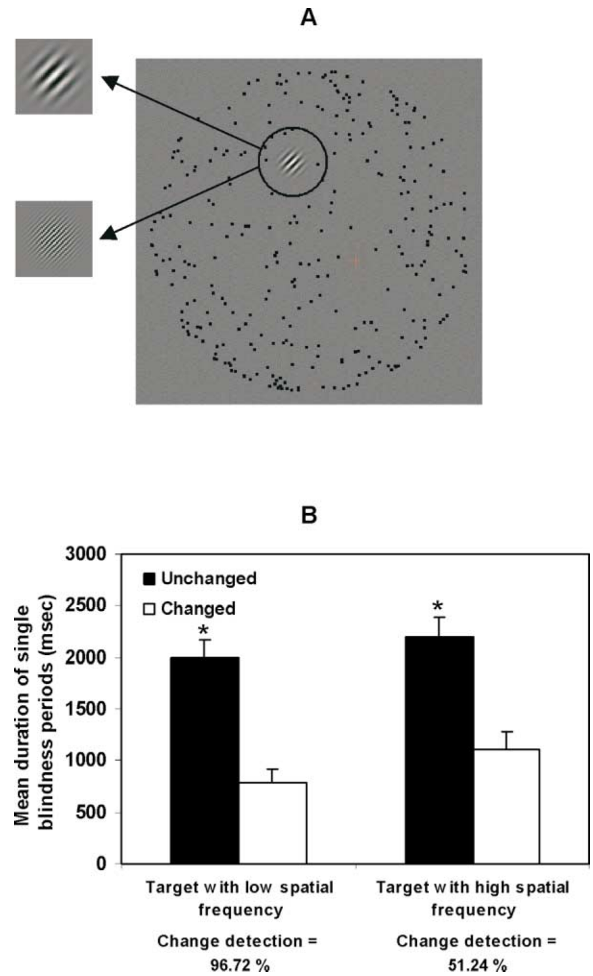

Figure 5. MIB Display in Experiment 5 and Results of This Experiment

(A) MIB display contained a global moving pattern superimposed on a target Gabor patch (either resolvable or unresolvable). MIB display was presented for 1 min. Subjects had to report the invisibility pattern of the target. At the beginning of each blindness phase, the orientation of the target was suddenly changed to its orthogonal orientation or remained unchanged.

(B) Mean duration of single blindness periods has been shown in different conditions (changed and unchanged orientation in targets with low or high spatial frequency). Periods of invisibility in the changed condition were shorter than that in the unchanged condition, both with low and high spatial frequency targets (Gabor patches). Change detection was at chance level for high-frequency Gabor patches. Error bars indicate one SEM.

Change in orientation was detected in targets with low spatial frequency ($p < 0.05$ in individual subjects using χ^2 test), while change detection in targets with high spatial frequency was at chance level (50% correct)

($p > 0.05$ in individual subjects using χ^2 test, $d' = 0.07$, Criterion = 0.065). However, abrupt change in the orientation popped out in both conditions, and the target reappeared rapidly even when subjects were not aware of the change in orientation. Figure 5B shows the results of this experiment. Mean duration of single blindness periods in the changed condition was significantly shorter than that in the unchanged condition both when the change was perceptually detected and not ($p < 0.05$ using two-tailed t test, df = 10).

Further analysis showed the robust pop out effect in the changed condition either when subjects reported the change in orientation or when they missed the change ($p < 0.05$ using two-tailed t test, df = 10).

At the "change times," local change in the luminance may truncate the suppression phase of MIB instead of change in orientation. To investigate the pure role of "local change in the luminance," we designed a control experiment that was identical in all respects to experiment 5 except that the key press caused a sudden change in the "phase" of either the resolvable or unresolvable Gabor patch in half of the trials. The phase of the Gabor patch remained unchanged in the other trials. Local luminance information was altered by changing the phase of the Gabor patches. There was no significant difference between mean durations of single blindness periods in changed and unchanged conditions ($p > 0.05$ using two-tailed t test, df = 10). It seems that local change in the luminance provides a weak transient signal, which could not truncate the suppression phase of the MIB.

Therefore, the orientation change was implicitly detected in the visual system and caused the target to pop out in the temporal domain even in the absence of explicit change detection.

