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Time-locked Perceptual Fading Induced by Visual Transients

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Abstract

■ After prolonged fixation, a stationary object placed in the peripheral visual field fades and disappears from our visual awareness, especially at low luminance contrast (the Troxler effect). Here, we report that similar fading can be triggered by visual transients, such as additional visual stimuli flashed near the object, apparent motion, or a brief removal of the object itself (blinking). The fading occurs even without prolonged adaptation and is time-locked to the presentation of the visual transients. Experiments show that the effect of a flashed object decreased monotonically as a function of the distance from the target object. Consistent with this result, when apparent motion, consisting of a sequence of flashes was presented between stationary disks, these target disks perceptually disappeared as if erased by the moving object. Blinking the target disk, instead of flashing an additional visual object, turned out to be sufficient to induce the fading. The effect of blinking peaked around a blink duration of 80 msec. Our findings reveal a unique mechanism that controls the visibility of visual objects in a spatially selective and time-locked manner in response to transient visual inputs. Possible mechanisms underlying this phenomenon will be discussed. ■

INTRODUCTION

The visibility of visual objects is not simply a function of stimulus intensity or contrast. It also depends on internal states of the visual system, including adaptation levels of local feature detectors as well as high-level cognitive states, such as attention. Perceptual fading induced by prolonged fixation is one of the remarkable perceptual phenomena where the visibility of a visual object is drastically altered by changes in internal states of the visual system. When an observer maintains fixation while attempting to view a stationary object in the periphery, this peripheral object becomes fainter and disappears from awareness (Troxler, 1804). This phenomenon, known as the Troxler effect, is especially striking at low luminance contrast (Livingstone & Hubel, 1987).

The Troxler effect is commonly assumed to result from sensory adaptation of edge detectors (Ramachandran & Gregory, 1991; Krauskopf, 1963). The sensory adaptation procedure generally consists of two separable periods, namely, an adaptation period and a test period. In the Troxler effect, there is an adaptation period of a certain duration, followed by a test period in which the target disappears as a consequence of adaptation. Since slight eye movements after the fading can make the whole area of the target reappear, the Troxler effect is generally explained in terms of adaptation to an edge, as opposed to adaptation to a surface, followed by a filling-in of the background visual attributes across the attenuated edge.

Here, we report a new type of fading effect that is induced by presentation of a flash, without prolonged adaptation. The basic effect we discovered is illustrated in Figure 1. A stationary red disk (illustrated as dark gray) was presented on a near-isoluminant green background as in stimuli commonly used to induce the Troxler effect. A few seconds after the onset of the red disk, thus without sufficient adaptation to induce the Troxler fading, a white ring was flashed around the disk for 40 msec. Although the disk was physically present all the time, it was perceived to disappear when the flash was presented and stayed invisible for several seconds. This fading effect does not require a strict isoluminant background, but occurs even when the target disk is defined by a relatively high-contrast, achromatic edge as well. To obtain maximal and drastic fading effects, however, we used a near-isoluminant background of a different chromaticity in this study.

A notable characteristic of this fading effect is that the timing of fading is perfectly controlled. In studies of the Troxler effect, the fading time, the time required for the initiation of the perceptual fading from stimulus onset, is often used as an estimate of likeliness that the fading occurs in a given stimulus condition (Sakaguchi, 2001; Lou, 1999; De Weerd, Desimone, & Ungerleider, 1998; Clarke, 1961). The fading time is known to be typically long and its variability across trials to be large.

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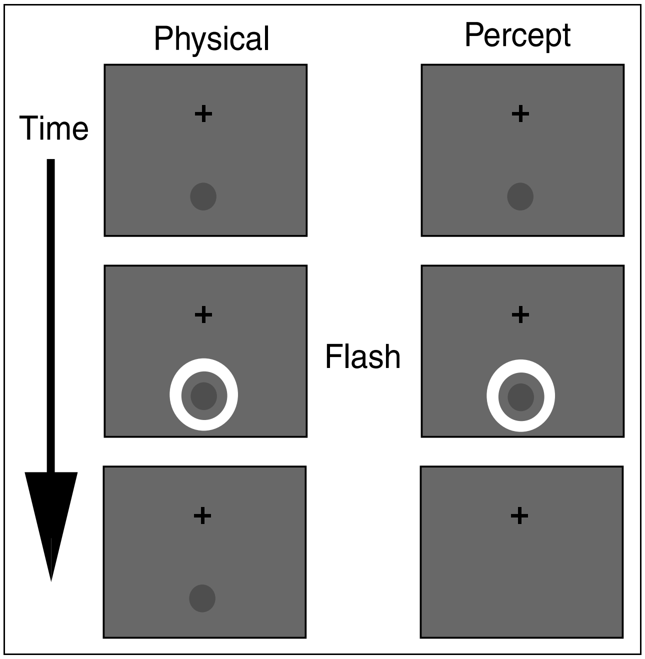

Figure 1. Perceptual fading induced by a flash. The left column illustrates the flash stimulus used to induce the perceptual fading. A red disk (illustrated as dark gray) was presented on the near-isoluminant green background (illustrated as light gray). After a short fixation on the cross, a white ring surrounding the red disk was flashed. The red disk was physically present throughout the observation. The right column shows a typical percept of this stimulus. The red disk perceptually disappeared when the flash was presented.

