Adaptation-induced blindness to sluggish stimuli

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It is well known that prolonged observation of a dynamic visual pattern raises the contrast threshold for a subsequently presented static pattern. We found that if the post-adaptation test was presented gradually, so that its onset transient was weak, the test pattern was undetectable even at high contrast. Although the smooth-onset patterns were invisible, they caused apparent shifts in the orientation and contrast of neighboring stimuli, indicating the implicit processing of the target features. However, this strong aftereffect was not obtained if the target grating drifted rapidly or was onset abruptly. These results suggest that when human observers become less sensitive to transients in stimuli due to dynamic adaptation, they cannot consciously perceive sluggish stimuli containing weak transients. This is consistent with the notion that the visual system cannot prompt a conscious awareness of a single stimulus unless triggered by enough transient or temporally salient signals.

Keywords: vision, consciousness, adaptation, threshold, illusion

Introduction

The visibility of a stimulus is believed to depend on the activity of neural sensors in the retina and the early visual cortex. The contrast detection threshold, or contrast sensitivity, has long been considered a basic behavioral measure of the function or dysfunction of these sensors. However, recent findings in psychophysics and brain imaging show that the activity of early visual channels is insufficient for the conscious perception of the target. For example, the early visual system can process the orientation and color of a grating pattern even if its spatiotemporal frequency is too high for observers to detect. (Fang & He, 2005; He & MacLeod, 2001; Jiang, Zhou, & He, 2007).

It is well known that the prolonged observation of a high-contrast stimulus raises the contrast threshold for subsequently presented stimuli (Blakemore & Campbell, 1969). Figure 1a shows a typical procedure to demonstrate the aftereffect. Following adaptation to a drifting grating pattern and a brief pause, a test grating is abruptly presented. If the adaptation is sufficiently deep, the contrast threshold for the test grating is elevated 2–10 times compared with that of the pre-adaptation state. This post-adaptation threshold elevation is thought to reflect the reduction in the gain of early visual units, such as simple cells and complex cells in V1 (Movshon & Lennie, 1979; Ohzawa, Sclar, & Freeman, 1982). On the basis of this explanation, contrast adaptation has long been used as a standard psychophysical tool for analyzing the nature of early visual channels in humans (Blakemore & Campbell, 1969; Ross & Speed, 1991).

Using the slightly modified display shown in Figure 1b, we found that the post-adaptation test grating often becomes undetectable even at high contrast when it is gradually presented outside the fovea (Motoyoshi & Hayakawa, 2008a, 2008b). A few previous adaptation studies have also used non-abrupt test gratings, but did not obtain a very strong aftereffect (Blakemore & Campbell, 1969; Stromeyer, Klein, Dawson, & Spillmann, 1982).

