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Attention During Adaptation Weakens Negative Afterimages

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The effect of attention during adaptation on subsequent negative afterimages was examined. One of 2 overlapped outline figures was attended during a 7–10-s adaptation period. When the figures were readily perceptually segregated (on the basis of color or motion), the subsequent afterimages were initially weaker for the previously attended figure. This effect was confirmed by demonstrations that the onset of a single afterimage was delayed when an afterimage inducer was attended during adaptation compared with when a central digit stream or an overlapped (brightness-balanced) figure that did not generate an afterimage was attended. The attention effect was further confirmed using a criterion-independent (dot-integration) paradigm. The fact that selective attention during adaptation weakened or delayed afterimages suggests that attention primarily facilitates the adaptation of polarity-independent processes that modulate the visibility of afterimages rather than facilitating the adaptation of polarity-selective processes that mediate the formation of afterimages.

After one stares at a pattern for several seconds, a faint afterimage appears when one's gaze is redirected to a blank surface. This afterimage is complementary to the original pattern in both brightness and color (e.g., Kelly & Martinez-Uriegas, 1993); such afterimages are thus called *negative* afterimages. Negative afterimages are a ubiquitous, though often unnoticed, component of visual perception. In this article, we present results suggesting that the neural adaptation underlying these afterimages is modulated by selective attention. We begin by reviewing evidence that, contrary to a commonly held belief, photoreceptor adaptation and cellular interactions in the retina alone cannot account for the formation of afterimages.

In the special case in which afterimages are generated by an intense flash of light, strong and persistent (lasting for minutes) afterimages can be explained primarily on the basis of bleaching of the retinal photoreceptors (e.g., MacLeod & Hayhoe, 1974; Rushton & Henry, 1968; Williams & MacLeod, 1979). However, even for these bleaching afterimages, photochemical processes alone cannot fully account for their appearance. For example, different temporal patterns of light flashes have produced afterimages differing in brightness and color even when the flash patterns were calibrated to generate equivalent photoreceptor bleaching (e.g., Brindley, 1959; Loomis, 1972, 1978). These results implied a role for postreceptoral neural adaptation. More important, the ubiquitous afterimages seen under normal circumstances, which are the focus of this study, should involve mechanisms different from photoreceptor bleaching, because cone bleaching[1] is insignificant under normal indoor lighting conditions (i.e., ambient lighting less than 120 cd/m^2; e.g., Schiller & Dolan, 1994; Virsu & Laurinen, 1977).

Wilson (1997) proposed that horizontal–cell gain control in the retina might play a role in the formation of these nonbleaching afterimages (henceforth simply referred to as *afterimages*). However, evidence also implicates cortical adaptation. For example, the colors of afterimages tend to be consistent with the perceived colors rather than with the spectral patterns of the adapting stimulus (e.g., Anstis, Rogers, & Henry, 1978; Loomis, 1972). In particular, color-induction effects used by Anstis et al. (1978) to induce afterimages are thought to be mediated by cortical cells (rather than by retinal and lateral geniculate nucleus [LGN] cells) because of the slow temporal characteristics of color-induction effects (R. L. De Valois, Webster, De Valois, & Lingelbach, 1986). Furthermore, a recent study demonstrated that the perception of illusory contours, and a related phenomenon of filling in of color, luminance, or both during adaptation, contributed to the structure and color of subsequent afterimages (e.g., a solid-colored square afterimage occurred after adaptation to an illusory square generated by colored sectors of four inducing "pacman" shapes; Shimojo, Kamitani, & Nishida, 2001). Both illusory contours and filling-in are known to be mediated by cortical processes (e.g., De Weerd, Gattass, Desimone, & Ungerleider, 1995; Gilbert, 1992; Peterhans & von der Heydt, 1991).

Given that cortical processes contribute to the formation of afterimages, which cortical visual area (or areas) might be involved? The visual pathway underlying perception of shapes and objects is thought to course through the ventral visual stream, extending through areas V1, V2, and V4 and terminating in the inferotemporal cortex (IT; e.g., Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). The complexity of pattern processing increases in the downstream visual areas. For example, processing is elaborated from local orientation and spatial frequency in V1 and V2 (e.g., Foster, Gaska, Nagler, & Pollen, 1985;

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[1] Rods contribute little to vision under normal lighting (photopic) conditions.

Hubel & Wiesel, 1968), to 2-D textures and contour features in V4 (e.g., Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Kobatake & Tanaka, 1994; Pasupathy & Connor, 1999), to geometric shapes and familiar shapes in IT (e.g., Fujita, Tanaka, Ito, & Cheng, 1992; Ito, Tamura, Fujita, & Tanaka, 1995; Logothetis & Sheinberg, 1996; Tanaka, 1996; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001; Vogels & Orban, 1994; Y. Wang, Fujita, & Maruyama, 2000; G. Wang, Tanaka, & Tanifuji, 1996; Young & Yamane, 1992). The size of receptive fields also increases in the downstream visual areas, from means of 1.1° in V1 and 3.0° in V2 parafoveal regions (e.g., Foster et al., 1985), to sizes 4–7 times as large in V4 (e.g., Desimone & Schein, 1987), to a median of about 30°, but up to about 100°, in IT (e.g., Desimone & Gross, 1979; Gross, Rocha-Miranda, & Bender, 1972; Ito et al., 1995), resulting in a considerable degree of translation and scale tolerance in IT.

The types of cortical cells that mediate afterimages must be *polarity selective;* that is, their responses must be selective for luminance polarity, color polarity, or both against the background. For example, a luminance-polarity–selective cell might respond to lighter-than-background bars but not to darker-than-background bars; a color-polarity–selective cell might respond to redder-than-background spots but not to greener-than-background spots. Then, selective adaptation of cells tuned to one polarity (e.g., light or red) would result in relatively stronger activity of cells tuned to the opposite polarity (e.g., dark or green) in the adapted region, contributing to negative afterimages on viewing of a uniform field (e.g., Schiller & Dolan, 1994).

The fact that afterimages are seen at the retinal locations of the adapting stimulus in fine detail (up to 9–12 cycles per degree of alternating light and dark patterns; e.g., Burbeck & Kelly, 1984; Kelly, 1979; Tulunay-Keesey, 1982) implicates cortical cells with small receptive fields that have distinct polarity-selective subregions, each of which responds to a specific luminance polarity (light or dark), color polarity (e.g., red or green), or both. These cells include simple cells and color-opponent cells in early visual areas, V1 and V2 (e.g., R. L. De Valois, Albrecht, & Thorell, 1982; Hubel & Wiesel, 1968; Schiller, Finlay, & Volman, 1976; Ts'o & Gilbert, 1988; Ts'o & Roe, 1995). Most cells in V1 undergo considerable adaptation; higher activity tends to lead to stronger adaptation (i.e., greater sensitivity reduction), but degrees of adaptation also depend on neural interactions (e.g., Albrecht, Farrar, & Hamilton, 1984; Bonds, 1991; Carandini, Movshon, & Ferster, 1998; Ohzawa, Sclar, & Freeman, 1985; Saul & Cynader, 1989a, 1989b; Sclar, Lennie, & DePriest, 1989). In addition to simple cells and color-opponent cells in V1 and V2, luminance-polarity–sensitive cells and color-tuned cells in higher visual areas with larger receptive fields, such as those in V4 (e.g., Desimone & Schein, 1987; Schein & Desimone, 1990) and IT (e.g., Ito, Fujita, Tamura, & Tanaka, 1994; Komatsu, Ideura, Kaji, & Yamane, 1992), might contribute to afterimages, potentially via feedback connections (e.g., Felleman & Van Essen, 1991). Adaptation has been demonstrated for some cells in IT (e.g., Miller, Gochin, & Gross, 1991; Miller, Li, & Desimone, 1993; Vogels, Sary, & Orban, 1995).

In addition to these polarity-selective cells that could potentially mediate afterimages, cortical cells include polarity-independent (or attribute-invariant) cells that respond to their preferred patterns relatively independently of luminance polarity, color, or both. For example, a polarity-independent cell tuned to a vertical bar would respond equivalently to a light vertical bar and to a dark vertical bar throughout its receptive field. These cells include complex cells in V1 and V2 and some proportions of cells in V4 and IT (Desimone & Schein, 1987; R. L. De Valois et al., 1982; Hubel & Wiesel, 1968; Ito et al., 1994; Komatsu et al., 1992; Schein & Desimone, 1990; Schiller et al., 1976; Ts'o & Gilbert, 1988; Ts'o & Roe, 1995). Polarity-independent cells cannot mediate the formation of afterimages because their adaptation does not induce polarity-specific reductions in visual sensitivity (e.g., reduced sensitivity to light patterns relative to dark patterns). Instead, adaptation of polarity-independent cells should reduce subsequent pattern visibility regardless of stimulus polarity.

