Psychological Science OnlineFirst, published on December 29, 2011 as doi:10.1177/0956797611422236

ASSOCIATION FOR PSYCHOLOGICAL SCIENCE

Research Report

Psychological Science
XX(X) 1–7
© The Author(s) 2012
Reprints and permission:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/0956797611422236
http://pss.sagepub.com
SAGE

Cortical Shape Adaptation Transforms a Circle Into a Hexagon: A Novel Afterimage Illusion

Hiroyuki Ito
Kyushu University

Abstract

After viewing a colored figure on a uniform gray background, an observer will see a negative afterimage after the colored figure disappears. This study shows that the shapes of afterimages vary systematically according to the shape of the adaptation stimuli, a phenomenon that could be caused only by cortical shape adaptation. In the experiments reported here, participants typically saw a hexagonal afterimage after viewing a circle and sometimes saw a circular afterimage after viewing a hexagon. When observers were adapted to rotating circles or hexagons, which produced the same circular retinal painting, they reliably reported that afterimages of circles appeared as hexagons, and vice versa. Furthermore, the fact that this effect also arose through interocular transfer confirms that a cortical process with binocular inputs must have contributed to it. This novel finding reveals that afterimage formation is determined mainly by a cortical process, not by retinal bleaching, and that rival mechanisms detect corners and curves of shapes in cortical processing.

Keywords

afterimage, illusion, shape perception, shape adaptation, perception, visual perception, vision

Received 1/17/11; Revision accepted 8/10/11

After viewing a colored figure on a uniform gray background, an observer will see a negative afterimage after the colored figure disappears (Anstis, Rogers, & Henry, 1978; Brindley, 1962; Craik, 1940; Hofstoetter, Koch, & Kiper, 2004; Kelly & Martinez-Uriegas, 1993; Loomis, 1972, 1978). Although researchers in the fields of psychology, physiology, and neuroscience have been interested in the origin of afterimages (i.e., retinal or cortical adaptation; Davis, 1973; MacKay, 1957; Shimojo, Kamitani, & Nishida, 2001), the fact that the shape of an afterimage is sometimes different from the adapted shape, not simply blurred, has been largely ignored. In the study reported here, I show that there is a systematic change in shape between an adapted image and its afterimage, a phenomenon that could only be caused by cortical shape adaptation.

I have found that adaptation to circular shapes produces afterimages that are perceived as polygons, typically hexagons (see Afterimage Demonstration in the Supplemental Material available online). Some observers may notice that the perceived deformation of a circle into a polygon starts even during adaptation. However, the perceived polygon in the afterimage is much clearer than the perceived polygon seen in the adaptation period. Alternately, some observers see circle afterimages after viewing hexagons.

A possible explanation for this phenomenon is related to the use of filled instead of unfilled circles: If observers are adapted to filled circles, the perceived afterimage will be deformed by invasion of the background color against which the circles are presented (cf. Pritchard, 1961; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). However, this *filling-in hypothesis* would not predict the same effect for unfilled circles. Filling-in of the background color could erase parts of an unfilled afterimage but could not distort the perceptual outline of the shape. Another hypothesis is that the visual system processes a circular stimulus as a group of straight lines. There are numerous orientation-tuned cells in area V1 of the cortex (e.g., Hubel & Wiesel, 1959). The receptive field of the orientation-tuned cells in peripheral vision is considered to be relatively large; therefore, a rough approximation of a circle's curvature produced by a small number of orientation-tuned cells or a limited number of orientation-tuned channels (Ellemberg, Allen, & Hess, 2006) might become visible after adaptation to curves. I call this explanation the *line-approximation hypothesis*.

Corresponding Author:
Hiroyuki Ito, Faculty of Design, Kyushu University, 4-9-1, Shiobaru, Minami-ku, Fukuoka 815-8540, Japan
E-mail: ito@design.kyushu-u.ac.jp

Experiment 1 explored the shape of the afterimage produced by viewing static circles or hexagons. To test the two hypotheses, unfilled circles and unfilled hexagons were used as adaptation stimuli. The filling-in hypothesis predicted that adaptation to unfilled circles should not produce afterimages of polygons, whereas the line-approximation hypothesis predicted that afterimages of hexagons should have the same hexagonal shape as the stimuli.

Experiment 1

Method

The author and 82 university students, including graduate students, participated in Experiment 1. All students were naive to the purpose of the experiment and provided written consent.

