
Effects of voluntary attention on structured afterimages

Liang Lou

Department of Psychology, Grand Valley State University, Allendale, MI 49401, USA;
e-mail: loul@gvsu.edu

Received 4 September 2000, in revised form 21 August 2001

Abstract. The effect of voluntary attention on afterimage fragmentation was explored in two experiments. The afterimage, in the form of a 30°-tilted star of David, was generated after prolonged steady fixation in the first experiment, and with a brief and intense flash in the second experiment. Subjects were instructed to select various target shapes in the afterimage for attention and, at the same time, observe what was visible or invisible. Verbal reports and manual responses to afterimage changes were analyzed. Attended shapes were found to disappear from awareness faster than unattended ones (experiment 1), and complementary shapes were found to predominate visual awareness when one of the pair was selected for attention (experiment 2). Voluntary attention was also found to affect closure (filling-in of enclosed regions) and smoothing of line figures in afterimages.

1 Introduction

Voluntary and involuntary eye movements continuously shift the location of an image on the retina. If the image is viewed under conditions that reduce the effect of eye movement, the image, or fragments of it, can disappear from awareness in a few seconds. An afterimage, being stabilized on retina, is under such a condition, and can be seen to disappear and reappear from awareness before it ultimately fades away. A curious observation about this process is that a figural afterimage typically disappears in units of its substructures and almost never in random pieces. This regularity, referred to as ‘structured afterimage fragmentation’, was believed by many to reveal perceptual organizations in the brain (eg Bennett-Clark and Evans 1963; Evans 1967; Hebb 1963; Piggins 1968), or some form of central inhibition (McDougall 1901). It is only a small step from here to ask whether one could affect afterimage fragmentation by voluntarily changing perceptual organization over a figural afterimage. The question is equivalent to asking whether voluntary attention affects afterimage fragmentation, since a change in perceptual organization entails a change in the distribution of attention (eg Tsal and Kolbet 1985).

The idea that attention may affect the afterimage visibility is age-old. The earliest documented observation can be traced to Newton (1691, in Wade 1998):

“I looked a very little while upon the sun in the looking-glass with my right eye, and then turned my eyes into a dark corner of my chamber, and winked, to observe the impression made, and the circles of colours which encompassed it, and how they decayed by degrees, and at last vanished. This I repeated a second and third time. At the third time, when the phantasm of light and colours were almost vanished, intending my fancy upon them to see their last appearance, I found to my amazement, that they began to return, and by little and little to become as lively and vivid as when I had newly looked upon the sun. But when I ceased to intende my fancy upon them, they vanished again. After this, I found that as often as I went into the dark, and intended my mind upon them, as when a man looks earnestly to see any thing which is difficult to be seen, I could make the phantasm return without looking more upon the sun ...” (page 165).

Seemingly contradicting the observation, Hyslop (1903) wrote:

“I often notice an after image of a bright object in the field of vision when I am not trying to produce it. It of course arrests my attention and I immediately turn to observe it. As usual it quickly fades” (page 296).

There has been little serious investigation into the role of attention in perceiving afterimages in more recent time, even in the 1960s and 1970s when there were considerable interests in structured afterimage fragmentation and related phenomena. Inspired by my recent finding of a deleterious effect of attention on peripheral vision (Lou 1999), I suspected that a similar effect could occur to afterimages. Two experiments with somewhat different methods were conducted consequently. Overall, these experiments confirmed that a voluntarily attended figural component in afterimage disappears faster than unattended components in the same afterimage. Voluntary attention was also found to lead to certain unexpected forms of ‘distortion’ of afterimages.

2 Experiment 1

2.1 Methods

Afterimages were generated by prolonged fixation of a luminous figure in a dark room. The stimulus design is shown in figure 1a. Its shape can be described as two outline triangles of opposite orientations superimposed on each other, forming a 30°-tilted star of David. One of the component triangles was drawn in green color and the other in orange color. Located in the center of the figure was a small white cross, serving as the fixation point. The outer corner of the figure was 1.5 cm from the fixation, subtending 2.9 deg at a viewing distance of 30 cm. The lines composing the figure were about 1 mm wide.