We thus hypothesized that perceived afterimages are due to at least three types of adaptation: (a) luminance-based adaptation of retinal cells, (b) polarity-selective adaptation of cortical cells, and (c) polarity-independent adaptation of cortical cells.[2] The first two types of adaptation generate and strengthen afterimages, whereas the third type reduces the visibility of afterimages. Previous psychophysical studies confirmed the combined and individual effects of these three types of adaptation. For example, static (stationary) adaptors should induce all three types of adaptation simultaneously. Static adaptors with higher contrasts or with longer durations (inducing greater adaptation) produced stronger afterimages (e.g., Georgeson & Turner, 1985; Kelly & Martinez-Uriegas, 1993), indicating that adaptation of retinal or cortical polarity-selective mechanisms (or both) was stronger, faster-growing, or longer-lasting (or any combination of these) than adaptation of cortical polarity-independent mechanisms. Further, by comparing adaptation (or masking) effects from grating patterns with those from uniform fields, Bowen and colleagues (e.g., Bowen, 1995, 1997; Bowen & de Ridder, 1998; Bowen & Wilson, 1993) psychophysically isolated pattern-based adaptation of cortical polarity-selective (on–off) mechanisms from luminance-based adaptation of retinal mechanisms. K. K. De Valois (1977) also demonstrated adaptation of cortical polarity-selective mechanisms by showing that bar-width aftereffects were selective for luminance polarity. Other researchers examined cortical adaptation effects by using spatiotemporally modulated adaptors (e.g., counterphased or drifting gratings), which presumably averaged out local luminance adaptation in the retina or, in earlier studies, by having observers free-scan a static adaptor (e.g., Blakemore & Campbell, 1969; Jones & Tulunay-Keesey, 1980; Kelly & Burbeck, 1980). These stimuli would simultaneously adapt both light-polarity–selective and dark-polarity–selective mechanisms, as well as polarity-independent mechanisms; they might adapt polarity-independent mechanisms more strongly, because drifting gratings tend to adapt

[2] Note that we have been discussing polarity-selective and polarity-independent cortical cells as if they were two distinct classes of cells. In fact, cortical cells exhibit various degrees of polarity selectivity, with complete polarity selectivity and polarity independence being the possible extremes. Even regarding V1, some researchers (e.g., Mechler & Ringach, 2002) recently have challenged the conventional dichotomy (e.g., Hubel & Wiesel, 1968; Schiller et al., 1976) between simple cells with distinct polarity-selective receptive-field subregions and complex cells with overlapped polarity-selective subregions (which are, thus, responsive to both light and dark polarities throughout their receptive fields). Prototypical simple and complex cells may be the extremes in a unimodal distribution of receptive-field properties in V1. The degree of polarity selectivity also appears to be continuously distributed in higher visual areas (e.g., in V4 [Desimone & Schein, 1987] and in IT [Ito et al., 1994]).

V1 complex cells more strongly than they do simple cells (e.g., Albrecht et al., 1984). Reductions in pattern visibility due to cortical adaptation were also greater following stronger (higher contrast or longer lasting) adaptors (e.g., Blakemore & Campbell, 1969; Blakemore, Muncey, & Ridley, 1973; Greenlee, Georgeson, Magnussen, & Harris, 1991; Rose & Lowe, 1982). Finally, adaptation to a grating defined by luminance, subjective contours, or motion produced tilt aftereffects on a test grating defined by a different attribute (e.g., Berkley, Debruyn, & Orban, 1994; Paradiso, Shimojo, & Nakayama, 1989), demonstrating adaptation of attribute-independent (i.e., polarity-independent) cortical mechanisms tuned for orientation.

Thus, both physiological and psychophysical results support the idea that polarity-selective as well as polarity-independent cortical mechanisms adapt during prolonged viewing of a pattern. We thus propose, as others have suggested previously, that the strength of an afterimage should be increased by greater adaptation of retinal mechanisms and cortical polarity-selective mechanisms, whereas the visibility of an afterimage should be reduced by adaptation of cortical polarity-independent mechanisms (e.g., Burbeck & Kelly, 1984; Georgeson & Turner, 1985; Leguire & Blake, 1982). For example, during observation of a bright spot, lighter polarity–selective cells as well as polarity-independent cells would continue to adapt. During viewing of a blank field, greater adaptation of lighter polarity–selective cells would induce a darker afterimage. At the same time, greater adaptation of polarity-independent cells would make the dark afterimage appear weaker (lower in perceived contrast). In the current study, we examined how attention facilitated adaptation of polarity-selective and polarity-independent mechanisms by taking advantage of the fact that the adaptation of the two mechanisms would have opposite effects on subsequent afterimages. Attention during adaptation should strengthen afterimages if attention primarily facilitates adaptation of polarity-selective mechanisms. In contrast, attention during adaptation should weaken afterimages if attention primarily facilitates adaptation of polarity-independent mechanisms. The physiological results discussed below indicate that adaptation of either mechanism could plausibly be facilitated by attention.

Throughout the cortical visual areas along the ventral object-processing stream (V1, V2, V4, and IT), cells tend to respond more strongly to their preferred stimuli when those stimuli are attended, especially when competing stimuli are also presented within their receptive fields (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Haenny & Schiller, 1988; Luck, Chelazzi, Hillyard, & Desimone, 1997; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Motter, 1993; Reynolds, Chelazzi, & Desimone, 1999; Reynolds, Pasternak, & Desimone, 2000; Roelfsema, Lamme, & Spekreijse, 1998). Though physiological studies have tended to report greater attentional modulations in higher visual areas, and some have failed to demonstrate attention effects in V1, recent functional magnetic resonance imaging (fMRI) studies have confirmed retinotopic attentional modulations in V1 (e.g., Gandhi, Heeger, & Boynton, 1999; Somers, Dale, Seiffert, & Tootell, 1999). There is, however, no conclusive evidence regarding the question of whether attention effects might be different for polarity-selective and for polarity-independent mechanisms.

When attentional modulation was examined in higher visual areas such as in V4 and IT, attention effects were never analyzed as a function of cells' polarity selectivity. In V1 and V2, polarity-selective cells and polarity-independent cells can be mapped broadly onto simple cells and complex cells, respectively (but see Footnote 2). Motter (1993), Luck et al. (1997), and Reynolds et al. (1999) demonstrated attentional modulation of V2 cells, but they did not distinguish between simple and complex cells. Roelfsema et al. (1998) demonstrated attentional enhancements of V1 cells responding to portions of an attended curve during a mental curve-tracing task. Motter (1993) sampled V1 cells from all layers except Layer 4 and showed attentional modulations while attention was manipulated in multiple-item displays. However, these studies also did not distinguish between simple and complex cells. Ito and Gilbert (1999) demonstrated attentional enhancements of contextual effects in V1 while recording from complex cells in the superficial layers. Vanduffel, Tootell, and Orban (2000) used a metabolic staining technique to show that neural activity of cells responding to unattended regions was suppressed in V1 Layer 4 as well as in the magno layers of the LGN. Di Russo and Spinelli (1999a, 1999b) measured visual evoked potentials while observers attended to temporally modulated luminance or chromatic gratings; their results suggested that attention enhances responses of both parvocellular and magnocellular pathways (potentially through different mechanisms). Taken together, the current physiological evidence indicates that attention tends to enhance the relative activity of cells responding to attended stimuli at multiple levels of processing (LGN, V1, V2, V4, and IT), potentially for both polarity-selective and polarity-independent mechanisms.

Because attention facilitates neural responses, it is expected that attention should also facilitate neural adaptation. Though direct physiological evidence of attentional modulation of adaptation has yet to be obtained, studies of tilt aftereffects (e.g., Spivey & Spirn, 2000), shape aftereffects (Suzuki, 2001, 2003), position aftereffects (e.g., Yeh, Chen, De Valois, & De Valois, 1996), depth-interpretation aftereffects (e.g., Shulman, 1992, 1993), motion aftereffects (e.g., Alais & Blake, 1999; Chaudhuri, 1990; Lankheet & Verstraten, 1995; Von Grünau, Bertone, & Pakneshan, 1998), and motion-coherence–threshold elevation effects (e.g., Raymond, O'Donnell, & Tipper, 1998) have demonstrated stronger aftereffects when the adaptor was attended relative to when distractor stimuli were attended. These studies provide psychophysical evidence that attention facilitates neural adaptation at multiple stages of processing.

The experimental goal of the present study was to determine whether a stimulus selectively attended during adaptation produced stronger, weaker, or equivalent afterimages compared with a stimulus ignored during adaptation. As discussed earlier, if attention primarily enhances adaptation of polarity-selective mechanisms, the attended stimulus should produce stronger afterimages than the ignored stimulus. If attention primarily enhances adaptation of polarity-independent mechanisms, the attended stimulus should produce weaker afterimages than the ignored stimulus. It is also possible that attentional modulations of neural adaptation might not be measurable as perceptible changes in the strength of subsequent afterimages.