The present study shows that this extremely profound aftereffect occurs only when a test grating with a low temporal frequency is presented gradually following adaptation to gratings with high temporal frequencies (Experiment 1). More importantly, we show that the test grating, made invisible by adaptation, strongly affects the apparent orientation and contrast of the neighboring visible patterns (tilt illusion and surround contrast suppression; Experiment 2), indicating the neural activity with respect to the invisible target. Thus, when human observers become less sensitive to transients in stimuli due to dynamic adaptation, they cannot consciously perceive sluggish stimuli with weak transients. This adaptation-induced blindness cannot be solely explained in terms of sensory gain control or perceptual
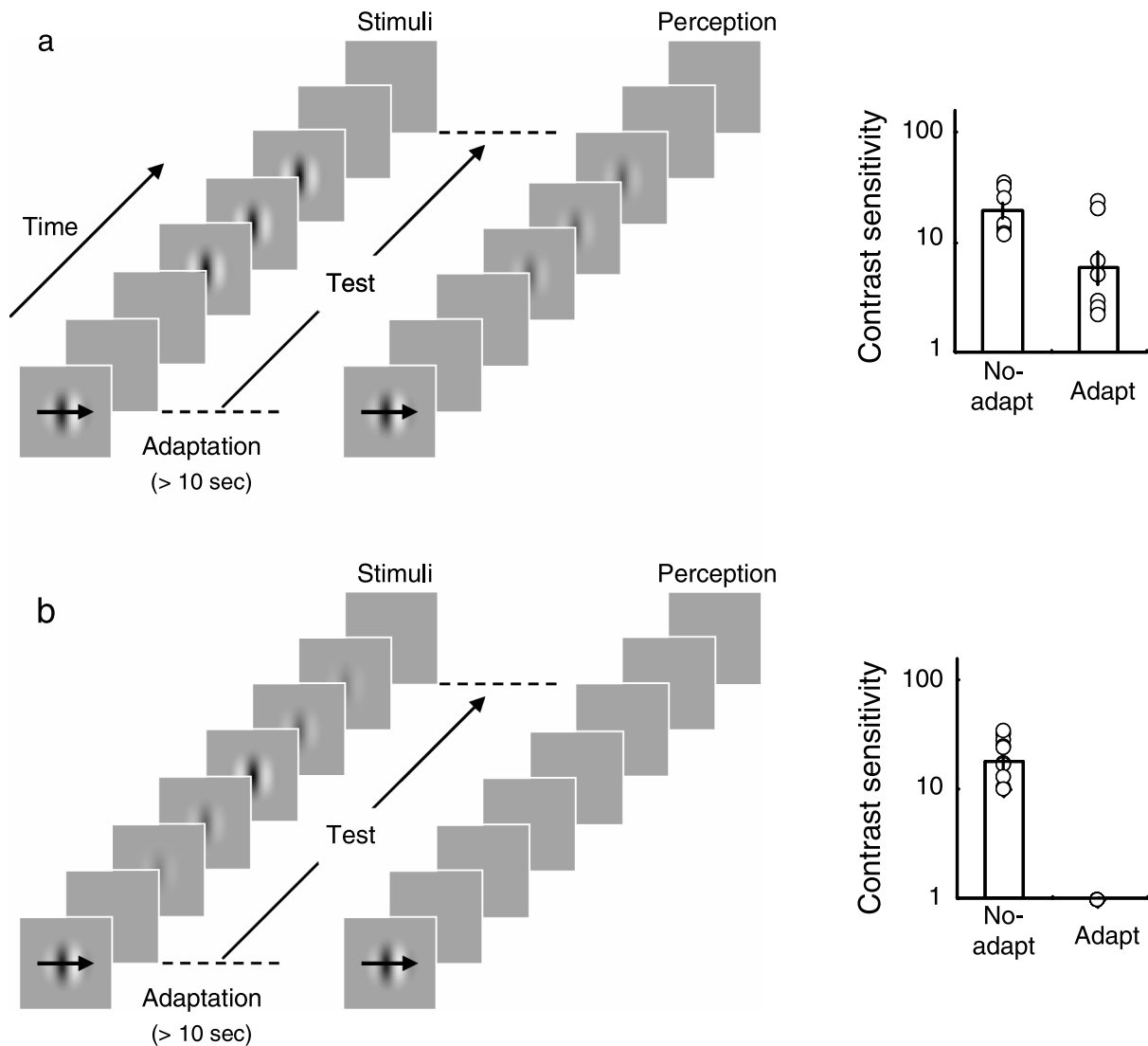
Figure 1. (a) After adaptation to a drifting grating, the subjects were abruptly presented with a static test grating. The contrast sensitivity after adaptation is lower than prior to adaptation. (b) If the test grating is presented within a gradual temporal window, it becomes undetectable even at full contrast, and the sensitivity is too low to measure. In both (a) and (b), the right panel shows the results. Open circles are the data collected from individual observers and the bar shows the averaged data for all subjects. Error bars are ±1 *SE*.

rivalry or masking. The results lead us to a notion that the visual system can only prompt the phenomenal awareness of a visual stimulus when triggered by transient signals.

Experiment 1

We first examined the aftereffects by measuring the pre- and post-adaptation contrast thresholds under several stimulus conditions.

Methods
Apparatus and stimuli

Visual stimuli were presented on a CRT (Sony GDMF520, 160 Hz, 14 bit) controlled by a graphics card (CRS ViSage). The adapting stimulus was a vertical sinusoidal grating pattern drawn within a circular patch. This circular grating had a diameter of 2.0 deg and the edge was blurred by a cosine with a wavelength of 1.4 deg. The grating had a spatial frequency of 1.5 c/deg, and drifted at a temporal frequency of 8.0 or 0.5 Hz. The test grating was the same circular grating, but was either static or drifted at various temporal frequencies.