The stimulus was presented on a 21-inch monitor. Subjects sat in a comfortable chair with their chin and forehead supported. The experiment was conducted in a darkened room. Each trial had two consecutive periods. In the first period, the one for afterimage generation, the stimulus was presented against a black background for 30 s, during which the subjects’ task was to “maintain best possible fixation and disregard the stimulus”.⁽¹⁾ The second period, the test period, started with a plain gray screen (16 cd m⁻²) replacing the stimulus display except for the fixation point. Against this background, the afterimages of the green and orange triangles looked pink and blue, respectively. During this period, subjects were instructed to maintain attention to one specified triangle and ignore the other in the afterimage. The selective attention was aided by the instruction “try to perceive the pink triangle above the blue triangle”, for the pink triangle in the afterimage, and vice versa for the blue triangle in the afterimage. In the meantime, they were told to maintain fixation, in order to prevent or reduce the apparent drift of the afterimage. The part of the instruction regarding response was this: “Press a key when one or both triangles have disappeared and keep the key pressed until you see any of the disappeared parts again”. There was a 40 s deadline for the response. Immediately following the release of the key, the subject was asked to recall the color of the disappeared triangle(s) that he/she had indicated by key press, which could be pink, blue, or both. Each subject was tested on six trials, with each color (pink and blue) selected for attention on three consecutive trials. There was a 50% chance for the two triangles composing the stimulus to switch colors from each other from the preceding trial.

⁽¹⁾ This part of the instruction was intended to discourage selective attention to a particular triangle in the inducing stimulus, though there has been no evidence so far that such selective attention could affect the initial intensity of component shapes in the afterimage. Moreover, any spontaneously engaged attention in the first period (the afterimage generation period) is very unlikely to be consistently correlated with the attention in the second period (the test period).

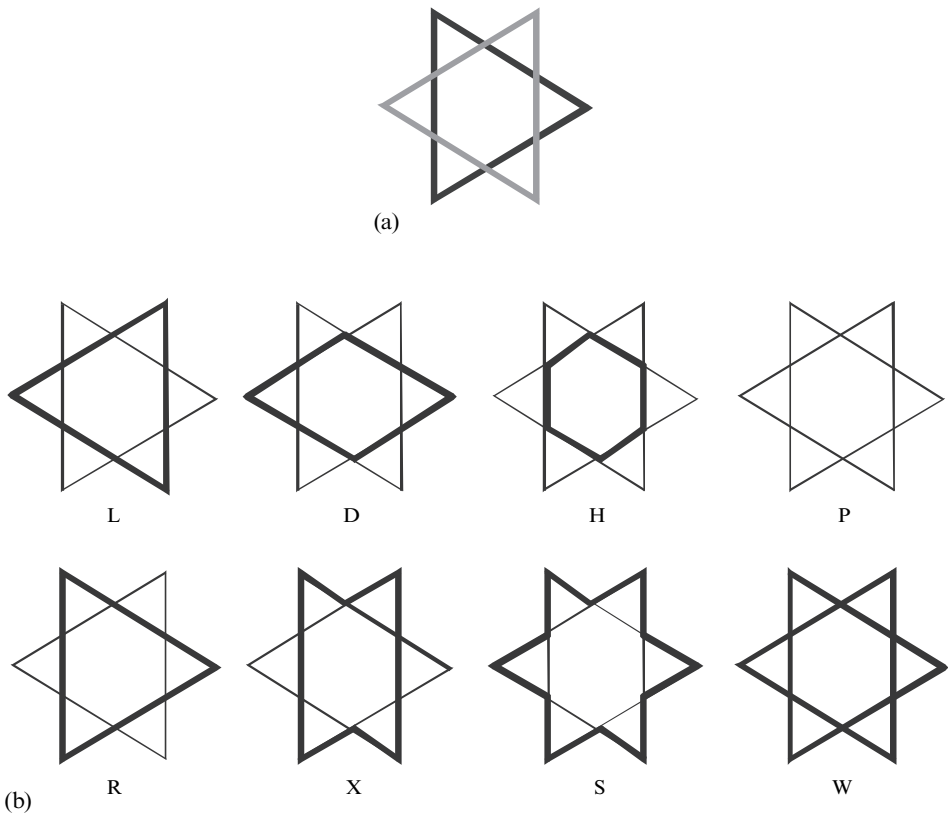


Figure 1. Panel (a) illustrates the stimulus used in experiment 1 (interlocked orange triangle and a green triangle). Panel (b) illustrates the stimulus and the conditions of attention for viewing the afterimage of the stimulus. The thick-line figures were selected for attention and the thin-line figures were unattended. The letter labels (except P) refer to the selected shapes: left triangle (L), right triangle (R), diamond (D), X-shape (X), hexagon (H), hexangular star (S), the whole figure (W), and passive viewing (P).