In Experiments 1A, 1B, and 3, the afterimage inducers consisted of two overlapped outline figures, and observers were instructed to attend to one figure and to ignore the other figure. In Experiment 2, the inducer was a single figure, and attention was manipulated by having observers attend either to the inducer or to a central, rapid digit stream. In Experiment 4, the inducer was an array of discs, and observers attended either to the discs or to a central ring around the fixation marker. In Experiments 2–4, observers' atten-

tion was tracked by having them count the number of times a certain feature appeared on the attended stimulus. The strength of afterimages was measured using subjective ratings (Experiments 1A and 1B) and by recording the onset and offset latencies of afterimages (Experiments 2 and 3). In addition, a criterion-independent procedure was used in Experiment 4; the initial visibility of afterimages was measured using a dot-integration paradigm (e.g., Eriksen & Collins, 1967, 1968; Hogben & Di Lollo, 1974), in which a gap in a circular array of discs could be detected only if the presented half array could be integrated with the complementary array generated by afterimages.

Experiment 1

Observers adapted to two overlapped outline inducer triangles, one upright and one tilted, and were instructed to attend to one of them and to ignore the other (see Figure 1). Upon disappearance of the inducer triangles, observers described the afterimages that they saw. A pilot study revealed that afterimages were relatively weaker for the inducer triangle that was attended during adaptation. However, this effect tended to be rather small, presumably because it was difficult to perceptually segregate the two overlapped triangles and then maintain attention on only one of them during the 7-s adaptation period. We observed that when different colors were assigned to the two triangles or when the two triangles were oscillated out of phase, the color-based and motion-based perceptual segregation of the two triangles made it easier to maintain attention on one of them. Thus, in Experiment 1A, the two inducer triangles either were the same color (dark blue or dark green) or were different colors (one dark blue and one dark green). In Experiment 1B, the two inducer triangles were vertically oscillated in opposite phase.

Experiment 1A: Color-Based Segregation of Overlapped Afterimage Inducers

Method

Observers. In all experiments except Experiment 4, undergraduates at Northwestern University gave informed consent to participate for course credit. They were tested individually in a dimly lit room (ambient luminance of a white wall = 1.5 cd/m^2). They all had normal or corrected-to-normal visual acuity and normal color vision. Twenty-four observers participated in this experiment.[3]

Stimuli. The afterimage-inducing stimuli (referred to as *inducers*) consisted of an outline drawing of two overlapped triangles, one upright and the other tilted 20° clockwise. The dimensions of the stimuli are shown in Figure 1. In this configuration, in which the overall shape was not symmetric about the cardinal axes, the two individual triangles (rather than the global pattern or other possible contour organizations) tended to form the primary perceptual organizations. The dark triangles were centered around a black fixation marker and were presented against a light gray background (45.7 cd/m^2, Commision Internationale de l'Eclairage, or CIE [.311, .333]).

There were two conditions. In the *same-color* condition, both inducer triangles were dark blue (CIE [.146, .074]) or dark green (CIE [.306, .585]). In the *different-color* condition, one of the inducer triangles was dark blue and the other was dark green. The two colors were adjusted so that the dark blue (7.5 cd/m^2) and the dark green (28.4 cd/m^2) appeared equally salient (subjectively) and so that both produced reliable bright afterimages.

Procedure. The same-color condition and the different-color condition were tested in a blocked design (five trials per block). The blocks were ordered as follows: (a) blue upright triangle with green tilted triangle, (b) green upright triangle with green tilted triangle, (c) blue upright triangle with blue tilted triangle, and (d) green upright triangle with blue tilted triangle. These four blocks were tested twice, once while observers attended to the upright inducer triangle and once while observers attended to the tilted inducer triangle during adaptation, with the order of attention counterbalanced across observers. Two practice trials were given prior to each attention instruction. When the two inducer triangles had different colors, which triangle (upright or tilted) appeared in front was also counterbalanced across observers.

Observers were seated 64 cm from a computer monitor. A chin rest was used to maintain viewing distance. Stimuli were displayed on a 17-in. (43.18-cm) color monitor (75 Hz), and all experiments were controlled with a Macintosh PowerPC 8600 (300 MHz) computer using Vision Shell software (Micro ML, Inc., Version 3.0).

The experimenter initiated each trial. During the adaptation period, the overlapped inducer triangles were presented for 7 s. On the disappearance of the inducers, observers described their afterimages, and the experimenter transcribed their reports. The following verbal instructions were given to encourage observers to describe their afterimages in detail:

> What you may see in the afterimage can vary a lot. You may see both triangles just as they look here [experimenter pointed to the dark inducer triangles], except in bright yellow or orange; you may see one or the other triangle, or perhaps parts of one or both triangles. You may even see motion, or one triangle changing into the other. We are interested in what you see, particularly in what you see first and in any changes in the image. There are no right or wrong answers.

When an observer's responses were unclear, he or she was asked to clarify and elaborate them.

We also instructed observers to fixate the central marker throughout a trial and to minimize blinking (especially toward the end of the 7-s adaptation period and while they examined the afterimage). The experimenter monitored eye blinks and coarse eye movements by watching observers' eyes in a mirror located above the monitor; the resolution of this method of eye tracking was at least 1.3°,[4] sensitive enough to detect eye movements from the fixation marker to the triangle contours, which lay at 1.9°–3.7° eccentricity. Persistent fixation drifts were also detected by observers' reports of afterimages appearing off center. All of the trials in which observers' fixation drifted or in which they blinked at the end of the adaptation period or during report of the afterimage were replaced. The experimenter waited until observers reported that afterimages from the previous trial had disappeared before initiating a new trial.

Data analysis. To quantify observers' verbal descriptions, we adopted the following scheme. When the afterimage was predominantly the previously attended triangle, a maximum positive score of 2 was given. When the afterimage was predominantly the previously ignored triangle, a maximum negative score of −2 was given. Intermediate scores were assigned on the basis of the relative dominance of the two afterimages. Because afterimages tended to fluctuate as they faded away (especially when observers blinked), we assigned these scores on the basis of the initial perception (the first several seconds) of the afterimages. The scoring details

[3] In all experiments reported in this article (except Experiment 4, in which experienced psychophysical observers participated), we initially recruited a larger number of participants. Whenever participants were unable to hold steady fixation, tended to blink with unusual frequency, were unable to monitor rapid streams of digits or colors (Experiments 2–3), or chose to withdraw from the study, they were excused from the experiment.

[4] This resolution was determined by having an observer deliberately shift gaze from a central marker to contours at varying eccentricities while the experimenter reported occurrences of eye movements. The estimate of 1.3° resolution is conservative in that fixation shifts of 1.3° and above were consistently detected, although shifts of less than 1.3° were also sometimes detected.

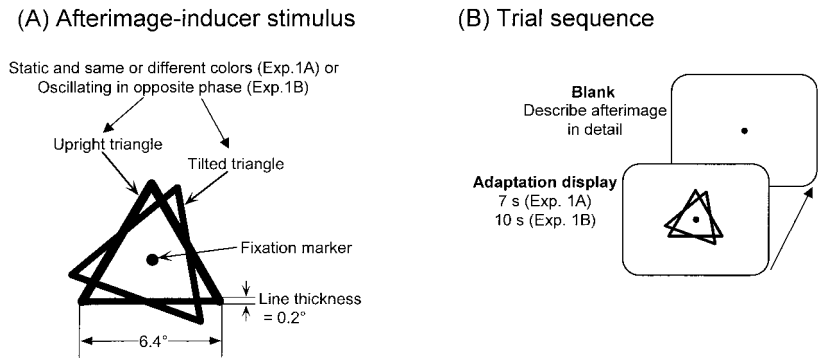

Figure 1. Afterimage-inducer stimulus (A) and trial sequence (B) for Experiments 1A and 1B. Observers fixated the central marker throughout the trial. During the 7-s (Exp. 1A) or 10-s (Exp. 1B) adaptation period, observers attended either to the upright triangle or to the tilted triangle. The two afterimage-inducing triangles were static and had either the same color or different colors (dark blue and dark green) in Experiment 1A. The two (dark blue) triangles were oscillated vertically out of phase in Experiment 1B. Upon disappearance of the inducer triangles, observers described the afterimages that they saw. Exp. = Experiment.

and distribution of responses (across Experiments 1A and 1B) are given in Figure 2.

We chose to use observers' verbal reports in our initial pair of experiments because these allowed us to gain insights into what unbiased[5] observers would see when they were free to report any particular aspect of an afterimage (e.g., duration, brightness, and fragmentation). As shown in Figure 2, observers spontaneously used relative strength (relative brightness) and duration in their reports.

Results

Consistent with the pilot observations, when the two inducer triangles were the same color, observers' selective attention during adaptation had little effect on the subsequent negative afterimages (see Figure 3; mean rating = −0.01, $SE = 0.08$), $t(23) = -0.101$, *ns*. However, when the two inducer triangles were different colors, afterimages were significantly weaker for the inducer triangle that was attended during adaptation (mean rating = −0.25, $SE = 0.08$), $t(23) = -3.314$, $p < .005$.

Experiment 1B: Motion-Based Segregation of Overlapped Afterimage Inducers

Method

Observers. In all experiments except Experiment 4, undergraduates at Northwestern University gave informed consent to participate for course credit. They were tested individually in a dimly lit room (ambient luminance of a white wall = 1.5 cd/m^2). They all had normal or corrected-to-normal visual acuity and normal color vision. Twenty-four observers participated in this experiment. (See Footnote 3.)