Procedure

During adaptation, eight drifting gratings were presented on a uniform background of 72 cd/m². The gratings were evenly spaced on a virtual circle with a radius of 5.9 deg. The subjects fixated on a small black dot in the center of this display. On each trial, after the initial 2 min adaptation, the re-adapting gratings were shown for 10 sec,

and the test grating was presented at one of the eight possible locations during a period of 2 sec. In one case during this period, the test grating was presented within a Gaussian temporal window that peaked at 1 sec after the adaptor offset with a standard deviation of 200 ms (gradual). In the other case, the test grating was presented within a rectangular waveform from 0.85 to 1.15 sec after the adaptor offset with a duration of 300 ms (abrupt). The subjects indicated the location of the grating by pressing a button. We adopted this eight-alternative forced choice task because it is relatively independent from the observer's response criterion (Lau, 2008) and because it achieves efficient data collection. The contrast of the test grating was varied in accordance with the staircase (one-up and one-down, 0.1 log unit step) randomly interleaved for each condition. The contrast thresholds, determined by a proportion of 56.3 % correct responses, were estimated by means of the maximum likelihood method, based on at least 120 trials (30 trials for the full-contrast test). The threshold was defined as immeasurable, and the test was regarded as invisible, if the proportion of correct responses did not reach 56.3% at full contrast (>0.99) or if the maximum-likelihood estimation of the threshold exceeded 1.0. We used these criteria even when the proportion of correct responses was higher than the chance level (12.5%). We employed a bootstrap estimate of the standard error.

Observers

In total, eleven naives and one of the authors (IM) served as subjects. All had normal or corrected-to-normal vision. All experiments were conducted with completed consent forms and permission from the NTT CS Labs Ethical Committee (2007, 2008).

Results

The results are shown in Figure 1. The contrast sensitivity (1/threshold) for the abrupt test grating was reduced by adaptation, but was still measurable (Figure 1a). On the other hand, the sensitivity for the gradual test grating became too low to measure after adaptation (Figure 1b). The proportion of correct responses for the full-contrast test grating was on average 34.0%. The subjects typically reported that they saw nothing but a uniform background, even if the test grating was presented at full contrast.

Using drifting test gratings, we also examined the contrast sensitivity for the gradually presented test grating as a function of its temporal frequency, both before and after adaptation. The results are shown in Figure 2. The test grating with a low temporal frequency (<~0.5 Hz) became undetectable after adaptation to drifting gratings with high (8 Hz, black circles), but not low (0.5 Hz, gray squares), temporal frequencies.

We additionally checked to determine whether the post-adaptation test grating was undetectable even if the subjects knew its location and paid attention to it. We presented a small dot (0.2 deg in diameter) at the location where the test grating would appear 4 sec prior to its presentation. The cue duration of 4 sec was long enough for subjects to allocate their attention to the test location (Carrasco, Penpeci-Talgar, & Eckstein, 2000). The subjects were asked to indicate if they saw the test grating (yes/no task). The results showed that after adaptation to 8 Hz gratings, the subjects rarely perceived the gradual test grating (8% average across three subjects) even when cued to the correct location.

Experiment 2

Threshold elevation following adaptation is usually ascribed to the gain reduction of neural sensors in the early visual cortex (Movshon & Lennie, 1979; Ohzawa et al., 1982). According to this theory, the present aftereffect
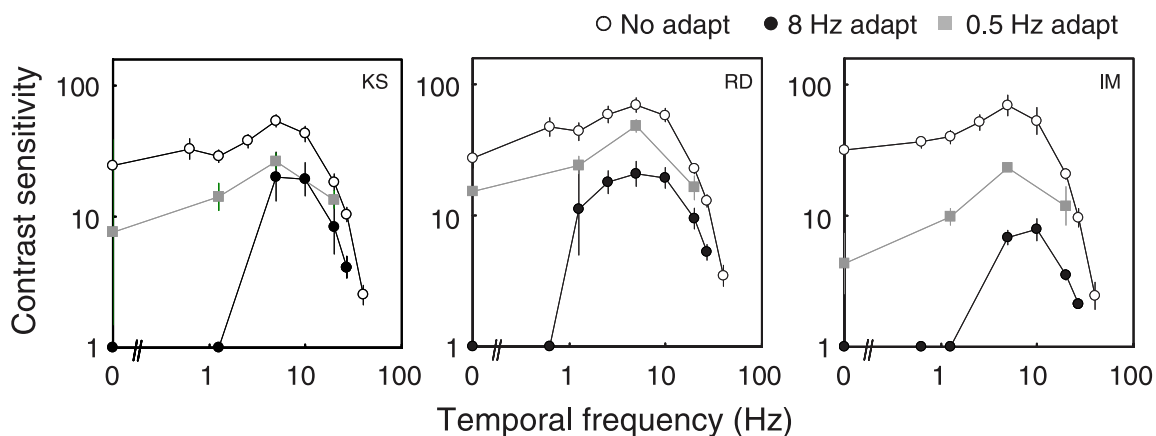