Thus, the fading time in the Troxler effect is not readily predictable. On the other hand, the fading induced by a flash is time-locked to the flash, and thus allows more flexible experimental designs to study perceptual fading and filling-in phenomena by triggering a fading at an experimenter's desired timing.

More importantly, the fading induced by a flash provides insights into the mechanisms that mediate our conscious visual perception. Although the fading is driven by a brief visual stimulus, the invisible period lasts substantially longer than the duration of the flash. Therefore, the fading seems to reflect not just interactions between concurrent visual inputs, but a sustained change in internal states of the visual system. Furthermore, since the spatial overlap between the edges of the flash and the target disk does not seem essential, it is unlikely that the fading is induced by the same mechanism as the Troxler effect, which is thought to involve adaptation of edge detectors.

In this article, we present data demonstrating that a flashed object can induce the fading of a low-contrast target in a well-controlled manner both in space and time. It is also shown that even a brief removal of the object itself (blinking) leads to the fading: Thus, transient sensation, not the presentation of an additional object, is essential to induce the fading. We discuss possible mechanisms underlying this phenomenon, as well as the relation to other fading phenomena.

RESULTS

We first measured the frequency of fading as a function of the distance between the flashed stimulus and the target. The dependency on the spatial distance is informative in identifying the level of processing involved in the fading effect, since high- and low-level processes are generally characterized by global and local interactions, respectively. If high-level processes are involved, the fading would occur rather irrespective of the distance, while if low-level processes are involved, it would occur only at short distances. In addition, a different type of distance dependence may be predicted by an account based on spatial attention: If the fading is caused by diverting attention from the target to the flash, the fading would be observed even more frequently when the distance is large.

We used stimuli illustrated in Figure 2A. The target red disk (1.06° in diameter) was presented on a near-isoluminant green background at one of eight directions at an eccentricity of 10.6°. Subsequent to 1500 msec of fixation, a white disk of the same size was flashed for 40 msec at the same eccentricity in a variable direction relative to the target disk (θ, in Figure 2A). After the presentation of the flash, the target disk remained for another 1500 msec. The strength of the effect in triggering the fading was quantified as the percentage of the trials in which the observers reported that fading occurred at the timing of the flash. In a control experiment where no flash disk was presented, subjects were asked to report whether they experienced a fading at any time during the viewing time (3000 msec). In addition, to control for a potential shift in response bias depending on the distance between the target and the flash, a separate session was conducted in which the target disk was physically removed at the onset of the flash.

Figure 2B and 2C shows the results averaged over different target positions. In all four subjects, the frequency of perceptual fading monotonically decreased as the spatial separation between the flash and the target increased (Figure 2C; Spearman rank-order correlation coefficient $R = -.898, p < .001$). The results of the control condition show that a fading rarely occurred within 3000 msec of fixation alone. The frequency of fading was 1.7%, 6.7%, 23.3%, and 3.3% for the subjects CP, MR, RK, and WH, respectively (dashed lines in Figure 2C). The mean frequency of fading across the subjects was 8.8% (dashed line in Figure 2B). In the trials where the target disk was physically removed at the onset of the flash, the subjects rarely failed to detect the physical fading (2.3%), and the detection ratio did not depend on the target-flash distance. Thus, the decrease in the frequency of the perceptual fading as a function of the target-flash distance is not simply due to response bias

