Orientation-selective adaptation during motion-induced blindness

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Abstract. When a global moving pattern is superimposed on high-contrast stationary or slowly moving stimuli, the latter occasionally disappear for periods of several seconds (motion-induced blindness, MIB). Here, an adaptation paradigm was used to determine if orientation-selective adaptation still occurs for the stimulus that is no longer visible. Two slowly drifting high-contrast Gabor patches were presented to observers. As soon as both patches disappeared, one was eliminated from the screen. After 2 s, two low-contrast Gabor patches were presented as tests at the same locations and observers were asked to report their orientations. The observers’ performance was significantly higher when the orientation of the low-contrast test patch was orthogonal to the orientation of the high-contrast adapting patch (p < 0.0001) for the location where the patch was present during MIB, even though it was perceptually invisible. The observers’ performance was not significantly different at the adjacent control location where the stimulus was absent during the MIB. Although no stimulus was visible at either location, orientation-selective adaptation was preserved only for the location at which the patch remained present. Since orientation information is processed in low-level visual areas such as the primary visual cortex (VI), we conclude that MIB originates in an area higher than VI.

1 Introduction
Salient visual stimuli can be blocked from conscious perception under a number of special conditions such as spatial masking (Dehaene et al 2001), spatial crowding (Toet and Levi 1992), binocular rivalry (Logothetis 1998), attentional blink (Raymond et al 1992), repetition blindness (Kanwisher 1987), change blindness (Rensink et al 1997), inattentional blindness (Mack and Rock 1998), and, last, motion-induced blindness (MIB, Bonneh et al 2001).

MIB is observed under normal viewing conditions. When a global moving pattern is superimposed on high-contrast stationary or slowly moving stimuli, the latter disappear and reappear alternately for periods of several seconds. When two adjacent, collinear or parallel Gabor patches are presented, they disappear and reappear simultaneously, but when two orthogonal Gabor patches are presented their disappearances are independent (Bonneh et al 2001).

The properties of MIB do not seem to reflect sensory suppression or adaptation, as opposed to the Troxler fading. First, highly supraliminal targets with high luminance contrast disappeared more often than low-contrast targets. Therefore, MIB cannot be explained by a contrast-gain-control mechanism. Second, MIB does not always require prolonged presentation of the stimulus, and it sometimes occurs in a couple of seconds. Third, moving or dynamic targets may also disappear in MIB, producing the striking phenomenon of target dots that disappear in one quadrant and reappear in another after a few seconds. Such disappearance is unlikely to be explained by local adaptation or retinal stabilisation effects. Last, the effect does not depend on local masking, as targets continued to disappear even when surrounded by background-coloured circular ‘protection zones’ that occluded the moving mask (Bonneh et al 2001).
argued that the disappearance of stimuli during MIB might reflect the higher-level attentional selection or disruption of attentional processing (Bonneh et al 2001; Pettigrew and Funk 2001).

Visual adaptation has been used repeatedly for determining whether visual disappearance phenomena like binocular rivalry or spatial crowding occur in cortical areas higher than the primary visual cortex (V1) (Blake and Fox 1974; He et al 1996). Preservation of orientation-selective adaptation in either crowding or the suppression phase of binocular rivalry would suggest that these phenomena occur at a later stage than orientation processing in the visual stream (ie after V1).

We used an adapting paradigm to determine if an oriented stimulus that is perceptually invisible during MIB activates orientation-specific responses. If MIB originates after the level where orientation adaptation occurs, then it should not disrupt orientation-selective adaptation.

According to the adaptation paradigm, exposure to visual patterns of high-contrast Gabor patches creates adaptation of units tuned to the adapting orientation. Consequently, observers become temporarily insensitive to low-contrast test patterns of similar orientation (Blakemore and Campbell 1969). In our experiment, observers viewed two adjacent parallel Gabor patches superimposed on a ‘global moving pattern’ (figure 1). When the two patterns disappeared together, one of the Gabors was removed to serve as a control for the adaptation generated by the other. Nothing was visible at either location. If the disappearance lasted for 2 s, the display was blanked and two low-contrast test stimuli were presented, either aligned with or orthogonal to the adapting orientations. The location that had no stimulus present during the 2 s MIB interval served as a control for the location where the stimulus remained (but was invisible).

The 2 s MIB interval was short compared with the time required for adaptation. However, we found that it was long enough for any adaptation that had built up over the previous exposure to dissipate. In particular, we observed in a control experiment (as described later) that, even following a long period of adaptation to visible Gabor patches (in the absence of global moving pattern), a 2 s blank interval was sufficient for significant recovery from the orientation-specific adaptation. To be more specific then, in this test we examined whether the invisible Gabor maintains orientation-specific adaptation.