Stimuli. The two inducer triangles (both dark blue, 7.1 cd/m^2, against a light gray background, 49.2 cd/m^2) oscillated vertically out of phase (amplitude = ± 0.085°; frequency = 4.7 Hz). The opposite-phase motion facilitated perceptual segregation of the two inducer triangles. Because the motion slightly reduced the strength of afterimages, we increased the duration of adaptation from 7 to 10 s.

Procedure. Observers attended to the upright triangle and the tilted triangle in a blocked design. Half of the observers attended to the upright triangle first, and the other half attended to the tilted triangle first. Each block consisted of 2 practice trials, followed by at least 10 experimental trials. The scoring of responses was the same as it was for Experiment 1A.

Results

As shown in Figure 3, when the two inducer triangles oscillated out of phase, afterimages were significantly weaker for the inducer triangle that was attended during adaptation (mean rating = −0.42, $SE = 0.17$), $t(11) = 2.505$, $p < .03$.

Discussion of Experiments 1A and 1B

We demonstrated that selective attention during adaptation tends to weaken the subsequent afterimage of the attended inducer. This attentional modulation was reliable when perceptual segregation of the two overlapped inducers was facilitated by assigning them slightly different colors or opposite motions. In both of these experiments, however, observers verbally reported the relative strengths of the two afterimages, one generated by the attended inducer and the other generated by the ignored inducer, while the two afterimages were being inspected simultaneously. To rule out the possibility that the results might be tied to this particular methodology, in the next experiment we manipulated attention using a central, rapid digit stream without overlapped inducers and, thus, did so without generating competing afterimages. Because only one afterimage was seen, we were able to use the onset and offset latencies of afterimages as indices of their strengths (e.g., Atkinson, 1972; Leguire & Blake, 1982; Wade, 1972, 1973, 1974) rather than rely on verbal descriptions. Furthermore, observers' attention during adaptation was tracked using a continuous feature-detection task in all of the subsequent experiments, whereas we relied on observers' compliance with task instructions in Experiments 1A and 1B.

[5] To confirm that observers were indeed unbiased about the potential effects of selective attention during adaptation on subsequent afterimages, we recruited an additional group of 24 undergraduates and surveyed their predictions on the outcome of the experiment. Most (13) predicted no effects of attention; 7 predicted that afterimages would be strengthened, and 4 predicted that afterimages would be weakened by attention during adaptation. Thus, observers apparently had no consistently biased expectation to see weaker afterimages for a previously attended inducer.

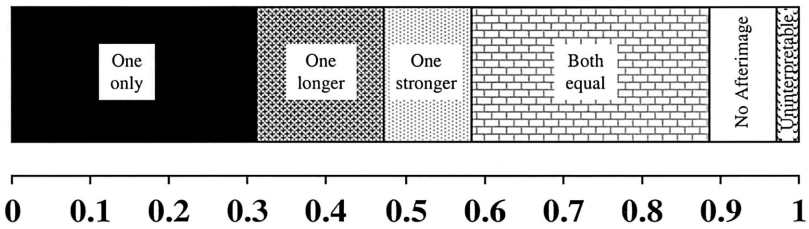

Figure 2. Proportional distribution of responses for Experiments 1A and 1B. The scoring scheme was primarily based on the strength and duration of the initial organization of the afterimage because in some cases the relative dominance of the two triangles in the afterimage changed over time. If the previously attended triangle was first seen alone, the response was assigned a score of 2. If both triangles were seen together, but the previously attended triangle appeared brighter or to last longer, the response was assigned a score of 1. When the previously ignored triangle was dominant, the same scoring scheme was used but with a negative sign. Reports of both triangles seen as equivalent, reports of no afterimage, and uninterpretable descriptions were assigned a score of 0. When the dominant afterimage was fragmented (only parts of the triangle were seen), the score was shifted toward 0 by 0.5. For example, when the previously ignored triangle was seen exclusively in the afterimage but it was fragmented, a score of −1.5 (rather than −2) was assigned because we considered the dominance to be weaker than when the afterimage was intact. Overall, observers reported the initially dominant afterimage to be fragmented less than 5% of the time.

Experiment 2: Attending to an Afterimage Inducer Versus Attending to a Central, Rapid Digit Stream

During the 7-s adaptation period, the dark inducer triangle frequently changed its color, while the centrally presented digits also changed synchronously (see Figure 4). The color-changing inducer triangle produced an afterimage that appeared light gray.

There were two attention conditions. In the *attend-triangle (attend-inducer)* condition, observers counted the number of times the inducer triangle turned gray. In the *attend-digit (ignore-inducer)* condition, observers counted the number of times the central digit became *5*. When the inducer triangle disappeared (the last digit remained), observers pressed the space bar of the computer keyboard when a coherent afterimage emerged and pressed the space bar again when the afterimage disappeared. The onset and offset latencies were recorded. Observers then told the experimenter the number of times that the inducer triangle turned gray (in the attend-triangle [attend-inducer] condition) or the number of times that the central digit became *5* (in the attend-digit [ignore-inducer] condition). The trial was replaced if the count was off by more than two.

If attention during adaptation weakens subsequent afterimages, afterimages in the attend-triangle (attend-inducer) condition should have had a delayed onset, a truncated duration, or both relative to afterimages in the attend-digit (ignore-inducer) condition.

Method

Observers. Thirty undergraduates at Northwestern University participated.

Stimuli. The inducer triangle was centered around the fixation marker, and its color was changed randomly every 270 ms among dark red (8.8

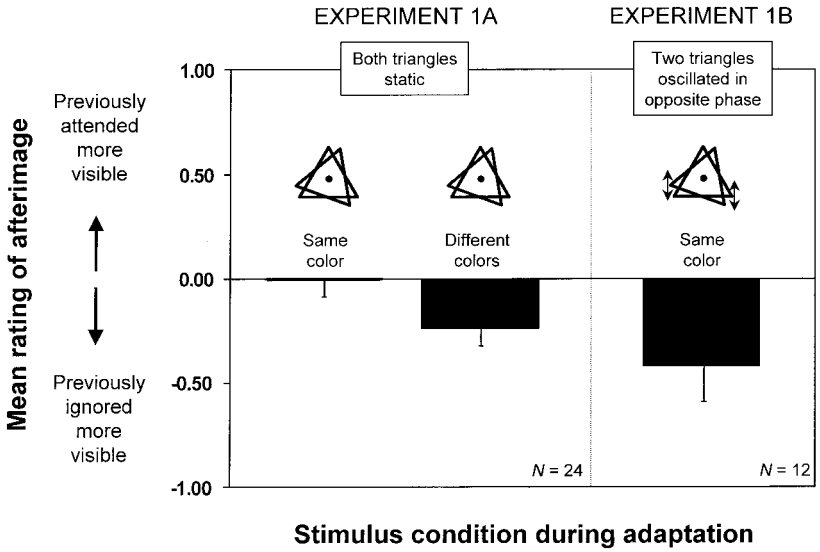

Figure 3. Mean ratings of afterimages under different adaptation conditions in Experiments 1A and 1B. Negative ratings indicate that the previously ignored triangle dominated in the afterimage. Error bars represent plus or minus one standard error.

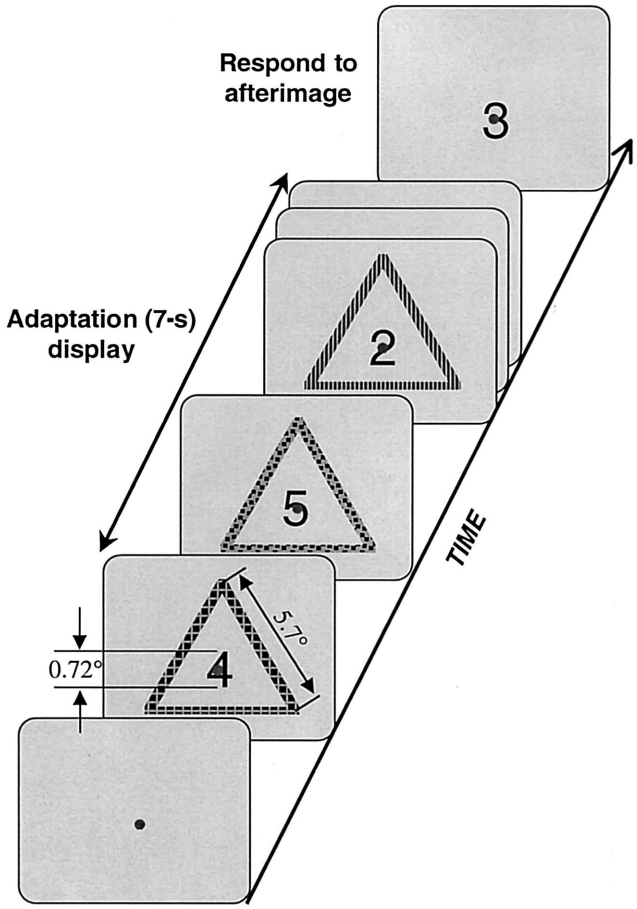

Figure 4. The stimuli and trial sequence for Experiment 2. During the 7-s adaptation period, the color of the inducer triangle was changed randomly among dark red, dark blue, dark green, and dark gray (depicted here with different textures) while the central digit was also changed randomly among 2, 3, 4, and 5 at the rate of 270 ms per display frame. Observers either counted the number of times the triangle turned gray (in the attend-triangle [attend-inducer] condition) or counted the number of times the central digit turned "5" (in the attend-digit [ignore-inducer] condition). When the inducer triangle disappeared (while the last digit remained), observers pressed the space bar when a coherent afterimage appeared and again when it disappeared. Observers fixated the central marker throughout each trial.