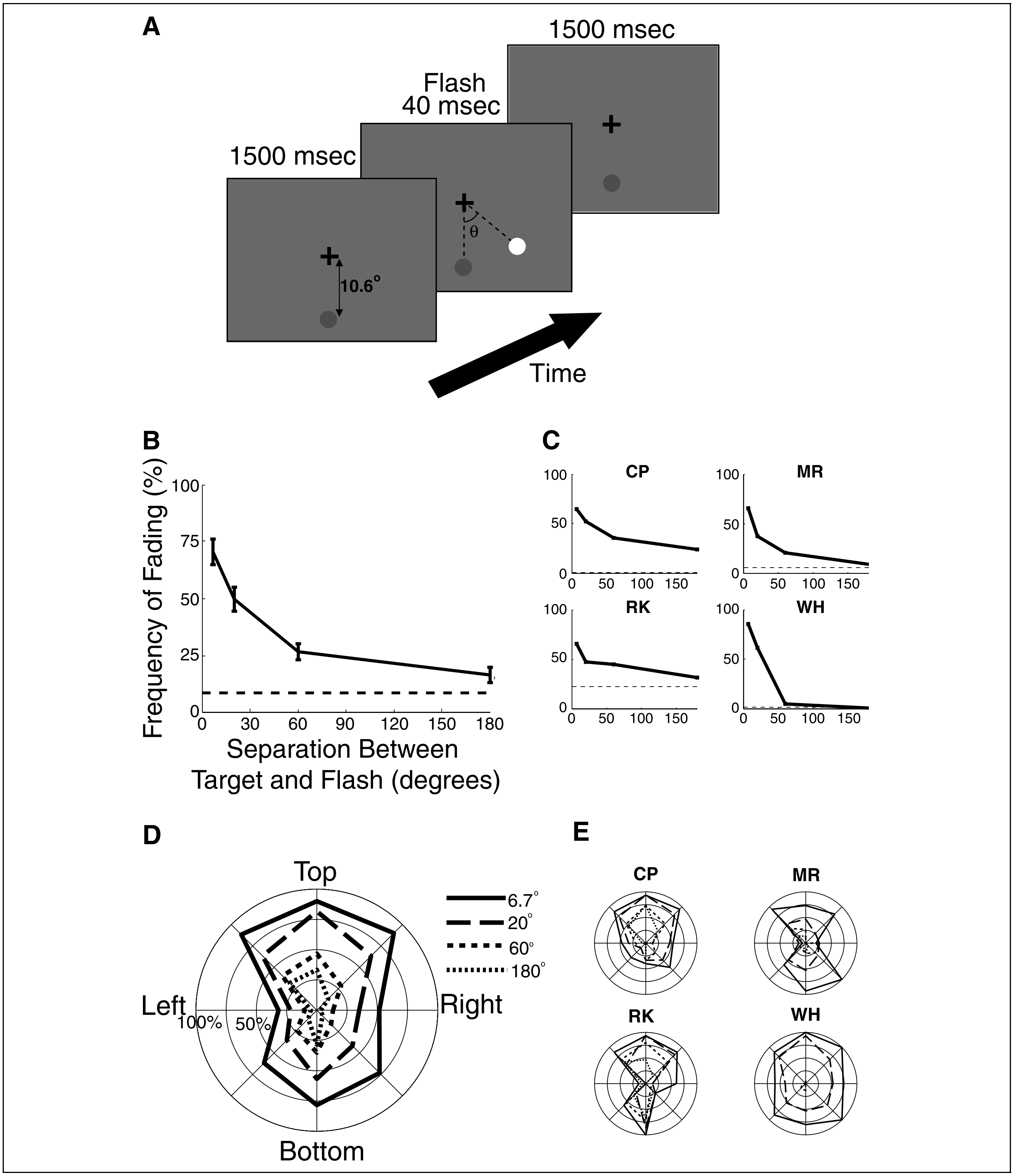

Figure 2. Flash-induced fading experiment. (A) Schematic illustration of the stimulus. A red disk (illustrated as dark gray) was presented at an eccentricity of 10.6° from the fixation point. The disk was presented at one of eight directions (the downward direction in this figure). After 1500 msec from the onset of the red disk, a white disk of the same size as the red disk was flashed for 40 msec. The separation between the target and the flash, denoted by θ, was varied (6.7°, 20°, 60°, or 180°). After the flash, the red disk remained for another 1500 msec until the end of trial. (B) Mean frequency of fading as a function of the separation between the flash and the target disks. The dotted line is the baseline frequency of fading obtained from the control condition where no flash was presented. The error bar indicates the standard error of the mean. (C) Individual results of four subjects. (D) Mean frequency of fading as a function of the target location. The radial axis corresponds to the frequency of fading from 0% (center) to 100% (outer circle) and the angular axis corresponds to the direction where the target disk was presented. Concentric circles are drawn at every 25%. (E) Results of individual subjects.

associated with the spatial separation. The results support the idea that the fading is mediated by local interactions between the flash and the target stimuli, as opposed to nonselective cognitive effects or diverted attention by the flash.

Figure 2D and 2E shows the frequency of fading as a function of the target position and the distance between the target and flashed disks. In certain stimulus conditions, the frequency of perceptual fading reached 100%. The maximum frequency of fading was 93.3%, 100%, 100%, and 100% for CP, MR, RK, and WH, respectively (Figure 2E). Although such a ''hot-spot'' was quite variable across subjects, there were two general tendencies. First, subjects experienced a fading more often when the target was along the vertical axis, than when along the horizontal axis. This may be accounted for by the anisotropy cortical magnification factors between the horizontal and vertical meridians. The representation of visual image in the visual cortex is biased with a greater emphasis on the horizontal meridian than on the vertical meridian (Van Essen, Newsome, & Mounsell, 1984). In other words, a larger part of visual processing areas is devoted to stimuli presented on the horizontal meridian than on the vertical meridian, when compared at the same eccentricity. This may let the visual representation of objects on the horizontal meridian be more stable and resistant to perceptual fading. Second, fading occurred more frequently in the upper visual field than in the lower visual field, as can be seen in the mean of all subjects (Figure 2D). Such asymmetry has been found in other psychophysical measurements. For example, it is known that illusory contours are detected better when presented in the lower visual field than in the upper visual field (Rubin, Nakayama, & Shapley, 1996). In addition, upper/lower asymmetry is found in the neurophysiology of the visual pathway in terms of the cortical magnification factor: There is a slight overemphasis on inferior relative to superior parts of the visual field in the visual cortical areas (Van Essen et al., 1984).