Experiment 6: Absence of Interactions among Orientation Signals of Two Unresolvable Gabor Patches during Motion-Induced Blindness

In the MIB paradigm, when two adjacent collinear Gabor patches (Gabor patches with the same orientations) are presented, they tend to disappear and reappear simultaneously, but when two orthogonal Gabor patches (Gabor patches with different orientations) are presented, their disappearance would be independent or anticorrelated (Bonneh et al., 2001). This property of MIB (effect of orientation configuration on simultaneous blindness) has been examined in a previous study where orientations of the Gabor patches were maintained visible for the subjects (Bonneh et al., 2001). Theoretically, interactions (rivalry or cooperation) between the two sources of orientation signals (two adjacent Gabor patches) could explain this property of MIB (Bonneh et al., 2001). In this experiment, two resolvable or unresolvable Gabor patches were located in the periphery (in the same eccentricity as Gabor patches of the previous experiments), and their invisibility patterns were compared. In such eccentricity, unresolvable Gabor patches are detectable but not resolvable (Thibos and Bradley, 1995), so subjects could report disappearance or reappearance of unresolvable Gabor stimuli during MIB.

The MIB paradigm was constructed by using two adjacent Gabor patches superimposed on a global moving pattern (see Figure 5A). The two Gabor patches were either collinear/parallel or orthogonal and have either low spatial frequency (visible orientation) or high spatial frequency (indiscriminable orientation); hence, there were four conditions for MIB display. In each trial of the experiment, subjects were asked to fixate on the fixation point while one of the randomly chosen MIB conditions was displayed for 1 min. Subjects had to press one key on the computer keyboard when the two Gabor patches disappeared simultaneously, hold the key down during simultaneous blindness, and release it when at least one Gabor patch reappeared. Such a response pattern could be repeated several times during the 1 min observation period. "Overall" duration of simultaneous blindness within each trial was measured separately for each MIB condition and then was averaged across all trials (note that mean duration of single blindness periods has been calculated in experiment 5 and here we have measured mean duration of simultaneous blindness during "1 min trial").

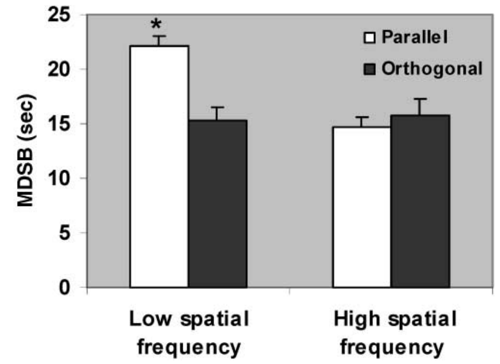

Figure 6. Results of Experiment 6

Mean duration of simultaneous blindness (MDSB) during 1 min observation of MIB display was calculated separately for parallel and orthogonal Gabor patches with either low or high spatial frequency. Simultaneous blindness occurred for parallel Gabor patches only when they had low spatial frequency. Error bars indicate one SEM.

A two-way ANOVA revealed a significant effect of spatial frequency (low or high spatial frequency) on mean duration of simultaneous blindness [$F(1,5) = 38.97$, $p < 0.05$]. There was also a significant effect of orientation configuration (parallel or orthogonal) on mean duration of simultaneous blindness [$F(1,5) = 7.80$, $p < 0.05$]. Interaction of spatial frequency and orientation in relation to mean duration of simultaneous blindness was significant as well [$F(1,5) = 18.72$, $p < 0.05$]. Using the Scheffe test as a post hoc analysis, the difference between mean duration of simultaneous blindness for parallel and orthogonal Gabor patches with low spatial frequency was significant ($p < 0.05$), but this difference for parallel and orthogonal Gabor patches with high spatial frequency was not significant ($p > 0.05$). Figure 6 demonstrates the mean duration of simultaneous blindness in four conditions of MIB display.

One may conclude that the disappearance and reappearance pattern of unresolvable Gabor stimuli in the MIB is purely luminance based, and thereby, two adjacent unresolvable Gabor patches have no correlation in the invisibility patterns since in this case the orientation

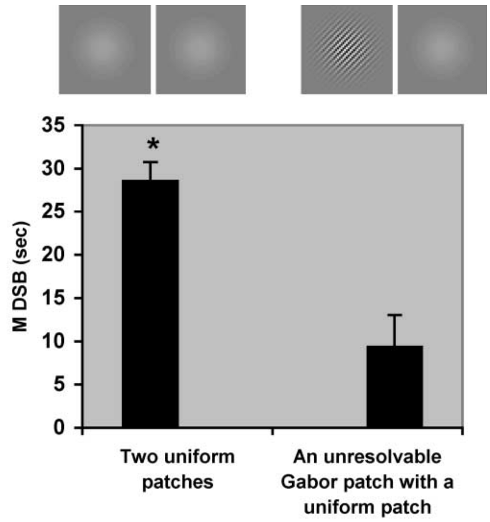

Figure 7. MIB Experiment with Two Control Conditions

Subjects could not distinguish an unresolvable Gabor patch from a uniform luminance patch; however, two physically uniform patches tended to disappear simultaneously but a physically uniform patch adjacent to a perceptually uniform one tended to disappear asynchronously. Error bars indicate one SEM.