cd/m^2, CIE [.609, .344]), dark green (14.1 cd/m^2, CIE [.301, .580]), dark blue (5.1 cd/m^2, CIE [.146, .074]), and dark gray (11.5 cd/m^2, CIE [.298, .313]), with the constraint that the same color was never repeated in consecutive display frames. The central digits were shown behind the small fixation marker, and they were changed (in sync with color changes on the inducer triangle) randomly among *2, 3, 4,* and *5,* with the constraint that the same digit was never repeated in consecutive display frames. The digits were dark gray (18.0 cd/m^2, CIE [.298, .316]). Note that the target color (gray) and the target digit (*5*) both occurred with 0.25 probability (per display frame) during the 7-s adaptation period (consisting of twenty-six 270-ms display frames). The target thus occurred 6.5 times on average, with a standard deviation of 2.2. The luminance of the light gray background was 45.7 cd/m^2, as in Experiment 1B. The stimulus dimensions are shown in Figure 4.

Procedure. Observers attended to the inducer triangle or the digits in a blocked design. Half of the observers attended to the inducer triangle first, and the other half attended to the digits first. The first block consisted of two practice trials for the second block, then two practice trials for the first block, followed by at least five experimental trials. The second block consisted of one practice trial for that block, followed by at least five experimental trials.

Results

As shown in Figure 5, afterimages occurred with significantly later onsets (by 335 ms), $t(29) = 3.084$, $p < .005$, and significantly earlier offsets (by 450 ms), $t(29) = 2.583$, $p < .02$, when the inducer triangle was attended (in the attend-triangle [attend-inducer] condition) relative to when the inducer triangle was ignored (in the attend-digit [ignore-inducer] condition) during adaptation.

Discussion

The results when we used different methods of manipulating attention and measuring afterimages confirmed our findings in Experiments 1A and 1B that selective attention during adaptation weakened subsequent afterimages. However, we were concerned that eye fixation during adaptation might have been more stable in the attend-digit (ignore-inducer) condition, in which observers attended to centrally presented digits, than in the attend-triangle (attend-inducer) condition, in which observers attended to the relatively large inducer triangle (parafoveal contours). Though coarse eye movements (1.3° or larger) were monitored by the experimenter, it is possible that small retinal slips may have been more frequent in the attend-triangle (attend-inducer) condition, resulting in weaker afterimages. We offer several pieces of evidence against this possibility.

First, differential stability of eye fixation cannot explain the attention effects obtained in Experiments 1A and 1B (in which the relative strengths of afterimages for the attended and the ignored inducers were compared simultaneously) because any fixation instability during adaptation would have equally affected the afterimages of both the attended and the ignored inducer triangles. Also note that fixation shifts of 1.3° or larger were rare, and whenever they occurred the trials were replaced. Second, in this experiment, the onset of afterimages occurred later and the offset

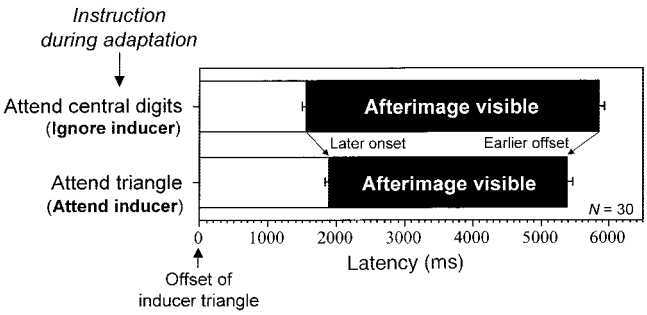

Figure 5. Onset and offset latencies of the afterimage of the inducer triangle in the attend-digit (ignore-inducer) and attend-triangle (attend-inducer) conditions in Experiment 2. The afterimage onset occurred significantly later and the offset occurred significantly earlier in the attend-triangle (attend-inducer) condition relative to the attend-digit (ignore-inducer) condition. Error bars represent plus or minus one standard error. Variances due to differences in baseline latencies among the observers have been removed.

occurred earlier in the attend-triangle (attend-inducer) condition relative to the attend-digit (ignore-inducer) condition. If these weakenings of the early and the late components of afterimages were both due to a single mechanism, such as instability of eye fixation, the size of onset and offset shifts should have been positively correlated across observers (i.e., observers with weaker adaptation should have seen afterimages that were both more delayed and shorter lasting); this was not the case, $r = -.127$, $t(28) = -0.679$, *ns.* The delay and truncation of afterimages thus appear to have been due to separate mechanisms. In other words, even if differential fixation stability explains either the delay effect or the truncation effect, the other (unexplained) effect is likely to be attributable to attention. It is also possible that both effects are due to attention, influencing adaptation by means of two separate mechanisms. Third, we verified the results of Experiments 1A, 1B, and 2 using three experienced psychophysical observers (including S.S.). It is known that fixation fluctuations are small (standard deviations of about 2–5 min of arc) for experienced observers with a foveal fixation marker (e.g., Steinman, Haddad, Skavenski, & Wyman, 1973). If anything, attentional weakening of afterimages was more substantial for these observers. Thus, the consistent attention effects we obtained to this point are unlikely to be explained by differential eye fixation.

Nevertheless, in the next experiment we combined the overlapped-inducer method of Experiments 1A and 1B, to equate the potential effects of fixation instability across attention conditions, with the single-afterimage method of Experiment 2, to allow measurement of attention effects in terms of delayed onset and truncated duration of a single afterimage.

Experiment 3: Attending to an Afterimage Inducer Versus Attending to an Overlapped (Brightness-Balanced) Figure That Does Not Produce an Afterimage

The stimuli consisted of an overlapped inducer triangle and a *noninducer* circle. During the adaptation period (7 s), each figure frequently changed its color; the color changes on the two figures were synchronous but uncorrelated (see Figure 6). As before, all colors on the inducer triangle were darker than the background so that it generated a light gray afterimage. The colors on the noninducer circle were brightness balanced (some colors being darker and others being brighter than the background) so that the circle produced no visible afterimage.

There were two attention conditions. In the *attend-triangle* (*attend-inducer*) condition, observers counted the number of times the dark inducer triangle turned gray. In the *attend-circle* (*ignore-inducer*) condition, observers counted the number of times the brightness-balanced noninducer circle turned gray. Because the overlapped triangle and circle were comparable in size and contour eccentricity, the stability of eye fixation at the central marker during adaptation should have been similar whether observers attended to the inducer triangle or to the noninducer circle.

If attention during adaptation weakens subsequent afterimages, the afterimage produced by the inducer triangle should have had a delayed onset, a truncated duration, or both in the attend-triangle (attend-inducer) condition relative to the attend-circle (ignore-inducer) condition.

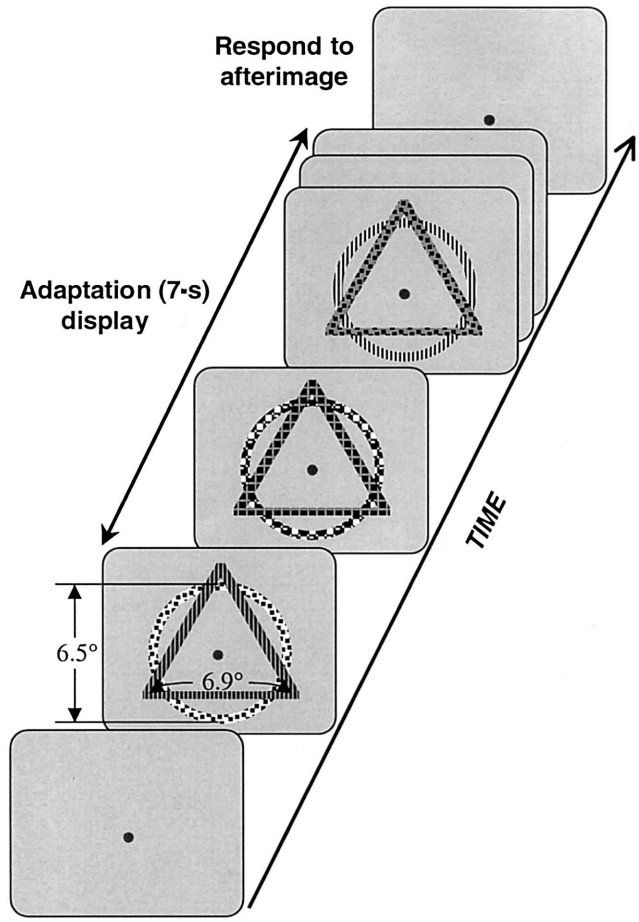

Figure 6. The stimuli and trial sequence for Experiment 3. During the 7-s adaptation period, the color of the inducer triangle was changed randomly among dark red, dark blue, dark green, and dark gray while the color of the noninducer circle was changed randomly among red, blue, green, and gray (brightness balanced to prevent afterimages) at the rate of 270 ms per display frame; different colors are depicted here with different textures. Observers either counted the number of times the dark inducer triangle turned gray (in the attend-triangle [attend-inducer] condition) or counted the number of times the brightness-balanced noninducer circle turned gray (in the attend-circle [ignore-inducer] condition). When the adaptation display disappeared, observers pressed the space bar when a coherent afterimage appeared and again when it disappeared. Observers fixated the central marker throughout each trial.