The fact that the fading was induced more frequently by spatially close flashes indicates that the spatial extent where the fading is induced can be well controlled by the location of the flash. To further demonstrate the fine control of perceptual fading by a flash in space as well as in time, we designed the following stimulus configuration. The stimulus consisted of an array of target disks, and flashed disks that were presented sequentially between the target disks, producing apparent motion of a single disk over the target disks (Figure 3A). We observed that the target disks disappeared one by one as the flash passed through, as if they were swept by a moving disk.

In an experiment to support this observation, we used four target disks and varied the number of flashed disks that were presented sequentially to produce apparent motion. Hereafter, we refer to the four target disks as D1, D2, D3, and D4, and to five flashes as F1, F2, and so on. Apparent motion was produced by presenting the flashes in this order, and the extent to which the target disks were covered by the apparent motion was manipulated by varying the number of flashes beginning from F1 (F1-only, F1–2, F1–3, F1–4, and F1–5). Subjects were asked to report which target disk(s) perceptually disappeared after the last flash for each condition was presented.

The results show that the fading of a disk was induced only when the moving flash was presented near the disk (Figure 3B,C). In the condition F1-only, the fading of D1 was frequently induced, whereas most of the other disks remained visible. In the condition F1–2, D1 and D2 faded frequently, whereas others remained largely visible. In the same manner, as the extent covered by apparent motion increased, the fading of a larger number of disks was triggered. We applied a repeated measures ANOVA and a post hoc Tukey multiple comparison test for each flash condition. For all conditions, the ANOVA results were significant ($p < .05$). The post hoc tests revealed between which disks the frequency of fading was significantly different for each condition: for the F1-only condition, between D1 and D2–4 ($p < .01$); for F1–2, between D1–2 and D3–4 ($p < .01$); for F1–3, between D1–3 and D4 ($p < .05$); for F1–4, between D1–3 and D4 ($p < .05$); for F1–5, no significant difference between disks ($*p < .05$, $**p < .01$, in Figure 3A). Thus, the locus of statistical significance shifted in accordance with the extent of apparent motion.

These results support the phenomenology that the consecutively flashed disks appear to erase target disks one by one along the path of apparent motion. The highly specific manner of fading demonstrated here is in contrast with rather unpredictable fading observed in the conventional Troxler effect and another type of motion-induced fading that will be discussed later.

Is the presentation of an additional object necessary to produce the fading effect? To address this issue, we next examined the effect of a brief removal of the target stimulus (blinking), instead of flashing an object. Blinking of a stimulus gives rise to transient sensation similar to a flashed stimulus. Thus, if transient sensation is sufficient to produce the fading effect, such blinking should induce a fading as well. On the other hand, it is also possible that such blinking interrupts adaptation, and thus leads to less fading.

To produce strong transient sensation, the duration of a blink should neither be too short nor too long: If it is too short, the blink is undetectable, whereas if it is too long, the disappearance and reappearance of the target are perceived as separate events, thus would not produce a single, vivid, transient event. If transient sensation is important in the fading effect, we expect that the frequency of fading should show dependency on the blink duration. Therefore, we explored a variable duration of a blink (26, 80, 240, or 720 msec) to manipulate