2 General methods

2.1 Participants

Five observers, 20–25 years old, with normal or corrected-to-normal vision, participated voluntarily in the experiments. All participants were trained psychophysical observers. They were, however, naïve with respect to the purpose of this experiment.

2.2 Apparatus

The stimuli and the psychophysical experiment were programmed in Delphi 5 on a Pentium III 800 MHz PC running Windows 98. Images were displayed on an RGB colour monitor, 800 (horizontal) × 600 (vertical) pixel resolution at 60 Hz frame rate (795FT Plus, LG: Korea). The observers were placed in a dark room and viewed displays binocularly while their heads were fixed in a chin-and-forehead rest. The viewing distance was 40 cm.

2.3 Stimuli

We designed the MIB paradigm using two adjacent parallel Gabor patches superimposed on a global moving pattern (see figure 1).

The global moving pattern consisted of 180 black square dots, each 0.3 deg × 0.3 deg in size, rotating in a random direction on an imaginary sphere, 15.4 deg in diameter. The background of the moving pattern was grey with a mean luminance of 32 cd m⁻².
A red crosshair fixation point was located in the bottom-right quadrant of the moving pattern. Adapting stimuli consisted of two parallel or coaxial Gabor patches superimposed on the top-left quarter of the sphere. The Gabor functions were composed of a Gaussian envelope with the standard deviation of 28 min of arc, with a cosine modulation of 28 min of arc wavelength \((2.12 \text{ cycles deg}^{-1})\). Both Gabor patches were oriented either 45° or 135° within a ‘protection-zone’ with diameter of 1.7 deg. The centre-to-centre distance between the adjacent patches was 3.2 deg and the eccentricity of each Gabor patch from the fixation point was 10.2°. The peak contrast of the adapting stimuli was 100%. To avoid local adaptation, the phase of each Gabor patch was slowly changed in a smooth motion over time \((0.35 \text{ s}^{-1})\). Test stimuli consisted of two Gabor patches with the same properties of adapting stimuli but with a peak contrast of 30%. They could be either parallel or orthogonal. In a pilot experiment we found that this contrast for test stimuli was optimal for achieving a significant difference between the ‘same-adapt Gabor patches’ (Gabor patches with the same orientation as the adapting Gabor patches) and ‘different-adapt Gabor patches’ (Gabor patches with a different orientation from the adapting Gabor patches).

3 Procedure
Each trial began with the presentation of the MIB display (see figure 1). Gabor patches superimposed on the moving sphere were parallel (and sometimes coaxial) so they had a robust tendency to disappear and reappear simultaneously (Bonneh et al 2001). Observers were asked to press and hold down a key on the keyboard when the Gabor patches disappeared simultaneously and release it when either of them reappeared.

As soon as the observers pressed the key, the Gabor patch on the right side was eliminated from the screen and replaced by a homogeneous grey background while the left Gabor patch remained physically present. Subjects could not detect the elimination, as both patches were already perceptually invisible because of the MIB. The Gabor patch on the right side served as a control stimulus. Observers kept reporting the disappearance and reappearance of Gabor patches until they achieved a 2 s MIB. Once the MIB lasted 2 s (ie the subject held down the key for 2 s), the global moving pattern and the remaining adapting Gabor patch were eliminated and, after a delay interval of 300 ms, the test stimuli were introduced.

The two test stimuli were presented for 500 ms. Each test Gabor patch was oriented either in the same or in the orthogonal orientation (with equal probability) with respect to the adapting orientation. Observers were asked to first report the orientation of the right test stimulus by pressing one of the two keys on the computer keyboard with

![Figure 1. Schematic diagram demonstrating the temporal succession of visual stimuli in a typical trial of MIB experiment. (a) The adaptation phase in the MIB condition consisted of two adjacent parallel/coaxial Gabor patches superimposed on the global moving pattern. (b) Delay period between adaptation and test phases (300 ms). (c) The test phase in which moving dots were removed and two test Gabor patches presented in the same locations of adapting stimuli for 500 ms. The orientation of each test Gabor patch could be the same or different with respect to the adapting orientation.](image-url)
their right hand, and then report the orientation of the left one with their left hand (two 2AFC tasks). No feedback was given to the observers about their performance. The next trial began 2 s after a blank intertrial interval.