information has no contribution to the MIB. To rule out this possibility, we showed, in a control experiment, that the indiscriminable orientation of a single unresolvable Gabor patch could affect the pattern of blindness during MIB. We repeated the MIB experiment with two other control conditions. In one of the control conditions, two adjacent physically uniform patches (i.e., simple luminance patches) were presented; in the other control condition, a physically uniform patch was presented adjacent to a perceptually uniform one (i.e., unresolvable Gabor patch). It was shown in a pilot experiment that observers were unable to distinguish the two patches from each other. The performance of subjects in discriminating two different pairs of patches (physically uniform pair and mixed pair) was at chance level (50% correct) ($p > 0.05$ in individual subjects using χ^2 test).

Results revealed that the mean duration of simultaneous blindness for the physically uniform pair was significantly longer than the mixed pair ($p < 0.05$ using two-tailed t test, $df = 10$). Figure 7 depicts the results of the control experiment. This experiment confirmed that the pattern of disappearance and reappearance of unresolvable Gabor patches was not purely luminance based.

The results of experiment 6 demonstrated that, in an unresolvable condition, orientation per se influenced the temporal pattern of disappearance in MIB, but “orientation context” (orientation-based grouping) failed to influence MIB.

Discussion

In a set of experiments, we used unresolvable high-frequency orientation patches to investigate different aspects of unconscious orientation processing. Various experimental paradigms were designed to show that orientation information of a single unresolvable patch penetrates the visual system and affects the neuronal processing at different levels.

Our findings in experiment 1 demonstrate that unresolvable Gabor patches are able to induce a robust orientation-selective adaptation in the peripheral visual field. Therefore, orientation-selective adaptation to unresolvable oriented items found in the central vision (He and MacLeod, 2001) occurs in the peripheral vision as well. As primary visual cortex is the first locus detecting orientation signals (Hubel and Wiesel, 1977), this experiment confirms that orientation information is registered in—at least—primary visual cortex, even when the orientation patches could not be perceptually resolved. This finding is consistent with previous studies implying that area V1 could be selectively activated by perceptually indiscriminable visual stimuli (Blake and Fox, 1974; He et al., 1996; He and MacLeod, 2001).

Experiment 2 shows another type of orientation adaptation with unresolvable patterns. According to this experiment, not only orientation signals of unresolvable Gabor patches are detected in the cortical level but also they have interactions with color information. Color-contingent orientation adaptation requires more complex computations than simple orientation adaptation and it seems that even such processes could take place without explicit conscious access to the orientation information. To generate color-contingent orientation adaptation, binding of color and orientation information of a single unresolvable pattern might be necessary. Our results confirm the idea that this form of interaction (binding of spatially superimposed feature pairs) could be performed in early visual areas without the necessary need for attentional and awareness-based mechanisms (Holcombe and Cavanagh, 2001).

The effect of orientation of resolvable and unresolvable stationary Gabor patches on perceptual direction preference of an ambiguous motion was shown in experiment 3. The fact that oriented lines can bias a bistable apparent motion to be perceived in a direction parallel to the lines' orientation had been explained by the possible activation of motion-selective neurons whose preferred direction is parallel to the lines' orientation (Francis and Kim, 1999). The effect of orientation information on the activity of motion-selective cells seems to occur in the higher cortical areas because encoding of long-range apparent motion direction generally originates from higher-level motion processing areas like area V5 (Kaneoke et al., 1997). Therefore, experiment 3 reveals a high-level perceptual priming mediating by orientation-based cues with either resolvable or unresolvable spatial patterns. These results are consistent with some evidence pointing out that spatial cueing and semantic/perceptual priming may exist without awareness (Luck et al., 1996; Blake et al., 1999; Kentridge et al., 1999). Equal magnitudes of priming effects of resolvable and unresolvable Gabor patches indicate that perceptually unresolved orientation signals registered in—at least—primary visual cortex are strong and equally effective as perceptually resolvable signals in high-level priming.