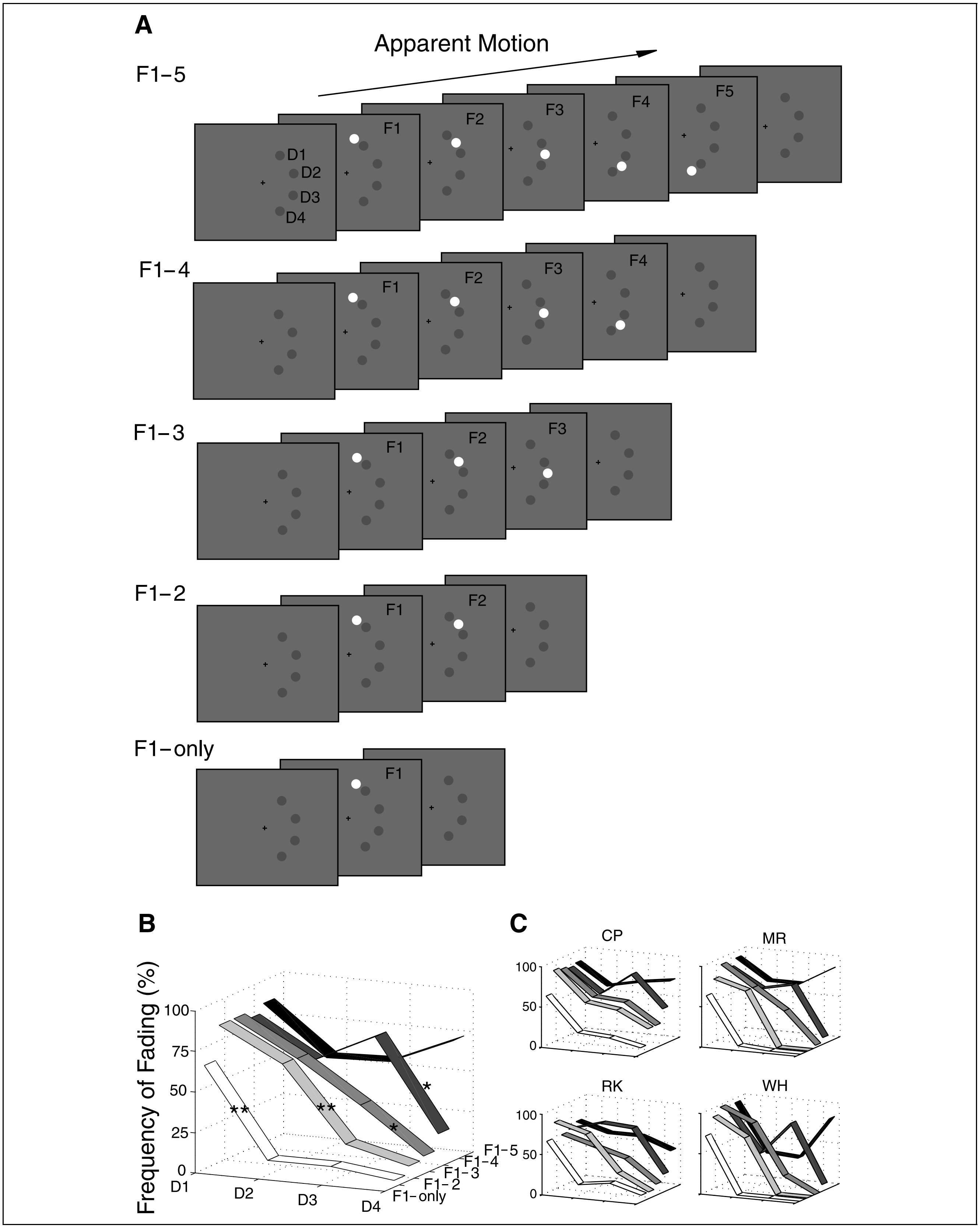

Figure 3. Perceptual fading induced by apparent motion. (A) Five experimental conditions differing in the number of flashes are illustrated schematically (the size is not to the scale). Four red disks (D1–4) appeared at the beginning of a trial. After 1500 msec, flashes were presented sequentially between disks, producing apparent motion in the clockwise direction. (B) Mean frequency of fading as a function of the target location and the flash condition. The results of pairwise comparison (Tukey test) are marked by * and ** for $p < .05$ and $p < .01$, respectively. (C) Individual results of four subjects.