Method

Observers. In all experiments except Experiment 4, undergraduates at Northwestern University gave informed consent to participate for course credit. They were tested individually in a dimly lit room (ambient luminance of a white wall = 1.5 cd/m^2). They all had normal or corrected-to-normal visual acuity and normal color vision. Twenty-four observers participated in this experiment. (See Footnote 3.)

Stimuli. The dimensions of the overlapped triangle and circle are shown in Figure 6. The color of the dark inducer triangle was changed randomly every 270 ms among red (8.8 cd/m^2, CIE [.609, .344]), green (14.1 cd/m^2, CIE [.301, .580]), blue (5.1 cd/m^2, CIE [.146, .074]), and gray (11.5 cd/m^2, CIE [.298, .313]). The color of the brightness-balanced noninducer circle was changed (in sync with color changes on the inducer triangle) randomly among red (24.3 cd/m^2, CIE [.560, .338]), green (54.0

cd/m^2, CIE [.298, .594]), blue (24.0 cd/m^2, CIE [.218, .177]), and gray (25.0 cd/m^2, CIE [.302, .320]). The same color never repeated in consecutive display frames on either figure. As before, the target color (on either figure) occurred 6.5 times on average, with a standard deviation of 2.2, during the 7-s adaptation period. The luminance of the gray background was 45.7 cd/m^2, as in Experiment 2.

Procedure. The procedure was identical to that of Experiment 2, except that observers attended either to the inducer triangle or to the noninducer circle (ignored inducer).

Results

As shown in Figure 7, the afterimage onset was significantly delayed (by 390 ms) in the attend-triangle (attend-inducer) condition relative to the attend-circle (ignore-inducer) condition, $t(23) = 2.719$, $p < .02$, replicating the results of Experiment 2. However, the afterimage offset was not significantly different in the two conditions, $t(23) = 1.475$, *ns;* if anything, the offset was delayed (by 275 ms) in the attend-triangle (attend-inducer) condition. The overall duration of the afterimage was shorter in the attend-triangle (attend-inducer) condition (by 115 ms), but this difference was not significant, $t(23) = 0.709$, *ns.*

Discussion

Attention to an afterimage inducer during adaptation again diminished the visibility of the early component of the afterimage, as reflected in its delayed onset even though contributions from differential eye fixation were unlikely in this experiment (because the afterimage inducer and noninducer figures were overlapped, and both consisted of contours of equivalent eccentricity). Attention during adaptation also reduced the late component of the afterimage in Experiment 2 (as reflected in truncated durations), but it did not do so in this experiment. Thus, we cannot rule out the possibility that differential stability of eye fixation may have contributed to the truncation of afterimages in Experiment 2. Alternatively, it is also possible that strong manipulation of attention during adaptation is required to affect the late component of afterimages. In Experiment 2, when observers did not attend to the inducer triangle, their attention was focused at a small region around the fixation marker (on the digits), away from the contours of the inducer triangle. In contrast, the contours of the inducer triangle and the competing noninducer circle were closely overlapped in Experiment 3, potentially causing weaker (or leaky) attentional selection. Without knowledge of the effects of small fixation jitter during adaptation on the strengths of afterimages (which would require measuring afterimage strength as a function of frequency and amplitude of eye jitter during adaptation while eye jitter is manipulated independently of attention), we cannot distinguish between these two possibilities.

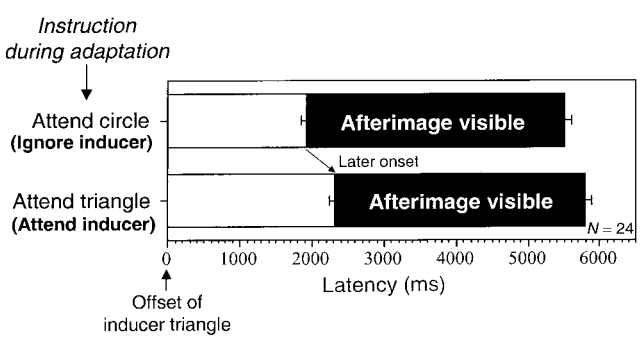

Figure 7. Onset and offset latencies of the afterimage of the inducer triangle in the attend-circle (ignore-inducer) and attend-triangle (attend-inducer) conditions in Experiment 3. The afterimage onset occurred significantly later in the attend-triangle (attend-inducer) condition relative to the attend-circle (ignore-inducer) condition. Error bars represent plus or minus one standard error. Variances due to differences in baseline latencies among the observers have been removed.

The results from all four experiments so far have demonstrated that attention during adaptation weakened the initial component of subsequent afterimages. A potential weakness of the procedures used to this point, however, was that they all required observers to set a criterion in making responses. In Experiments 1A and 1B, observers judged the relative strength of two competing afterimages. In Experiments 2 and 3, observers decided when an afterimage appeared and disappeared, setting criteria for visibility. Though results of criterion-dependent procedures can potentially be confounded by response bias, we have several pieces of evidence against the possibility that our results may have been so affected. First, observers did not have specific expectations as to whether attention during adaptation should strengthen or weaken subsequent afterimages (see Footnote 5). Second, in Experiments 1A and 1B, attention effects were obtained only in the conditions in which perceptual segregation of the two inducer triangles was facilitated by assigning them different colors or by antiphase oscillation; a simple response bias would have produced equivalent attention effects in all stimulus conditions. Third, detection of onset and offset of a single afterimage, used in Experiments 2 and 3, was a relatively simple perceptual task, previously used in studies of afterimages (e.g., Atkinson, 1972; Leguire & Blake, 1982; Wade, 1972, 1973, 1974). It is thus unlikely that a simple response bias could account for the converging results from the four experiments. Nevertheless, in the final experiment, we attempted to replicate the main finding, a reduction in the visibility of the initial component of afterimages due to attention during adaptation, using a criterion-independent procedure.

Experiment 4: Measuring Afterimages Using a Criterion-Independent Dot-Integration Paradigm

We adapted a dot-integration paradigm (e.g., Eriksen & Collins, 1967, 1968; Hogben & Di Lollo, 1974) in which a gap in a regular array of discs could be found only if complete afterimages were visible. We used a circular array that consisted of 12 positions, as of a clock face. In each trial, 6 of the 12 positions were selected to present bright inducer discs during the adaptation period. These 6 positions were selected randomly, with the constraint that no more than two positions intervened between any pair of inducer discs. Following adaptation, the bright inducer discs produced afterimages seen as six dark discs. At the same time, dark test discs, which were virtually indistinguishable from the afterimage discs, were placed in five of the six remaining positions. Thus, when the afterimage discs were completely visible and integrated with the test discs, there was a single visible gap in the clock array. Note that because of the constraint that no more than two positions intervened between any pair of afterimage discs, the gap was never flanked by two test discs and, thus, could not be detected unless the afterimage discs were visible. Observers indicated the position of

this gap, and the accuracy of this judgment was used as an indirect measure of the visibility of the afterimages (see Figure 8).

During the course of the adaptation period, observers either attended to the inducer discs (in the *attend-discs [attend-inducer]* condition) or to a ring placed around the fixation marker (in the *attend-ring [ignore-inducer]* condition). A ring rather than a central digit stream (as in Experiment 2) was used so that, in both attention conditions, observers attended to stimuli surrounding the central fixation marker, thereby making the fixation demand similar under both attention conditions. The colors of the discs and the ring were frequently changed synchronously but independently and randomly. When observers attended to the inducer discs, they pressed the space bar of the computer keyboard whenever all of the discs became the same color; this required that observers attend to all discs. When observers attended to the ring, they pressed the space bar whenever the ring became yellow.

If attention during adaptation weakens subsequent afterimages, the gap-detection performance should have been poorer when observers attended to the inducer discs relative to when they attended to the ring (ignored inducer) during adaptation.