Twenty-six naïve subjects were tested. They were Hong Kong University third-year undergraduate students, who had normal or corrected-to-normal visual acuity and normal color vision, according to self-report. They were divided into three groups, each given a slightly different introduction to the experiment for inducing a possible bias in their reports. The first (neutral) group was told nothing beyond what was necessary for carrying out the observation. The second (negative) group was biased against a deleterious effect of attention by being told that the experiment was designed for testing possible effects of attention in retaining or enhancing visual awareness. The third (positive) group was biased in the opposite direction by being told that the experiment was about confirming a previously reported surprising finding of a deleterious effect of attention on visual awareness. If the effect of attention on afterimage disappearance is genuinely perceptual, these biased instructions should make no difference. There were eight subjects each in the neutral group and the negative group and ten subjects in the positive group. For each group, half of the subjects started with selecting the pink triangle in the afterimage for attention, and another half started with selecting the blue triangle in the afterimage for attention.

2.2 Results

On average, it took 4.65 s (95% confidence interval = 0.418 s) for one or both triangles of the afterimage to disappear from awareness and the disappearance lasted 3.64 s

(95% confidence interval = 2.66 s) on average. As shown in figure 2, in most cases the attended triangle in the afterimage, either the blue or the pink one, disappeared from awareness first. The probability for the attended one to disappear first was 91.03% (95% confidence interval = 8.13%) for the pink triangle, and 69.24% (95% confidence interval = 8.45%) for the blue triangle. The biases embedded in the instruction had no significant influence on the result. The probabilities for the attended triangle to disappear from awareness were 86.46% (95% confidence interval = 6.38%) for the neutral group, 72.92% (95% confidence interval = 19.27%) for the negatively biased group, and 80.84% (95% confidence interval = 9.34%) for the positively biased group. No statistically significant difference between the three groups was found ($F_{2,23} = 1.51, p > 0.2$). Although overall it took longer for the blue triangle in the afterimage to disappear from awareness than for the pink one, it did not reverse or cancel the tendency for the attended one to disappear earlier.

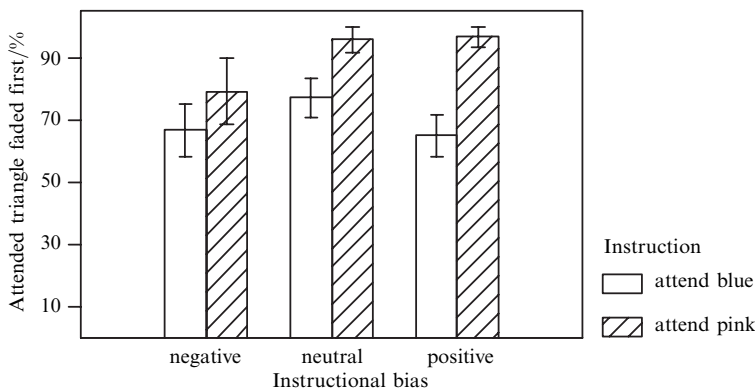


Figure 2. Experiment 1. Probabilities for the attended triangle in afterimage to disappear earlier than the ignored triangle. The three groups given differentially biased instructions are indicated on the abscissa: ‘negative’ refers to a possible bias to see the attended triangle more frequently than the unattended one, and ‘positive’ refers to the opposite possibility.

3 Experiment 2

3.1 Methods

The afterimage was produced with a brief intense flash through a cardboard cutout of the figure used in experiment 1. The cutout lines were 2 mm wide and its outer corners were 3 cm from the center, corresponding to 2.9 deg at a viewing distance of 60 cm. A studio photoflash unit (GuangBao EH1500—Wenzhou Photographic Equipment Ltd, Wenzhou, China; www.guangbao.com) was used. The flash rise time, energy, and temperature were 2.5 ms, 188 J, and 5200 K, respectively.