Figure 2. Contrast sensitivity functions for gradual test gratings drifting at various temporal frequencies, before and after adaptation to 8 Hz (black circles), and 0.5 Hz (gray squares). Error bars are ±1 *SE*.

should indicate the absence, or sub-threshold responses, of those sensors. We tested this notion using two spatial-induction effects, in which the apparent orientation (tilt illusion) (Blakemore & Tobin, 1972; Wenderoth & Johnstone, 1988) and contrast (contrast suppression) (Chubb, Sperling, & Solomon, 1989) of a stimulus is altered by surrounding stimuli (see Figures 3a and 3c). These effects are believed to be based on interactions between functional units in the early visual cortex (Blakemore & Tobin, 1972; Gilbert & Wiesel, 1990; Zipser, Lamme, & Schiller, 1996), and should not be present if such units fail to respond due to adaptation.

Methods

Tilt illusion

The adapting stimulus was an annular patch of vertical grating with a spatial frequency of 1 c/deg, which drifted at a temporal frequency of 10 Hz. The annulus had an inner diameter of 3.0 deg and an outer diameter of 7.1 deg; both the inner and outer edges were blurred. A single adapting grating was centered at 5.9 deg above the fixation dot on a background of 36 cd/m^2. During each trial, after an initial adaptation of 1 min, the adapting grating was shown for 12 sec, followed by the test stimulus, which was gradually presented within a Gaussian window ($SD = 200$ ms). The test stimulus was a small vertical grating (2.2 deg diameter) surrounded by the annular grating that tilted at ± 12 deg (chosen randomly). The subjects were asked to indicate if the central grating appeared to be tilted clockwise or counter-clockwise, and whether they could see the surrounding grating. The tilt illusion was defined as occurring when the subjects judged the central grating to be tilted contrarily to the surrounding grating. Data were collected for surrounding gratings with various levels of contrast. The occurrence of the tilt illusion in the post-adaptation condition was calculated only from trials in which the surround was not seen. The subjects were three naives and one of the authors (IM).