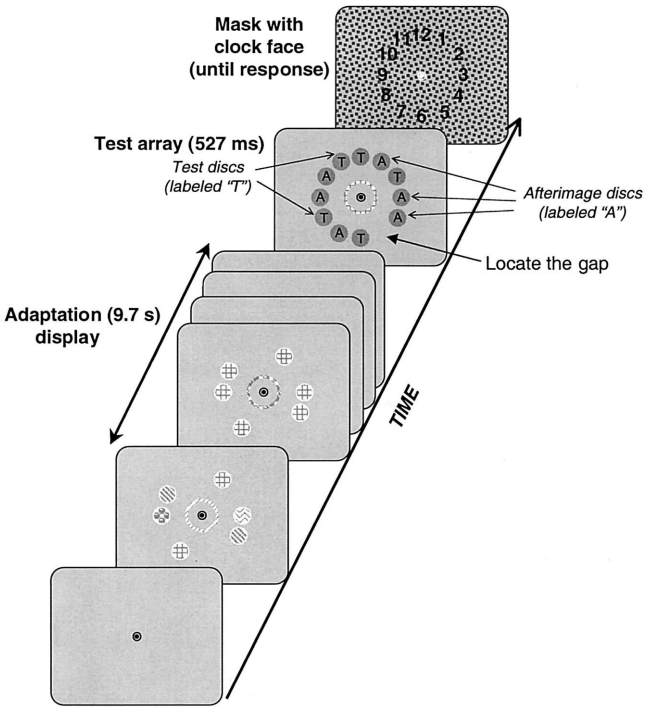

Figure 8. The stimuli and trial sequence for Experiment 4. During the 9.7-s adaptation period, colors of the six bright inducer discs (randomly chosen from the circular array of 12 discs) and the color of the central ring were changed independently and randomly among pink, light green, light blue, and yellow at the rate of 270 ms per display frame; different colors are depicted here with different textures. Observers pressed the space bar whenever all of the 6 inducer discs became the same color (in the attend-discs [attend-inducer] condition) or whenever the ring turned yellow (in the attend-ring [ignore-inducer] condition). Following adaptation, the test array containing faint dark gray test discs was presented for 527 ms; the test discs (labeled "T" in the figure) and the afterimage discs (labeled "A" in the figure) together formed a circular array with a gap at one position. When the mask with the clock face appeared, observers indicated the location of the gap by pressing the computer key corresponding to the clock hour at the gap. Observers fixated the central marker throughout each trial, and were allowed to blink only once during adaptation through the test display.

Method

Observers. Six observers (Os) experienced in psychophysical experiments participated. Except for O1 (one of the authors), the observers (O2–O6) were naive as to the purpose of the experiment. They were tested individually in a well-lit room and with a viewing distance of 76 cm.

Stimuli. The stimuli are depicted in Figure 8. The diameter of the circular array was 5.7°, and the diameter of each disc was 1.1°. The central ring was 0.17° thick and 1.7° in diameter. The colors of the inducer discs and the ring were changed independently and randomly every 270 ms during the adaptation period among pink (CIE [.335, .303]), light green (CIE [.307, .569]), light blue (CIE [.252, .240]), and yellow (CIE [.412, .493]). All these colors were equiluminant (as measured by a photometer) and brighter (48.5 cd/m^2) than the background (29.5 cd/m^2). With 0.25 probability, all of the inducer discs became the same color in any given display frame, with the constraint that the same-color display did not repeat in consecutive frames; otherwise, the colors of the individual inducer discs were changed randomly among the four colors. The color of the ring was also changed randomly among the four colors, with the constraint that the same color did not repeat in consecutive frames.

The afterimages produced by the inducer discs appeared as a faint dark gray; the luminance of the test discs (28.0 cd/m^2) was adjusted to appear indistinguishable from that of the afterimage discs. A full-screen random-dot mask was used to terminate the afterimages; small black squares (0.17° × 0.17°, 4.6 cd/m^2) randomly covered 50% of the screen. Clock numbers (font: 40-point Helvetica) on the mask were drawn in red so that they stood out against the random squares. The bull's eye fixation marker (outer diameter = 0.45°) was black, but it turned white in the mask so that it was readily visible.

Procedure. Observers pressed a computer key to initiate a trial. The adaptation display was presented for 9.7 s, during which the colors of the inducer discs and the ring changed (see Figure 8). While maintaining central eye fixation, observers attended either to the inducer discs (in the attend-discs [attend-inducer] condition) or to the ring (in the attend-ring [ignore-inducer] condition). In the attend-discs (attend-inducer) condition, observers pressed the space bar of the computer keyboard whenever all of the inducer discs became the same color. In the attend-ring (ignore-inducer) condition, they pressed the space bar whenever the ring turned yellow. On average, either of these target events occurred nine times, with a standard deviation of 2.6; a target event never occurred in the final frame of the adaptation period, so as to prevent its detection from interfering with the subsequent gap-detection task. On termination of the adaptation period, the test display was presented for 527 ms, and observers attempted to locate a gap in the circular array of faint dark gray discs. The mask then replaced the test display. While viewing the clock face on the mask, observers pressed the keyboard key corresponding to the position of the perceived gap. They were encouraged to guess if necessary. Once no residual afterimage was visible (with a minimum 30-s intertrial interval), the next trial was initiated.

During the adaptation period (up to the test display), eye blinks were controlled. Exactly halfway into the adaptation period, the computer sounded a beep, and observers were instructed to blink once at its sound; otherwise, they were not allowed to blink until the mask appeared.[6]

At least 20 practice trials were given, during which the durations of adaptation and test periods were adjusted (if necessary) to avoid floor and ceiling effects on the gap-detection performance. The adaptation and the test durations were shortened to 8.3 and 403 ms, respectively, for O5. The

[6] It was necessary for O4 to blink more frequently. Thus, O4 was allowed to blink freely until two thirds of the way into the adaptation period, at which time his beep sounded. Following the beep, he refrained from blinking until the mask appeared.

test duration was lengthened to 671 ms for O4. The tracking of the target events also improved during practice such that in the experimental trials, on average, observers missed the uniform-color discs only 1.6 times (when the inducer discs were attended) and the yellow rings only 0.3 times (when the ring was attended) per adaptation period.

The attend-discs (attend-inducer) condition and the attend-ring (ignore-inducer) condition were tested in blocks of 10 trials. Blocks for the two conditions were alternated four times so that 40 trials were run for each condition. Half of the observers began with the attend-discs (attend-inducer) block, and the other half began with the attend-ring (ignore-inducer) block. At least a 15-min break was given between blocks.

Results

The accuracy of gap detection (chance = 1/12) in the attend-ring (ignore-inducer) condition and the attend-discs (attend-inducer) condition is shown separately for individual observers in Figure 9. Though there were individual differences, all observers showed the same effect; the gap detection was less accurate when the inducer discs were attended during adaptation than it was when they were ignored (and the ring was attended) during adaptation (mean difference = 33.3%), $t(5) = 3.639$, $p < .02$. Because the gap detection required the afterimage discs to be reliably visible, the results indicate that the afterimages of the inducer discs were less visible when the discs were attended (relative to when they were ignored) during adaptation.

General Discussion

In five experiments, we consistently demonstrated that an afterimage was initially delayed or weaker when the afterimage-inducing figure was attended during adaptation. In Experiments 1A and 1B, observers adapted to overlapped triangles (one upright and the other tilted 20°) while attending to one triangle. Observers then described the initial impression of the subsequent afterimages produced by the two inducer triangles. They rated the afterimage of the previously attended triangle to be weaker (absent, less visible, or less persistent) than the afterimage of the previously ignored triangle. The attention effect was robust, so long as the perceptual segregation of the two inducer triangles was supported by assigning them different colors (Experiment 1A) or by oscillating them in opposite phase (Experiment 1B).

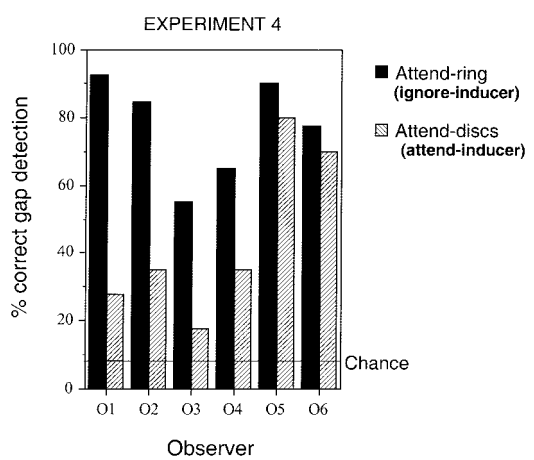

Figure 9. Gap-detection performance (percentage correct) under the attend-ring (ignore-inducer) and attend-discs (attend-inducer) conditions in Experiment 4. Data from the 6 observers are plotted separately; for convenience, the observers are labeled O1–O6 in the order of decreasing attention effects. Gap detection was worse in the attend-discs (attend-inducer) condition for all observers (a 33.3% overall decrement in gap detection when the inducer discs were attended relative to when they were ignored during adaptation).