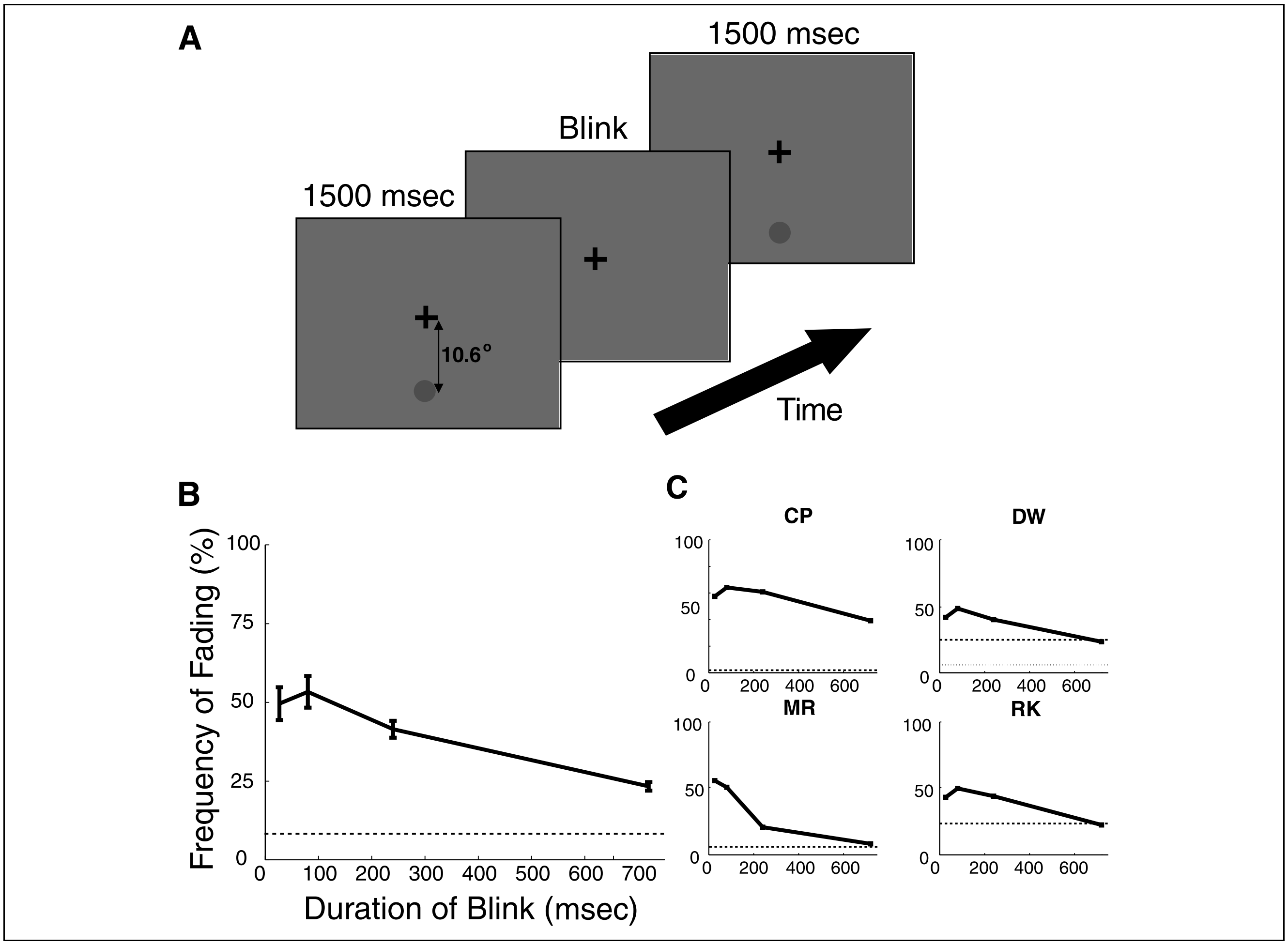

Figure 4. Blink-induced fading experiment. (A) A schematic illustration of the stimulus. A red disk (illustrated as dark gray) was presented at an eccentricity of 10.6° from the fixation point. The disk was presented at one of eight directions (the downward direction in this figure). After 1500 msec from the onset, the target disk physically disappeared for a variable duration (26, 80, 240, or 720 msec). After this blink period, the target disk reappeared and stayed on for another 1500 msec, until the end of trial. (B) Mean frequency of fading as a function of the blink duration (26, 80, 240, or 720 msec).

the strength of transient sensation and thereby examined what range of blink duration is effective at triggering a fading (Figure 4A).

The results show that the blink indeed induced perceptual fading (Figure 4B,C). The frequency of fading was evidently higher in the blink condition as compared to the control condition in which observers were asked to judge whether fading occurred at any time during the same observation duration without blinking. Thus, blinking increased the probability of fading, rather than decreasing it by interrupting adaptation. Note, however, that blinking was not as effective as flashing a stimulus nearby. Nonetheless, the increased frequency of fading by blinking the target disk supports the idea that transient sensation is sufficient to trigger the fading effect.

A general tendency of the results was that the fading effect decreased as the blink duration increased (Spearman rank order correlation coefficient $R = -.570$, $p = .011$). However, the shortest blink duration we tested was not necessarily the most effective. In three out of four observers, a stronger fading effect was found at the blink duration of 80 msec, rather than at the shortest blink duration of 26 msec (Figure 4B,C).

The dependency of the fading frequency on blink duration may reflect the strength of transient sensation induced by a blink of a different duration. In our informal observation, subjects reported that the impression of a blink, which was presented in the fovea to avoid fading, was strongest when the duration was 80 msec. The strength of a blink may also be related to flicker sensitivity as described in the literature. Flicker sensitivity at a temporal frequency could correspond to the strength of a blink with a duration of half the flicker period (the reciprocal of frequency). The sensitivity to a chromatic flicker is known to start decreasing around a temporal frequency of 7 Hz (van der Horst, 1969). This provides a rough estimation that the detectability of a blink begins to decay around 71 msec (1000 msec/[2 × 7 Hz]), consistent with the slight decay of the fading frequency at the shortest blink (26 msec). While the chromatic flicker sensitivity is largely constant at lower temporal frequencies (van der Horst, 1969), our data show a decrease in fading frequency for the corresponding longer blinks. This may be explained by a possible contribution of temporal luminance modulation that may be implicated in the stimulus (see Methods): The visual system has a markedly less sensitivity to temporal luminance modulation at low temporal frequencies than at the optimal frequency (Kelly, 1979). Taken together, these results suggest that the frequency of fading depends on the strength of the transient sensation produced by a blink.