Contrast suppression

The adapting stimulus was an annular patch of vertical grating with a spatial frequency of 1.5 c/deg, which drifted at a temporal frequency of 10 Hz. The annulus had an inner diameter of 2.2 deg and an outer diameter of 3.9 deg; both the inner and outer edges were blurred. Two adapting
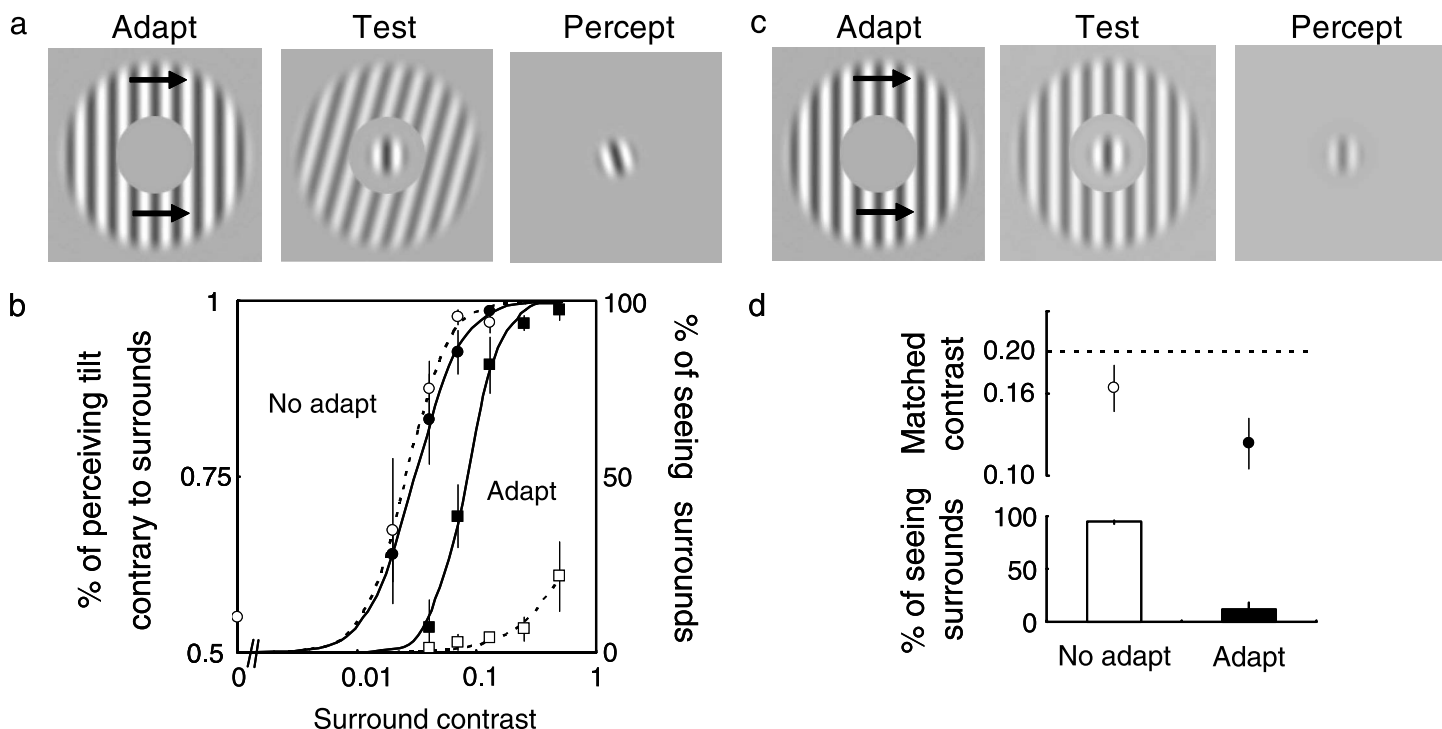

Figure 3. (a) After adaptation to an annular drifting grating (left), a vertical grating surrounded by a slightly tilted annular grating is gradually presented (middle). The central grating often appears to be tilted away from the invisible surrounding grating (right). (b) The occurrence of the tilt illusion (solid symbol) and the probability of seeing the surrounding grating (open symbol) as a function of the surrounding contrast before (circle) and after (square) adaptation. Error bars are ± 1 *SE* across subjects. (c) After adaptation to an annular grating (left), center–surround gratings are gradually presented (middle). The contrast of the central grating appears lower than it actually is with invisible surrounds (right). (d) The upper panel shows the matched contrast of the central grating before (open circles) and after (solid circles) adaptation. The lower panel shows the probability of seeing the surrounding grating. Error bars are ± 1 *SE* across subjects.

gratings were centered at 6.7 deg to the left and right of the fixation dot. In each trial, after an initial adaptation of 1 min, the adapting gratings were shown for 12 sec, followed by the two stimuli, which were gradually presented within a Gaussian window (SD = 200 ms). One (test grating) was a small vertical grating (1.7 deg diameter) with a low contrast (0.2) surrounded by an annular grating with a high contrast (0.4). The other (reference grating) was a central grating with a variable contrast. The locations of the two gratings were randomly switched. The subjects indicated which central grating appeared to have a higher contrast, and whether they could see the surrounding grating. The contrast of the reference grating was varied in accordance with the staircase procedure (one-up and one-down, 0.1 log unit step). The matched contrast was defined as the reference contrast that gives 50% in the logistic curve fitted to the psychometric function. The standard error was estimated by means of a bootstrap method. The matched contrast in the post-adaptation condition was estimated only from trials in which the surround was not seen. The subjects were two naives and one of the authors (IM).

Results

We found that the surrounding grating, which was rendered invisible by adaptation, produced spatial induction effects. As illustrated in Figures 3a and 3c (right images), the subjects often only saw the central grating, which appeared to be tilted or to have lower contrast without perceivable surrounds.