Experiment 4 shows that attentional or preattentive mechanisms are able to detect an unresolvable orientation patch among simple luminance patches while they are perceptually indistinguishable. Furthermore, this experiment provides evidence about effective orientation-dependent spatial cuing by an unperceived visual cue. We could conclude that attraction of attention to a visually salient location is possible even in the absence of perceptual saliency. This finding is contrary to evidence demonstrating that visually guided attention is neutralized when informative cues are unperceived due to presenting the cue to an eye during the suppression phase of binocular rivalry (Schall et al., 1993). This controversy can be explained by differences between the processing levels of the binocular rivalry paradigm and our task.

Experiment 5 also reveals that abrupt change in the orientation of an unresolvable Gabor patch is implicitly detected in the visual system. This processing could trigger a pop out mechanism and cancel motion-induced blindness. Results of experiments 4 and 5 support the idea that, at least in some situations, attentional mechanisms are sensitive to unconscious orientation processing.

In experiment 6, we investigated the disappearance pattern of two adjacent Gabor patches in a MIB paradigm in resolvable and unresolvable conditions. Previous studies had shown that perceptual disappearance induced in the MIB is not always "independent" for two adjacent orientation patches; indeed, the relative orientations of the two patches determine whether they disappear simultaneously or asynchronously. This fact is interpreted as a higher-level interaction (so-called rivalry or cooperation) between the two Gabor patches (Bonneh et al., 2001). Results of experiment 6 show that the disappearance patterns of unresolvable Gabors do not have any interaction with each other. This result is comparable to recent evidence reporting the absence of visual grouping effects during the suppression phases of binocular rivalry (Sobel and Blake, 2002). However, it has been shown that Gestalt grouping does occur during inattentional blindness (Moore and Egeth, 1997). Further investigations are needed to clarify differences between unawareness due to unresolvability and unawareness due to inattention.

The control condition of experiment 6 demonstrates positive correlation in the temporal patterns of disappearance of two simple luminance patches (the two physically uniform patches form a stronger gestalt). The same experiment shows that an unresolvable Gabor patch does have interaction with a simple luminance patch (they disappear and reappear asynchronously), while subjects are not able to distinguish between them. This result reveals that the difference between an unresolvable Gabor patch and a perceptually equivalent Gaussian blob is sufficient to affect the disappearance pattern during MIB, although the difference between a pair of unresolvable orthogonal Gabor patches is not.

How could we explain the overall results in experiment 6? Fourier transformation of a Gaussian luminance patch would have all orientation components equally and a low spatial frequency peak. The low spatial frequency Gaussian blob and the high spatial frequency Gabor are different in both orientation and spatial frequency contents. The parallel and orthogonal high spatial frequency Gabor patches are different in orientation but are identical in spatial frequency. In an unresolvable condition where two patches subjectively appeared identical, a difference in orientation alone (without a difference in spatial frequency) was not enough to reduce temporal correlation of disappearance in MIB, so discrimination of spatially separated items by orientation alone requires awareness, but discrimination of spatially separated items by both orientation and spatial frequency does not require awareness. In other words, the more difficult discrimination appears to require awareness, and therefore, in order for orientation-based grouping to influence MIB, orientation signals may need to be processed robustly enough to support their conscious perception.

Experimental Procedures

The stimuli were programmed on a Pentium III 800 MHz PC. Images were displayed on a γ corrected (calibrated) RGB color monitor, 800 H $\times$ 600 V pixel resolution, 85 Hz frame rate (795FT Plus, LG: Korea). The subjects were placed in a dark room, and their heads were comfortably fixed on a chin and forehead rest, and they viewed the displays binocularly. The distance between eyes and the screen was 45 cm.

Six naive subjects who were trained psychophysical observers with normal or corrected-to-normal vision participated voluntarily in all six experiments.

The Gabor functions were composed of a Gaussian envelope with 98.9% peak contrast (maximum contrast) and a standard deviation of 36 arcmin, with a cosine modulation of 24 arcmin wavelength (for Gabor patches with low spatial frequency) and 6 arcmin wavelength (for Gabor patches with high spatial frequency). The Gabor stimuli had either 45° or 135° orientation. The eccentricity of Gabor patches was 8.4° from the fixation point in all experiments except experiment 3, in which only Gabor patches located in the lower part of frames had such eccentricity. Luminance was 39 cd m^{-2} for the gray background.

Experiment 1

In the first experiment, each subject completed one block containing 50 trials. The adapting Gabor patch had high spatial frequency and was presented above the fixation point. The phase of Gabor patches was slowly changed by a smooth motion in the Gabor (speed of Gabor motion was 0.35°/s). This phase shift prevented the afterimage formation of long-lived adapting stimulus and lower-level adaptations. The test line was 1.43° in length and 0.05° in width, with an orientation either 45° or 135°. The contrast of test line was set to 2.4% for all subjects. Subjects responded for two tasks (adapting stimulus and test stimulus discrimination) using a two-alternative forced-choice (2-AFC) procedure.