DISCUSSION

In the first experiment, we examined the spatial property of the fading induced by a flash. The frequency of fading decreased drastically as the separation between the flash and the target increased, indicating that the effect of the flash is spatially local. In addition, the timing of the fading was perceptually time-locked to the flash. These characteristics were further confirmed in the second experiment in which apparent motion was employed as an inducer of the perceptual fading. In the condition where all the flashes were presented, red disks were often perceived to fade in the order from D1 to D4, as if they were swept away by the moving white disk. This clearly demonstrates the highly specific manner of the fading in both space and time. In the third experiment, we showed that a brief disappearance of the target stimulus itself causes the fading, indicating that transient sensation, as opposed to the presentation of an additional object, is sufficient to produce the fading effect. In our present study, we used near-isoluminant stimuli to obtain a maximum fading effect. However, a similar effect can be observed in relatively high-contrast, achromatic stimuli, and therefore the effect appears to reflect a more general property of our perception.

Although adaptation of edge detectors due to the stabilization of the retinal image by fixation may contribute to the fading by reducing the gain of edge signals, it is unlikely that this fully explains our results. The observed fading frequency was generally much higher in the conditions with visual transients than in those without visual transients, where only edge adaptation is thought to contribute to the fading. While spatial proximity between the flash and the target was shown to be important, the fading was readily observed although there was no overlap between the edges of the flash and those of the target. Edge adaptation is thought to be highly position specific, since it can be disrupted by small eye movements, as observed in the conventional Troxler effect. Hence, the flashed stimulus does not seem to cause fading by affecting the edge adaptation of the target. Our results of blink-induced fading are also evidence against the account based on edge adaptation, since adaptation would instead be interrupted by a blink. One might argue that the disappearance and reappearance of the target produced strong signals in edge detectors, which in turn expedited adaptation, and thus resulted in a fading. In our preliminary experiment, however, we observed a similar fading in a stimulus where only the central region of the target disk was briefly extinguished while the outer edge of the disk was unchanged. Therefore, transient signals close to the target, rather than edge adaptation, seem to play a crucial role in the blink-induced fading too.

Motion-induced blindness (MIB) would be another example of perceptual fading that cannot be attributed solely to edge adaptation (Bonneh, Cooperman, & Sagi, 2001). MIB is a visual illusion wherein salient objects placed on a motion stimulus disappear from visual awareness. In MIB, even a slowly moving object can perceptually disappear. Based on this observation, it is argued that MIB is not attributable to low-level edge adaptation. Our perceptual fading is similar to MIB in that the cause of fading is not simply due to edge adaptation, but rather due to the interaction between the target and a stronger stimulus, such as a flash, in our stimulus, and structure-from-motion, in MIB. However, in MIB, the timing of fading is unpredictable. In addition, when there are multiple stationary objects on the periphery, the location or the order of perceptual fading is not predictable from the motion stimulus. In contrast, our stimulus provides more control of fading in space and time, as demonstrated in our apparent motion configuration. The precise control in space and time may be a great methodological advantage over conventional stimuli used for perceptual fading and filling-in, especially when combined with electrophysiological and imaging techniques.

It may seem puzzling that transient stimuli caused a fading, or an inhibitory effect, whereas in many studies, they have been used to cue the target, or to facilitate behavior or perception by drawing attention to the target (Hikosaka, Miyauchi, & Shimojo, 1993; Posner, 1980). It should be noted, however, that in typical cueing tasks, a transient stimulus, such as a flash, precedes the onset of a high-contrast target, while in our stimulus, the low-contrast target is present throughout the trial and overlaps the transient stimulus in time. It is an open question what the critical conditions are for transients to cause facilitation or suppression. Competition between a low-contrast target and a spatially close and co-occurring salient, transient object, however, may play an important role in producing the suppressive effect in our fading phenomenon.

The biased competition model (Desimone, 1998; Desimone & Duncan, 1995), which has been proposed to explain the effect of selective attention on neural responses in areas V4 and IT, may provide an insight into the inhibitory aspect of the fading effect. According to the model, objects in the visual field compete for the responses of cells in the visual cortex. When two objects are presented in the same receptive field, the response of neurons to that region is determined by a mutually suppressive interaction between the two stimuli. Thus, a neural representation of visual objects is selected in favor of one over the other. In the fading induced by visual transients, the weak signal from the target disk may be suppressed by the salient, transient signal. Therefore, the cell's responses to the target disk would decrease to below threshold, resulting in the perceptual fading of the disk.