Across Experiments 2–4, this attention effect was replicated (a) while observers' attention was tracked using a feature-monitoring task, (b) when afterimage strength was measured by recording the onset and offset latencies of a single afterimage, and (c) by using a criterion-independent paradigm. In Experiment 2, attention was manipulated by having observers attend either to the inducer triangle or to the central, rapid digit stream. Afterimage onsets were delayed and durations were truncated when observers attended to the inducer triangle relative to when they attended to the digit stream (ignored the inducer triangle) during adaptation. In Experiment 3, we replaced the central digit stream by the non-afterimage-inducing overlapped circle (matched in size and contour eccentricity to the inducer triangle) to control for a possible contribution of differential stability in eye fixation; the onset-delay effect was replicated, but the duration-truncation effect was not. Thus, we cannot rule out the possibility that the attention effects on the late component of afterimages obtained in Experiment 2 may have been affected by differential stability in eye fixation (potentially more stable fixation when the central digit stream was attended than when the inducer triangle was attended). Alternatively, however, the results might suggest that both space-based and object-based attentional selection (e.g., Downing & Pinker, 1985; Duncan, 1984; Egly, Driver, & Rafal, 1994; Eriksen & Hoffman, 1974; Lamy & Tsal, 2000; Posner, Snyder, & Davidson, 1980; Schendel, Robertson & Treisman, 2001; Treue & Martinez Trujillo, 1999; Vecera, 1994, 1997; Vecera & Farah, 1994; see Cave & Bichot, 1999, for a review) during adaptation are necessary to influence the late component of afterimages; the central digits were well separated from the triangle contours in Experiment 2 (in which both space-based and object-based selection should have been effective), whereas the circle and the triangle contours were intertwined in Experiment 3 (in which primarily object-based selection should have been effective).

In Experiment 4, observers attended either to the afterimage-inducing discs in the outer array or the inner ring. Because psychophysically experienced observers participated, and because they attended to stimuli surrounding the bull's-eye fixation marker (whether they attended to the inducer discs or to the ring) fixation stability was presumed to be equivalent in both attention conditions. Furthermore, because the afterimage strength was measured indirectly, as the accuracy in gap-detection performance (which required integration of the afterimage discs and the test discs), this paradigm was criterion independent. We again demonstrated that the early component of afterimages (with ~500-ms test duration) was diminished by attention during adaptation.

We hypothesized that if selective attention primarily facilitates adaptation of polarity-selective mechanisms (responding to patterns darker or lighter than the background) that contribute to the formation of an afterimage, the previously attended figure should produce a stronger afterimage. Alternatively, if selective attention primarily facilitates adaptation of polarity-independent mechanisms that contribute to pattern visibility regardless of polarity, the previously attended figure should produce a weaker afterimage. The latter alternative was supported. More specifically, because

the effect of attention during adaptation primarily diminished the early component of afterimages (causing delayed onsets), our results suggest that attention primarily increases the adaptation of polarity-independent mechanisms, but this attention-augmented component of adaptation may decay relatively quickly (within several hundred milliseconds, based on the results of Experiments 2 and 3).

Previous studies have suggested that afterimages are induced by polarity-specific adaptation in one stage of processing but that their visibility also depends on the sensitivity of subsequent stages of processing. For example, Leguire and Blake (1982) reported a set of results using brief (100-ms) afterimage inducers, demonstrating that the visibility of afterimages depended both on the strength of afterimage inducers and on contrast sensitivity of the visual system (manipulated by using gratings with different spatial frequencies or by prior contrast adaptation). More relevant, using prolonged (several-second) afterimage inducers, Georgeson and Turner (1985) found that onsets of afterimages were delayed for square-wave gratings compared with sinusoidal gratings. They explained this result by postulating (a) that polarity-independent adaptation (contrast adaptation), which built up concurrently with the polarity-selective adaptation (mediating the formation of afterimages), might have been stronger for square-wave gratings than for sinusoidal gratings, and (b) that this polarity-independent component of adaptation decayed faster than the polarity-selective component of adaptation, thus delaying onsets of afterimages for square-wave inducers. The fact that attention during adaptation also consistently delayed afterimage onsets supports the idea that this rapidly decaying contrast-adaptation component is what is primarily enhanced by attention.

Neurophysiologically, simple cells and color-opponent cells in V1 and V2, and some cells in V4 and IT, respond in a polarity-selective manner (i.e., with luminance-polarity selectivity or sensitivity, or with color opponency or tuning), whereas complex cells in V1 and V2, and other cells in V4 and IT, respond in a polarity-independent manner (i.e., relatively independently of luminance polarity, color, or both; e.g., Desimone & Schein, 1987; Foster et al., 1985; Hubel & Wiesel, 1968; Ito et al., 1994; Komatsu et al., 1992; Levitt, Kiper, & Movshon, 1994; Ts'o & Gilbert, 1988; Ts'o & Roe, 1995). Although responses of both polarity-selective and polarity-independent types of cells appear to be modulated by attention (e.g., Luck et al., 1997; Motter, 1993; Reynolds et al., 1999; Roelfseme et al., 1998; Vanduffel et al., 2000), our results suggest that attentional modulation of adaptation appears to occur primarily for the polarity-independent class of cells. It is, however, not clear whether attention primarily increases adaptation in relatively early processing (V1 and V2), in late processing (V4 and IT), or at all levels of processing.

If attention selectively enhanced adaptation of polarity-independent cells as early as in V1 and V2, attention should have primarily enhanced adaptation of complex cells (rather than simple cells). At least one study has confirmed that responses of V1 complex cells were modulated by attention (Ito & Gilbert, 1999); unfortunately, other studies examining attention effects in V1 and V2 have not separately analyzed effects on complex and simple cells (e.g., Luck et al., 1997; Motter, 1993; Reynolds et al., 1999; Roelfsema et al., 1998). Perhaps more likely, however, is that attention might primarily enhance adaptation of polarity-independent cells in higher visual areas, because attentional modulations of neural responses tend to be larger in higher visual areas (e.g., Haenny & Schiller, 1988; Kastner, De Weerd, Desimone, & Ungerleider, 1998; McAdams & Maunsell, 1999; Treue & Maunsell, 1996); this may be partly due to increased receptive-field sizes in higher visual areas, because attentional modulations tend to be strong when competing stimuli are accommodated within a receptive field (e.g., Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al., 1999; Treue & Maunsell, 1996; but see fMRI results demonstrating robust attention effects in V1, e.g., Gandhi et al., 1999; Somers et al., 1999).

In addition to the fact that cells must be polarity-selective to mediate formations of afterimages, Kelly and Martinez-Uriegas (1993) provided psychophysical evidence suggesting that the parvocellular pathway (rather than the magnocellular pathway) is uniquely involved in the formation of afterimages. They demonstrated that although both chromatic and luminance afterimages masked a brief chromatic probe, neither type of afterimage masked a brief luminance probe, which was presumably processed by the magnocellular pathway. If afterimage formation was indeed mediated primarily by the parvocellular pathway, increased adaptation of this pathway should have strengthened afterimages; instead, our finding that attention weakened afterimages may suggest that attention primarily enhanced adaptation of the magnocellular pathway in our study. Though some electrophysiological evidence suggests that attention enhances neural responses for both the parvocellular and the magnocellular pathways (Di Russo & Spinelli, 1999a, 1999b), attentional enhancements of adaptation might primarily occur in the magnocellular pathway. However, the relevance of the magno–parvo division should be interpreted with caution because there is considerable interaction between the two pathways, beginning in V1, and the degree of preservation of the two pathways in cortical processing is controversial (e.g., Levitt et al., 1994; Livingstone & Hubel, 1988; Maunsell, Nealey, & DePriest, 1990; Merigan & Maunsell, 1993; Schiller, Logothetis, & Charles, 1990; Shapley, 1995; Yoshikawa, Levitt, & Lund, 1994).

Finally, our results may also provide an explanation for a related phenomenon. Lou (1999) reported that attention modulated Troxler fading, a phenomenon in which images gradually fade when stabilized on the retina (e.g., by projecting images at the same retinal spot or by viewing low-contrast images peripherally under careful fixation; see Gerrits, Stassen, & van Erning, 1984, for a review). Lou found that attended stimuli tended to fade faster than unattended stimuli. Fading could result from adaptation of polarity-selective cells (e.g., Burbeck & Kelly, 1984; Schiller & Dolan, 1994) as well as from adaptation of polarity-independent cells. For example, during inspection of a light spot, adaptation of light-polarity–selective cells resulting in dark afterimages will tend to erase the light spot, and at the same time, adaptation of polarity-independent cells will also reduce the visibility of the spot. Our findings suggest that the attentional facilitation of Troxler fading is due primarily to facilitation of the latter mechanism.

In conclusion, we demonstrated that ubiquitous negative afterimages are weakened by attention during adaptation, a result that may partly explain why they so often go unnoticed. Our results suggest that for perception of brightness, voluntary attention primarily facilitates adaptation of polarity-independent processing rather than adaptation of polarity-selective processing. The fact that attention during adaptation primarily delayed onsets of afterimages (by 300–400 ms) further suggests that the attention-augmented adaptation of the polarity-independent processing di-

minishes rapidly relative to adaptation of the polarity-selective processing that underlies the formation of afterimages.

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Errata

The "*Observers*" part of the "*Method*" section for Experiment 1A was mistakenly duplicated for Experiments 1B and 3.

Experiment 1B:
Observers. Twelve undergraduates at Northwestern University participated.

Experiment 3:
Observers. Twenty-four undergraduates at Northwestern University participated.

Figure captions:
Error bars represent one standard error (not plus or minus one standard error)