Figure 3b shows the occurrence of the tilt illusion and the probability of seeing the surrounding grating as a function of its contrast. In the pre-adaptation condition (circles), the tilt illusion occurs as the surrounding gratings become visible with increasing contrast. In the post-adaptation condition (squares), on the other hand, the tilt illusion clearly occurs even when the surrounding gratings are virtually invisible owing to adaptation. It should be noted that the results indicate a modest gain reduction of neural units following adaptation, as can be seen in the shift in the psychometric function of the tilt illusion in the post-adaptation condition (filled red circles) relative to the pre-adaptation condition (filled black circles). However, the robust occurrence of the tilt illusion indicates the activity of orientation-selective units.

Figure 3d shows the matched contrast of the central grating before and after adaptation (upper panel), and the probability of seeing the surrounding grating (lower panel). The matched contrast of the central grating tends to be perceived as being lower than the actual contrast (0.2, denoted by a dashed line), particularly when the surrounding grating is invisible due to adaptation (p = 0.09 for the pre-adaptation, and p = 0.01 for the post-adaptation, t-test).

Curiously, the matched contrast appears to become even lower after adaptation. In other words, the apparent contrast is more profoundly suppressed by invisible surrounds than by visible surrounds, although the difference was not significant ($p > 0.05$). The reason for this paradoxical induction enhancement is unclear. One intriguing possibility is that the central grating, surrounded by a visible grating with a blurry gap of only 0.8 deg, appears to be crowded when viewed peripherally, and involves assimilation (or filling-in) in addition to the contrast effects, whereas the contrast effects are dominant when the surrounds are invisible. This effect may be further investigated with more appropriate stimuli (e.g., texture) and with a larger number of subjects.

Discussions

The present study shows that after adaptation to dynamic stimuli, sluggish test stimuli are invisible to normal human observers, but continue to affect the apparent orientation and contrast of neighboring stimuli. The results demonstrate that adaptation can totally suppress the conscious perception of a stimulus while retaining the implicit visual processing of low-level features.

It is difficult to ascribe this aftereffect directly to the gain reduction of early visual channels. According to the physiological evidence, it is likely that our adapting stimuli have reduced the gain of the cortical neurons to some degree (Movshon & Lennie, 1979; Ohzawa et al., 1982). However, the evidence of implicit spatial inductions suggests that those units are not completely suppressed by adaptation. Thus, while the low-level mechanisms detected the gradual test stimulus, their outputs did not directly contribute to the perceptual awareness of the stimulus.

It also seems difficult to explain the results solely in terms of inattention to the test stimulus. First, our subjects reported that they clearly perceived the 'absence' of the post-adaptation test during the aftereffect. Second, this was true even if the subjects knew the target's location and paid attention. Third, we also confirmed in a separate experiment that removal of attention by a central letter recognition task, without adaptation, reduced the contrast sensitivity for gradual gratings only by ~0.3 log unit (Motoyoshi, in preparation). This sensitivity reduction is larger than previously reported data for flashed gratings (0.1–0.2 log unit) (Carrasco et al., 2000), but is too weak to account for the sensitivity reduction by adaptation.

The present aftereffect appears to be more closely related to illusory effects such as masking and rivalry, in which a supra-threshold visual target is rendered invisible (Blake & Logothetis, 2002; Breitmeyer & Ogmen, 2006; Kim & Blake, 2005). It is known that a salient target can

be perceptually suppressed when presented with another salient stimulus; e.g., binocular rivalry (Blake, 1989), flash suppression (Tsuchiya & Koch, 2005; Wilke, Logothetis, & Leopold, 2003; Wolfe, 1984), motion/ flicker-induced blindness (Bonneh, Cooperman, & Sagi, 2001; Caetta, Gorea, & Bonneh, 2007; Kawabe & Miura, 2007), transient masking (Breitmeyer & Ogmen, 2006). Similar to our aftereffect, these phenomena provide evidence for the implicit visual processing of invisible targets and corresponding neural activity (Blake & Fox, 1974; Clifford & Harris, 2005; Logothetis & Schall, 1989; Macknik & Martinez-Conde, 2004; Mitroff & Scholl, 2005; Montaser-Kouhsari, Moradi, Zandvakili, & Esteky, 2004; Rajimehr, 2004). The phenomena are often thought to originate from competition or mutual inhibition between high-level neural representations of the target and the masker (Leopold & Logothetis, 1999). However, we cannot directly apply neural competition to explain the present results in which the target became invisible without any competing stimuli.