The experiment was conducted in a dimly lit room. Subjects initially viewed the afterimage through a tunnel painted pitch-black inside (with the flash coming from behind the other end of the tunnel). Their chins and foreheads were supported. The afterimage looked glaring-white immediately after the flash. In a few seconds to half a minute, which varied across subjects, it turned blue. Thereupon the subject turned his/her head aside to view the afterimage against a plain light-gray display (10.6 cd cm^{-2}) on a 21-inch monitor. The afterimage looked darker than the background.

The subjects started the flash with a remote control while fixating the center of the cutout figure (details of which could barely be seen before the flash). They received instructions that differed with respect to the required state of attention when viewing the afterimage. Eight different conditions of attention were generated by manipulating the instructions (figure 1b). The first six conditions differed with respect to which embedded shape in the afterimage was designated as target for selective attention:

left triangle (L), right triangle (R), diamond (D), X-shape (X), hexagon (H), and hexangular star (S). The remaining two conditions were 'controls', in which subjects were asked to perceive the afterimage as a whole (W) or to view it passively (P). Except for P, subjects were told to 'actively attend' to the selected shape. In the case of P, the instruction was "try to perceive it as nothing other than what enters your eyes".

Under all conditions, subjects were required to report what they saw as accurately and continuously as they could. A list of labels was provided for describing visible shapes: L, R, D, X, H, S, which are illustrated by the thick lines in figure 1b, plus T for trapezoid, \hat{H} for pen point (H with a small triangle attached), and M (mixture) for any other figure. Among these labels, D, X, T, \hat{H} can each refer to two or more figures with different orientations. It was emphasized in the instruction that, except for M, these labels must be used consistently and only when the shape it refers to is clear and intact.

Four subjects (ZH, LL, SL, and AY) between 23 and 40 years of age participated in the study. All of them had normal vision with myopia compensated by glasses. LL (the author) and ZH were experienced observers. SL and AY had never participated in visual perception experiments.

Each subject viewed the afterimage in eight different ways. The order was L, D, H, W, R, X, S, P for ZH and R, X, S, P, L, D, H, W for AY, with the order reversed, respectively, for LL and SL. The observation was completed in two sessions, each containing four conditions of attention. Under each condition, the observation continued until the subject indicated that the afterimage was no longer clearly visible. Between the conditions there were breaks of about 5 to 10 min. Each of the two sessions lasted 40 min to 1½ h. Subjects were encouraged to report, at any time during the observation or the breaks, any phenomena that they thought interesting or unusual, or details that would qualify what they reported to have seen. The verbal reports were tape-recorded and transcribed for analyses.

3.2 Results

3.2.1 Main findings. The persistence of the afterimage varied across the subjects (mean = 5.21 min, sd = 2.87 min). Figure 3 shows, for each subject, the frequency of each of six different shapes seen in isolation under each of the eight conditions of attention. The six shapes constitute three complementary pairs. T (trapezoid) and \hat{H} (pen point) were rarely reported and therefore were not included in the analyses. The frequency measure was obtained from a period that excluded the last twenty or so seconds starting when subjects reported seeing blurred afterimages. Because the reports were fairly continuous and evenly paced, the frequency measure can be expected to be proportional to the total visible duration for each shape. The effect of attention on afterimage fragmentation was assessed by comparing the frequencies of seeing each of six different shapes (R, L, D, X, H, S) under each condition of selective attention, and by comparing the frequencies with those obtained from the baseline conditions (W or P). The results from the four subjects were quite consistent.

(i) When L or R was selected for attention, L and R were the most frequently reported among the three pairs of complementary shapes (L and R, D and X, and S and H). All four subjects reported that L and R appeared to oscillate in awareness with brief temporal overlap. Similarly, when either D or X was selected for attention, D and X were the most frequently reported. Upon questioning, all subjects reported that the Ds and the Xs they reported were of one orientation (upright) each. Selecting H or S for attention was less effective in causing either H or S to dominate visual awareness. Nevertheless, three of the subjects (ZH, LL, and SL) reported more Hs and Ss, either compared with the average of L, R, D, and X within the viewing conditions, or compared with the frequencies of H and S in the baseline conditions (W and P).