Each subject performed 150 trials. The proportion of correct orientation discrimination was obtained for same-adapt Gabor patches and different-adapt Gabor patches separately. The mean time of adaptation period was calculated after pooling all data (ie the time elapsed for observers including the 2 s MIB).

As the control condition, each participant performed another adaptation experiment using the calculated mean adaptation time obtained from the previous experiment. In this experiment, adapting Gabor patches were presented on a grey background without any dots. This condition is a classic experiment of orientation-selective adaptation in the absence of a moving pattern. 2 s before the end of adaptation phase, the right-side Gabor patch was physically removed while the other patch remained. Observers again reported the orientations of test stimuli, just as in the previous experiment (see figure 2).

4 Results

The proportion of correct orientation discrimination in the test phase was compared between same-adapt and different-adapt conditions in the MIB and the control experiment. In the MIB experiment (after pooling all observers’ data), a two-way ANOVA revealed that the overall effect of adaptation (same-adapt versus different-adapt conditions, regardless of the presence of the stimulus during subjective MIB) was significant (figure 3a: $F_{1,1430} = 99.60, p < 0.001$). The effect of stimulus (physically invisible versus perceptually invisible) was also significant ($F_{1,1430} = 124.89, p < 0.001$), and there was a significant interaction between adaptation and stimulus existence ($F_{1,1430} = 65.27, p < 0.001$). A posteriori analysis with Scheffé’s test revealed significant difference between the proportion of correct same-adapt and different-adapt conditions of the perceptually invisible Gabor patches ($p < 0.0001$, figure 3a). In contrast, no significant difference was found between performances of same-adapt and different-adapt conditions of physically invisible Gabor patches ($p = 0.61$).
The duration of adaptation period in the MIB condition was $8 \pm 5.3$ s. With a two-way ANOVA (pooled data), the effect of adaptation was found to be significant ($F_{1,670} = 22.23$, $p < 0.001$) in the control experiment. The effect of stimulus presence in the last 2 s was also significant ($F_{1,670} = 19.87$, $p < 0.001$). There was a significant interaction between adaptation and stimulus presence ($F_{1,670} = 11.58$, $p < 0.001$). A posteriori analysis showed that the difference between performances of same-adapt stimuli and different-adapt stimuli was significant only for the stimulus that remained present during the last 2 s ($p < 0.0001$), whereas there was no significant difference for the stimulus that had been removed in the last 2 s ($p = 0.83$; figure 3b). The effect on adaptation for the perceptually invisible Gabor in the MIB condition was very much like the effect of the visible patch in the control experiment. There was also no significant difference in adaptation to the left-side or right-side patch in the control experiment when both patches remained present during the adaptation period ($p = 0.15$).

5 Discussion

We demonstrated a robust maintenance of orientation-selective adaptation, even when the adapting stimulus was perceptually invisible for 2 s as a result of MIB. In contrast, adaptation was weakened after 2 s during which the adapting stimulus was physically removed. This result showed that 2 s of delay time between adaptation and test phases was adequate for dissipating the adaptation even when the stimuli were presented for prolonged time during the adaptation phase. Such dissociation was also seen in the control experiment in which adapting stimuli were presented for a similar period.

Preservation of orientation-selective adaptation for the perceptually invisible Gabor patch during the MIB as well as for the remaining stimulus in the control experiment suggests that neurons responding to the stimulus orientation are still active during the disappearance phase of MIB.

The phase shift of Gabor patches during the adaptation period prevented afterimage formation of adapting orientation in the delay period between adaptation and test phases and this excludes the possibility of local adaptation in areas earlier than V1 (i.e. retina and LGN). V1 is the first site of orientation processing and is a plausible candidate for being the first site of orientation-selective adaptation of the oriented Gabor patches used in our study (Hubel and Wiesel 1977). Since orientation adaptation occurs at or after V1, we conclude that the activity in V1 is not affected by MIB.
Orientation-selective adaptation occurs even though observers do not have conscious access to the orientation information. This result is consistent with other findings suggesting that V1 activation alone does not necessarily determine conscious perception and V1 neurons can adapt even in the absence of awareness of the adapting stimuli (Blake and Fox 1974; He et al 1996; He and MacLeod 2001). However, disappearance from awareness might not necessarily be due to the suppression of the neuronal activity; it could be the result of decrease in synchronisation. If MIB is the result of reduced synchronisation in V1, then it might be possible to have adaptation when the disappearance happens. Even in this case, we have shown dissociation between the mere activity in V1 and the content of visual awareness. Further experiments are necessary to test if awareness may correspond to specific modes of cortical activity in V1 and other visual areas.

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