It has also been reported that a target can disappear on a uniform visual field; e.g., stabilized retinal image (Ditchburn & Ginsborg, 1952) and Troxler fading (but only for faint or isoluminant targets) (Troxler, 1804). These phenomena are always ascribed to the desensitization of low-level visual sensors owing to adaptation (Martinez-Conde, Macknik, & Hubel, 2004; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). However, as noted earlier, the present aftereffect cannot be directly attributed to sensory gain control.

Why does adaptation block stimuli from awareness, but not from subliminal detection? Our main finding is that when the observers become less sensitive to transients in stimuli due to dynamic adaptation, they cannot consciously perceive less transient stimuli. This leads us to the notion that a visual stimulus, even if it activates low-level neural units, does not reach awareness unless triggered by transient, or temporally salient, signals. There may be a visual mechanism that gates neural signals and allows them to enter consciousness only when triggered by temporally salient signals. In normal viewing, transient signals are constantly produced by (micro-)saccadic eye movements even during fixation (Martinez-Conde et al., 2004). However, if adaptation to dynamic stimuli reduces the gain of low-level sensors for transients, sluggish stimuli may not produce transient signals that are strong enough to prompt the awareness.

The above idea is consistent with a common property of various invisibility phenomena. For all of the aforementioned illusions, it is well known that the target becomes less visible when it is more static or dominated by more dynamic stimuli (the opposite never happens). For example, transient masking and motion-induced blindness depend by definition on the presence of flashing or moving masks, and are more profound for stationary targets (Bonneh et al., 2001; Breitmeyer & Rudd, 1981; Kanai & Kamitani, 2003). Dynamic stimuli greatly increase the

inter-ocular suppression during binocular rivalry (Tsuchiya & Koch, 2005; Wilke et al., 2003; Wolfe, 1984). Transient retinal image displacements caused by microsaccades prevent Troxler fading (Martinez-Conde et al., 2006) and motion-induced blindness (Hsieh & Tse, 2009), and even facilitate perceptual alternation during binocular rivalry (van Dam & van Ee, 2006). All of these findings support the notion that the target's invisibility is partially a result of losing transient-trigger signals.

Recent psychophysical evidence suggests that temporal saliency plays a critical role for segregating an object or an event in time (Cavanagh, Holcombe, & Chou, 2008; Kanai & Kamitani, 2003; Motoyoshi, 2007; Nishida & Johnston, 2002). The present aftereffect may also be interpreted from this viewpoint. It is possible that our gradual target, following adaptation, becomes invisible because it does not produce a salience signal sufficient for the temporal segmentation of the target from the preceding uniform background.

The neural basis of the present aftereffect is unknown, but several physiological findings allow us to consider possible candidates. It is known that damage to the parietal cortex often causes 'extinction', namely the spontaneous fading of stimuli in a damaged visual field (Luria, 1959). Similar to our illusion, extinction occurs for stimuli even with a uniform background, and involves implicit processing of the unperceived stimuli (Mattingley, Davis, & Driver, 1997; Rees et al., 2000). More recent studies show that a TMS pulse on the parietal area causes visual targets to disappear in a manner that mimics extinction (Pascual-Leone et al., 1994). It is suggested that the parietal lobe is responsible for the processing of transient information and the temporal localization of dynamic stimuli ('when' pathway; Battelli, Pascual-Leone, & Cavanagh, 2007). These findings imply that the parietal lobe plays an important role in the present illusion. Other physiological studies also suggest that feedback neural activity plays a significant role in visual awareness (Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000). The parietal structure may control this feedback loop on the basis of temporal salience. It should be noted, however, that early cortical signals, such as those causing the spatial induction effect, should not necessarily be the source of neural signals correlated with the conscious perception of a stimulus. There is even a possibility that feature analysis and awareness are mediated by independent processes.

The present findings, together with recent evidence of cortical responses to stimuli beyond the observers' spatio-temporal resolution (Fang & He, 2005; He & MacLeod, 2001; Jiang et al., 2007), cast a doubt on the classical view that behavioral contrast sensitivity is determined solely by the activity of early visual channels (such as those responsible for the spatial induction effects). Even simple detection in the absence of external noise can be severely limited by later cortical processes.

Acknowledgments

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