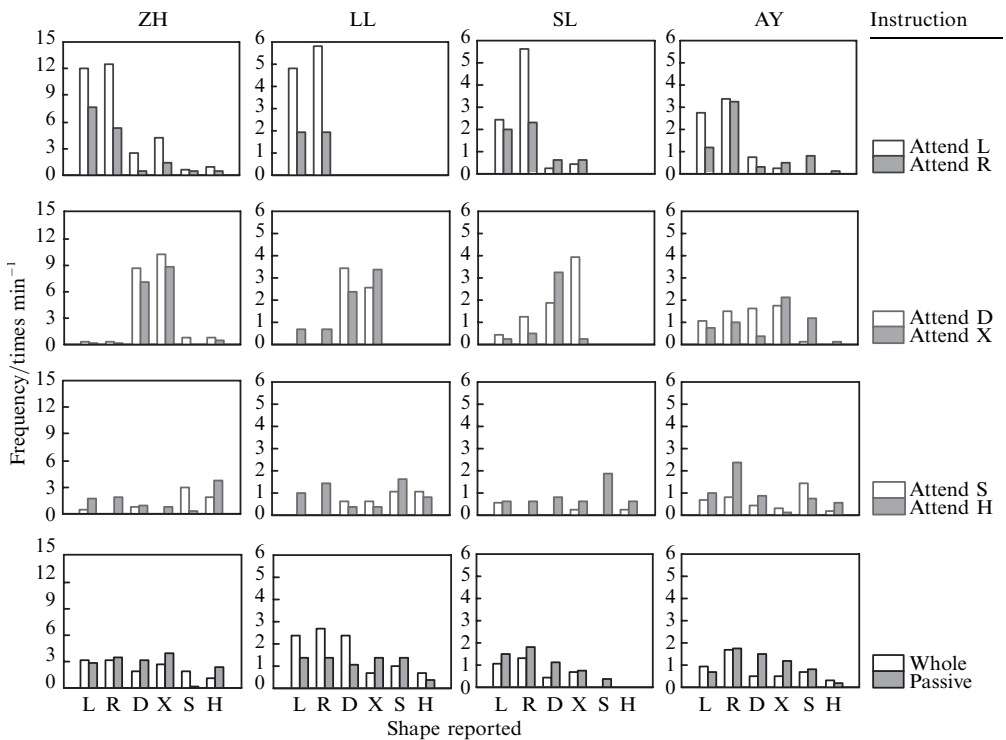


Figure 3. Frequencies of reporting each of six different shapes—L, R, D, X, S, and H under each of eight different conditions of attention in experiment 2. Each subject is represented by a column of four bar graphs.

(ii) Across the three pairs of complementary shapes (R and L, D and X, H and S), the shape selected for attention was reported about equally often as its unselected complementary.

(iii) Perceiving the afterimage passively, or as a whole, led to about equal frequencies of L, R, D, and X, and slightly less of S and H.

These findings, with the exception of the lower frequencies of reporting S and H in passive viewing, were confirmed by appropriate χ^2 tests ($\alpha = 0.01$) conducted separately on data from each subject. The small frequency difference in (iii) was confirmed by a χ^2 test ($\alpha = 0.01$) on observations pooled from the four subjects.

3.2.2 Spontaneous observations. In addition, the following phenomena were reported, without asking, by more than one subject. Although difficult to quantify, they could provide yet more clues regarding how voluntary attention affects visual sensory processes.

(a) All subjects reported that instead of seeing the entire X shape, they occasionally saw two parallel vertical lines.

(b) When H or S was selected for attention, each subject reported at least one of the percepts illustrated in figure 4. These phenomena invariably included two components: closure, or filling-in, of H, S, or some other line figures inbetween with what looked like a dark translucent coating, and smoothing of H, to the effect that the figure looked more like a circle. Sometimes the smoothing was seen before the closure, and sometimes the two phenomena were seen concurrently.