Although this particular model assumes that the competition occurs among visual objects rather than among local features, it is unclear whether the fading effect is object-based or not. The blink-induced fading indicates that fading can be triggered without presentation of an additional object. Thus, the competition between object representations does not seem to be essential. However, it should also be mentioned that the fading effect exhibits an object-based aspect as well. In our preliminary observation, we used stimuli similar to those used in the apparent motion experiment (see Figure 3A), except that four discrete target disks were replaced by a continuous bar. As the flash moved, the bar disappeared not gradually from one end to the other, but nearly in an all-or-nothing manner: Presenting just one flash was sometimes sufficient to cause the fading of the entire bar. This observation seems to favor object-based mechanisms, as it shows that the unit of fading is an object, rather than features in a local area. It remains to be seen what level of visual representations is critical for the fading effect.

Another important aspect of the fading effect is that a brief stimulus presentation (<100 msec; the visual transient) leads to a long invisibility of the target (2–3 sec). In this regard, the fading effect reported here is distinct from conventional visual masking phenomena, where a briefly presented target is suppressed by another temporally adjacent stimulus (Breitmeyer, 1984; see also Paradiso & Nakayama, 1991, for visual masking related to perceptual filling-in). Although it is possible that conventional visual masking, which reflects interactions between the target and the mask presented within a short time window, is involved in the initiation of the fading, it cannot explain the long invisible period. The fading effect seems to reflect a sustained process controlling the visibility of objects, the state of which could be drastically altered in response to transient visual inputs.

In this study, we have demonstrated a novel method to induce a perceptual fading using visual transients. It allows one to control the location and the timing of perceptual fading, and thus may prove useful in electrophysiological and imaging studies on fading or filling-in phenomena. The fading effect shows that a transient visual event can lead to a drastic and sustained change in the visibility of an object that is constantly presented. Our results suggest that it cannot be attributed to adaptation of local feature detectors or higher cognitive factors, but that it reveals a unique component of visual processing that crucially mediates conscious visual perception.

METHODS

Subjects

Four subjects participated in each experiment. All subjects had normal or corrected-to-normal visual acuity and reported no color vision abnormalities. R.K. is an author of the present article.

Stimuli and Procedure

Subjects were seated in front of a CRT monitor at a distance of 57 cm. Before each experiment, heterochromatic flicker photometry was used for each subject to obtain a green that was isoluminant to the maximum intensity of red (6.3 cd/m^2). In all experiments, the targets were red disks of the maximum intensity (1.06° in diameter) on a background of the near-isoluminant green, and presented at an eccentricity of 10.6°. Since we performed the flicker photometry for the entire display, not for each disk location, the disks may not be strictly isoluminant to the background, which thus may admittedly contain a small luminance component. To reduce accumulative adaptation across trials, a dynamic noise pattern was presented between trials.

In the experiment of the flash-induced fading, a white disk (23 cd/m^2) was flashed for 40 msec after 1500 msec from the onset of the target disk. This was followed by another 1500 msec of observation (Figure 2A). A beep was given to inform subjects of the end of a trial. The flash was placed at the same eccentricity as the target disk, and its relative angle from the target disk (θ, in Figure 2A) was varied (6.7°, 20°, 60°, or 180°). Each of 32 stimulus conditions (8 target positions $\times$ 4 relative flash positions) was repeated 15 times, and the order of presentation was randomized. Subjects were asked to report whether the fading of the red target was induced immediately following the flash. In the experiment of the blink-induced fading, the same procedure was adopted except that a blinking of the target of a variable duration (26, 80, 240, or 720 msec) was used instead of a flash. In the control experiment for these two experiments, the target disk stayed on for 3000 msec without a flash or a blink. Subjects were asked to report whether a fading of the target occurred at any time during the observation period of 3000 msec. Fifteen trials were repeated for each of the eight target positions.

In the experiment of the fading induced by apparent motion, four red target disks appeared on the green background. We refer to these disks as D1, D2, D3, and D4 in clockwise order (Figure 3A). These disks were presented at an eccentricity of 10.6° from the fixation point. The angle between adjacent two disks was 20°, therefore the angle between D1 and D4 subtended 60°. The position of the disks was randomly shifted across trials, while the eccentricity and the relative separation between disks were held constant. After 1500 msec, a series of white disks were flashed. We will refer to these white disks as F1, F2, and so on (Figure 3A). The presentation time of each flash was 66.7 msec and the interstimulus interval between the flashes was 0 msec. The flashes were positioned at the same eccentricity as the target disks. The range of apparent motion was varied (F1–5, F1–4, F1–3, F1–2, and F1-only), whereas the order of flash presentations was always clockwise. Immediately after the last flash, subjects were informed of the end of the trial by a beep and prompted to report which target disk(s) disappeared.

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