Experiment 2

In the second experiment, each subject completed one block containing 66 trials. The number of trials for one subject (R.Z.) was 70. In the Gabor patches, white stripes were substituted with colored stripes (either green or red). The saturation of color in different points of colored stripes was calculated by the two-dimensional Gabor function. In other words, the Gabor function produced the value of color saturation for colored stripes in different distances from the center of Gabor patch. The central colored stripe in the Gabor patch had the maximum saturation in comparison with other stripes (the color of red in the central stripe: X, 61.8680; Y, 31.9006; Z, 2.9001; and the color of green in the central stripe: X, 31.1095; Y, 62.2189; Z, 10.3698). Red and green Gabor patches with these C.I.E. values were isoluminant in the Heterochromatic Flicker Photometry (Ives, 1912; Wagner and Boynton, 1972). Adapting Gabor patch had high spatial frequency and maximum contrast. The Gabor function of test stimulus was composed of a Gaussian envelope with 34.8% peak contrast and a standard deviation of 36 arcmin, with a cosine modulation of 9 arcmin wavelength (the contrast and spatial frequency of test stimulus were lower than those of adapting stimulus). Adapting Gabor patch had a slight phase shift like that in experiment one. Subjects reported the orientation of adapting and test stimuli in the 2-AFC condition.

Experiment 3

In the third experiment, each subject completed six blocks, each containing 50 trials. In the first block, bistable motion display was presented per se, and subjects were trained to see possible directions of the motion quartet and switch between perceived directions of motion. In frames A and C, dots were located on the opposite corners of an imaginary diamond. In frames B and D, stimulus patches (low-frequency Gabor patches, high-frequency Gabor patches, or luminance patches) were placed on four sides of the imaginary diamond. Uniform patches had the same size as the Gabor patches, and their luminance was decreased from the center to surround by a Gaussian function. The mean luminance of uniform patches was adjusted for each subject so that the perceptual appearance of uniform patches and unresolvable Gabor patches were maintained equal when the subjects looked at them in the periphery. The center-to-center distance between two dots in each frame (A or C) was 8.09°. The center-to-center distance between two stimulus patches in each frame (B or D) was 4.06°. Each black dot was $1.0° \times 1.0°$ in size. The frames were $10.08° \times 10.08°$ in size. The luminance of the monitor screen was a little lighter than the background luminance of gray frames so frames were isolated. Frames were located above the fixation point. Subjects reported the orientation of stimulus patches in the 2-AFC condition.

Experiment 4

In the fourth experiment, each subject completed four blocks. Each block contained 96 trials counterbalanced for the presence of an oddball item (high-frequency Gabor patch), the location of the oddball item, the presence of serial search target, and cueing condition (cue-valid, cue-invalid, and neutral). Different types of trials were presented randomly. In the other experiment of this section (detection of the unique item in the stimulus array), each subject completed six blocks of 60 trials. Sixteen items of the stimulus array were regularly spaced around an imaginary circle at the same eccentricity used in the previous experiments. The letter array of serial search task contained eight items (Ts or inverted Ts) with either blue or yellow hues. The blue T was isoluminated with the yellow T using Heterochromatic Flicker Photometry. Letter items were located on an imaginary circle at the same eccentricity as the items of the stimulus array. The distance between two letters in the array was 6.9°. Each letter was $2.0° \times 2.0°$ in size.

Experiment 5

In the fifth experiment, each subject completed one block containing 20 trials. Subjects completed the same number of trials for the control experiment. The global moving pattern consisted of 300 black square dots, $0.3° \times 0.3°$ in size, moving coherently in a random direction on an imaginary sphere (3D moving mask) with 18.77° in diameter. The background of the moving pattern was gray. A red cross-shaped fixation point was located on the bottom-right quadrant of the moving pattern near the center of imaginary sphere. One Gabor patch with either low or high spatial frequency was superimposed on the top-left quadrant of the moving pattern.

Experiment 6

In the sixth experiment, each subject completed one block containing 20 trials. Subjects completed the same number of trials for the control experiment. MIB display was identical in all respects to the MIB display of the previous experiment except that two adjacent Gabor patches were presented on the top-left quadrant of the moving pattern. The center-to-center distance between two patches was 2.29°, and they had the same eccentricity from the fixation point. Two Gabor patches could have either low or high spatial frequency.

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