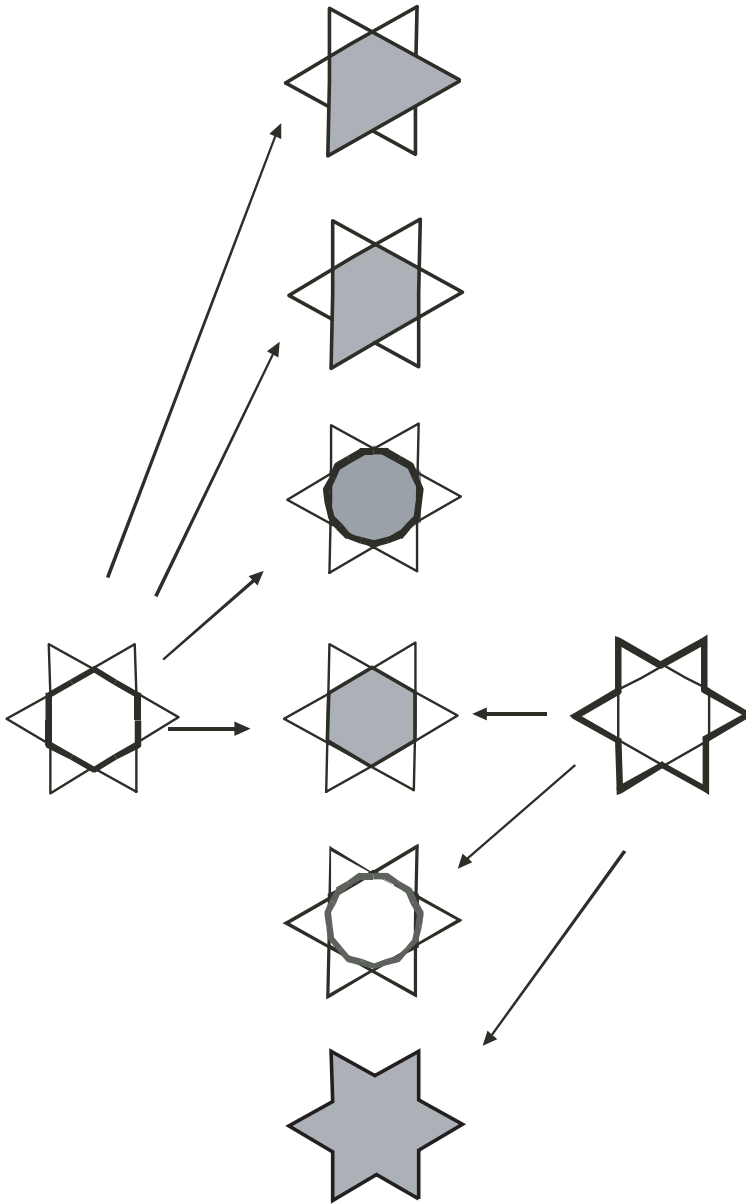


Figure 4. Closure and smoothing phenomena (the middle column) observed when H (the thick lines in the leftmost figure) or S (the thick lines in the rightmost figure) was selected for attention in experiment 2.

4 Discussion

4.1 Main effect of attention on afterimages and methodological considerations

It was an old observation that figural components of an afterimage tend to alternate in awareness. McDougall (1901) observed this phenomenon with an afterimage composed of an inner disc and an outer ring. Following Pritchard's influential report (1961) on structured fragmentation of artificially stabilized retinal images, similar phenomena were discovered with afterimages (Bennett-Clark and Evans 1963; Evans 1967; Piggins 1968) and steadily fixated images of line figures (McKinney 1963). The new observations from the current study indicate that the disappearance and reappearance of afterimage

components in awareness is largely subject to the influence of selective attention. The selective attention is object-based, since it affects spatially overlapping figural components selectively. Unlike in Troxler fading (Babington-Smith 1961; Lou 1999), the effect of selective attention was not limited to peripheral vision, as afterimage segments close to the fixation point were also affected. The inhibitory nature of this effect was most clearly suggested by experiment 1, where selecting a component triangle in afterimage for attention led to its faster disappearance from awareness. Interestingly, this observation is consistent with Hyslop's (1903) and not with Newton's (1691, in Wade 1998) introduced earlier.

An alternative interpretation to such observation is in terms of a bias of attention. A bias of attention is commonly thought to lead to heightened awareness of an object or image selected for attention without necessarily affecting the underlying sensory process. Had the attended triangle of the afterimage been found to stay longer in awareness than the unattended one, or more clearly seen, it would indeed be difficult to rule out the alternative interpretation. Fortunately, the opposite and counterintuitive was found: the attended triangle faded earlier than the unattended one. In particular, the disappeared triangle remained out of awareness for more than 3 s on average. 3 s is a very long period in attention literature. Had sensory adaptation occurred independently of attention and evenly across the entire afterimage, it would seem very implausible that a bias of attention somehow kept parts of the adapted afterimage visible for a further 3 s. It is much more likely that a sensory adaptation or inhibition occurred exclusively, or largely, to the attended triangle, leaving the unattended triangle unaffected. This argument is essentially the same as that presented in Lou (1999).

Despite the different methods used for afterimage generation and response, there is no doubt that the attentional effect obtained from experiment 1 would remain potent in experiment 2. Thus, during the 5 min or so continuous viewing, the target shape, ie the shape selected for attention, could fade out from awareness many times. Each time, if subjects remained faithful to the instruction, they would attempt to select the empty space previously occupied by the target shape for attention. However, such attempt would easily fail for two reasons. First, the disappearance of the shape from awareness would leave no distinctive cues for voluntary selective attention, especially when the selection is between two spatially overlapped shapes. Second, the shape that remained visible could capture attention involuntarily, canceling or interrupting the voluntary attention to the disappearing/disappeared image. This could account for why the target shape disappeared no more frequently than the to-be-ignored shape.

Remaining scepticism may be felt about the method for assessing visual awareness. Common to both experiments, the dependent measure was based on subjects' percepts, communicated either verbally (experiment 2), or through key depression (experiment 1). One aspect of the method that may be criticized was the distinct perceptual categories assigned for report, ie the red triangle and blue triangle in experiment 1, and the various geometric figures in experiment 2. A bias could be introduced in favor of exactly those categories in report. Schuck and Leahy (1966) used both verbal and non-verbal (tracing) methods to assess the fragmentation of a voluntarily fixated luminous figure and found the verbal method to favor reporting of namable fragments embedded in the figure. Similarly, Swanston and Wade (1981) found the duration of unitary disappearance of a stimulus to be longer when it is the only category of change to be reported than when the same measure is derived from concurrent reports of the disappearance of its parts. These results, however, do not seem to constitute a serious challenge to the validity of the present findings for two reasons.

First, the fragmentation of steadily fixated images, while qualitatively similar, is not strictly comparable to that of afterimages. Owing to the constant tremors of the eyes, a voluntarily fixated image is not perfectly stabilized on the retina and therefore

its disappearance from awareness appears transient and less compelling perceptually. There could be more room for an effect of response bias or response set in reporting fragmentation of steadily fixated images than that of afterimages. This argument is consistent with a quantitative comparison of observations on three different kinds of stabilized images (artificially stabilized retinal images, afterimages, and steadily fixated images) (MacKinnon et al 1969).

Second, the bias that those earlier studies cautioned about would not necessarily confound the effect of attention in the current study. The bias would presumably favor predefined percepts over ill-defined percepts. Likewise, the bias that might be considered an alternative interpretation of the effect of attention in the current study would favor certain predefined percepts over other predefined percepts. It could arise because of the selective attention to predefined percepts. However, such a bias would have existed for whatever percept selected for attention, which was evidently disproved by the finding: paying attention to S and H did not lead those two categories to dominate the reported percepts. Therefore, voluntarily attending to certain percepts (R, L, D, and X) in an afterimage must have an effect on underlying sensory processes. Whether such effect should be termed a bias of attention is precisely the kind of answer that this study has initially set to find.

4.2 *'Side effects' of voluntary attention*

Some interesting and unexpected findings from the current study are also apparently related to the main findings discussed above. In experiment 2, observers reported closure and smoothing of line figures when H or S was selected for attention. Because closure typically occurs to small closed areas in an afterimage of a complex line figure (Wade 1978), it seems to reveal certain limits in the visual system for processing high-spatial-frequency information. The new observations suggest, however, that the phenomenon is not entirely determined by the spatial frequencies and has to do with how attention is voluntarily distributed across the figural afterimage. The smoothing phenomenon could be accounted for along similar lines.

Voluntary attention is, on the other hand, not the only factor affecting the visibility of the afterimage components. In experiment 1, the pink triangle in afterimage disappears more easily than the blue triangle in afterimage—an effect that can only be attributed to stimulus properties. In experiment 2, L, R, D, and X were reported more frequently than H and S. These results suggest an effect of perceptual grouping that must have been either learned or inherent. Observers in experiment 2 also reported seeing the vertical parallel lines, even though the pattern was not among the set designated for selective attention or for report. It is noteworthy that the percept of parallel lines was frequently reported in at least two earlier studies on image fragmentation (MacKinnon et al 1969; Piggins 1968), strongly suggesting an underlying grouping factor at work.

4.3 *Implications*

A negative afterimage follows a sensory adaptation that involves contrast polarity reversal. Starting from retinal receptor bleaching, opponent mechanisms that exist at LGN and V1 levels may all contribute to negative afterimages (Anstis et al 1978; Gerling and Spillmann 1987; Loomis 1978). Different from these opponent processes, selective attention to afterimages or peripheral stimuli (Babington-Smith 1961; Lou 1999) leads to erasing of the image or image components, rather than the enhancement of their opposite polarity (in brightness or color). It can therefore be concluded that the effect of attention is external to the opponent processes underlying negative afterimages. It does not necessarily follow that the sensory adaptation under attention that leads to the image disappearance occurs in more central cortical areas than those of the opponent processes. Because the effect is due to voluntary attention, the source of

inhibition must come from activities in cortical areas associated with willed action, most likely the prefrontal cortex. However, the expression of the inhibition could occur downstream at various levels in the cortical or subcortical visual areas. Incorporating a piece of evidence from earlier psychophysical studies on Troxler fading (Clarke and Belcher 1962), I had speculated that the inhibition could follow directly from a breakdown of the cortical-LGN reverberation (Lou 1999). To account for the similar effect of voluntary attention on negative afterimages, this speculative mechanism must be considered nonspecific in contrast polarity.

Acknowledgements. This research was carried out at the Psychology Department of Hong Kong University while I was a postdoctoral fellow there. I thank Professor John Spinks for support, Richard Lee and Michael Tang for assistance, and Ms Serena Yang for a travel grant in her name that enabled me to present the findings reported here at two conferences. I also thank Nicholas Wade and an anonymous reviewer for helpful comments.

References

- Anstis S M, Rogers B J, Henry J, 1978 "Interaction between simultaneous contrast and colored afterimages" *Vision Research* **18** 899–911
- Babington-Smith B, 1961 "An unexpected effect of attention in peripheral vision" *Nature* **189** 776
- Bennett-Clark H C, Evans C R, 1963 "Fragmentation of patterned targets when viewed as prolonged after-images" *Nature* **199** 1215–1216
- Clarke F J J, Belcher S J, 1962 "On the localization of Troxler's effect in the visual pathway" *Vision Research* **2** 53–68
- Evans C R, 1967 "Further studies of pattern perception and a stabilized retinal image: the use of prolonged afterimage to achieve perfect stabilization" *British Journal of Psychology* **58** 315–327
- Gerling J, Spillmann L, 1987 "Duration of visual afterimages on modulated backgrounds: post-receptorial processes" *Vision Research* **27** 521–527
- Hebb D O, 1963 "The semiautonomous process: its nature and nurture" *American Psychologist* **18** 16–27
- Hyslop J H, 1903 "After images and applied phenomena" *Psychological Review* **10** 296–297
- Loomis J M, 1978 "Complementary afterimages and the unequal adapting effects of steady and flickering light" *Journal of the Optical Society of America* **68** 411–416
- Lou L, 1999 "Selective peripheral fading: evidence for inhibitory sensory effect of attention" *Perception* **28** 519–526
- McDougall W, 1901 "Some observations in support of Thomas Young's theory of light and colour vision" *Mind* **10** 210–245
- McKinney J P, 1963 "Disappearance of luminous designs" *Science* **140** 403–404
- MacKinnon G E, Forde J, Piggins D J, 1969 "Stabilized images, steadily fixated figures and prolonged after-images" *Canadian Journal of Psychology* **23** 184–195
- Piggins D J, 1968 "Perception of a square viewed as a prolonged after-image" *Atti della Fondazione Giorgio Ronchi* **23** 149–172
- Pritchard R M, 1961 "Stabilized images on the retina" *Scientific American* **204** (June) 72–78
- Schuck J R, Leahy W R, 1966 "A comparison of verbal and non-verbal reports of fragmenting visual images" *Perception & Psychophysics* **1** 191–192
- Swanston M, Wade N, 1981 "Consistency of response during steady visual simulation" *Perception* **10** 339–349
- Tsal Y, Kolbet L, 1985 "Disambiguating ambiguous figures by selective attention" *Quarterly Journal of Experimental Psychology A* **37** 25–37
- Wade N J, 1978 "Why do patterned afterimages fluctuate in visibility?" *Psychological Bulletin* **85** 338–352
- Wade N J, 1998 *A Natural History of Vision* (Cambridge, MA: MIT Press)