All stimuli were generated and presented on a computer (Sony VGN-Z91JS) with an LCD screen. Stimuli were displayed within an area of 1,200 × 900 pixels (20.5° × 15.5° of visual angle). Observers fixated on a center cross while their head was held steady by a chin rest. The viewing distance was 60 cm. Each adaptation display consisted of 16 yellow circles (55.0 cd/m^2) with a diameter of 2.86° of visual angle or 16 yellow hexagons with the same area subtended by the circles. These circles and hexagons were either filled or unfilled, depending on the condition, and were distributed on a gray background (26.1 cd/m^2; Fig. 1). Thus, there were four conditions, defined by the adaptation stimuli that were presented: unfilled circles, filled circles, unfilled hexagons, and filled hexagons. The outlines of the unfilled shapes had a thickness of 11.4 min of arc.

At the start of each trial, participants saw a blank gray screen with a fixation cross. Then, the adaptation stimuli were presented for 10 s, after which participants saw a blank gray field for 3 s. A click sound followed 1 s after the stimuli vanished, to prompt observers to attend to the shape of the afterimage. The gray field was then replaced by a 1-s mask consisting of a Mondrianesque pattern with various colors and shapes. Observers then chose one of seven shapes that was most similar to the shape of the afterimage they had seen. The seven choices, all with the same area, were triangle, square, pentagon, hexagon, octagon, dodecagon, and circle. These shapes were printed on a sheet of paper that was placed in front of the observer. The participants individually performed the task twice per condition. The observers were told not to pay attention to the orientation of the shapes in the afterimage in judging their similarity to the stimuli shapes. This direction was given because the perceived orientations of the polygon afterimages were ambiguous and followed no fixed pattern.

Results and discussion

As Figure 2 shows, both filled and unfilled circles typically produced afterimages of hexagons or octagons rather than circles. The filling-in hypothesis cannot explain why outlined corners were clearly perceived in the afterimages of unfilled shapes.

The notable difference between the distributions of the afterimage shapes seen after viewing hexagonal stimuli and those seen after viewing circular stimuli is that two peaks (i.e., for hexagons and circles) exist in the distribution resulting from adaptation to hexagonal stimuli, as compared with just one peak (for hexagons) resulting from adaptation to circular stimuli. In addition, when the adapted shape was a hexagon, circular afterimages were reported more frequently (especially for the unfilled hexagonal stimuli) than when the adapted shape was a circle. This perceived change of an adapted hexagon into a circular afterimage is a counterpart of the perceived change of an adapted circle into a hexagonal afterimage. The line-approximation hypothesis cannot explain this effect.

Pinna (1991) reported that radially arranged rectangles induced a circular subjective contour, but a physically drawn circle that replaced the subjective contour was seen as a polygon (Pinna termed this phenomenon the "illusion of angularity"). This phenomenon is consistent with the illusion seen here in showing perceptual ambiguity between corners and curvatures of shapes. However, the illusion of angularity originates from a difference in shape processing between real and subjective contours. In addition, the illusion of angularity in a real circle is produced by external inducers. However, the

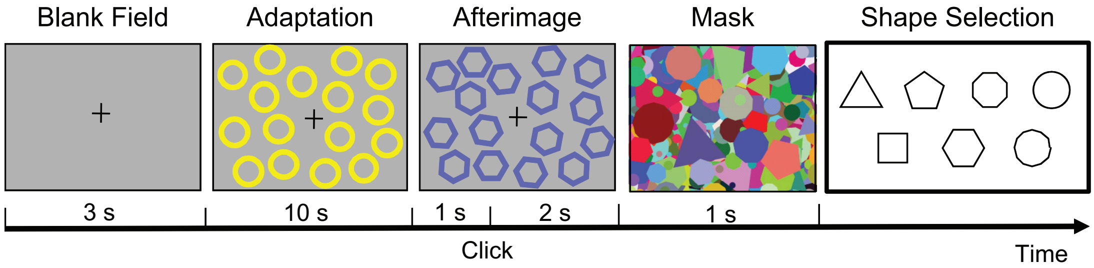

Fig. 1. Illustration of a sample trial in Experiment 1. Observers viewed a blank gray screen with a fixation cross for 3 s; then the adaptation stimuli (unfilled circles in the example shown here) appeared for 10 s. The screen then went blank for 3 s, during which most observers saw afterimages, such as the hexagonal shapes shown here. After the blank screen had been displayed for 1 s, a click sound prompted observers to attend to the shape of the afterimages. A 1-s mask consisting of a Mondrianesque pattern was then presented. Finally, observers selected the shape that most closely resembled the afterimage they saw, making their selection from seven possibilities printed on a sheet of paper.

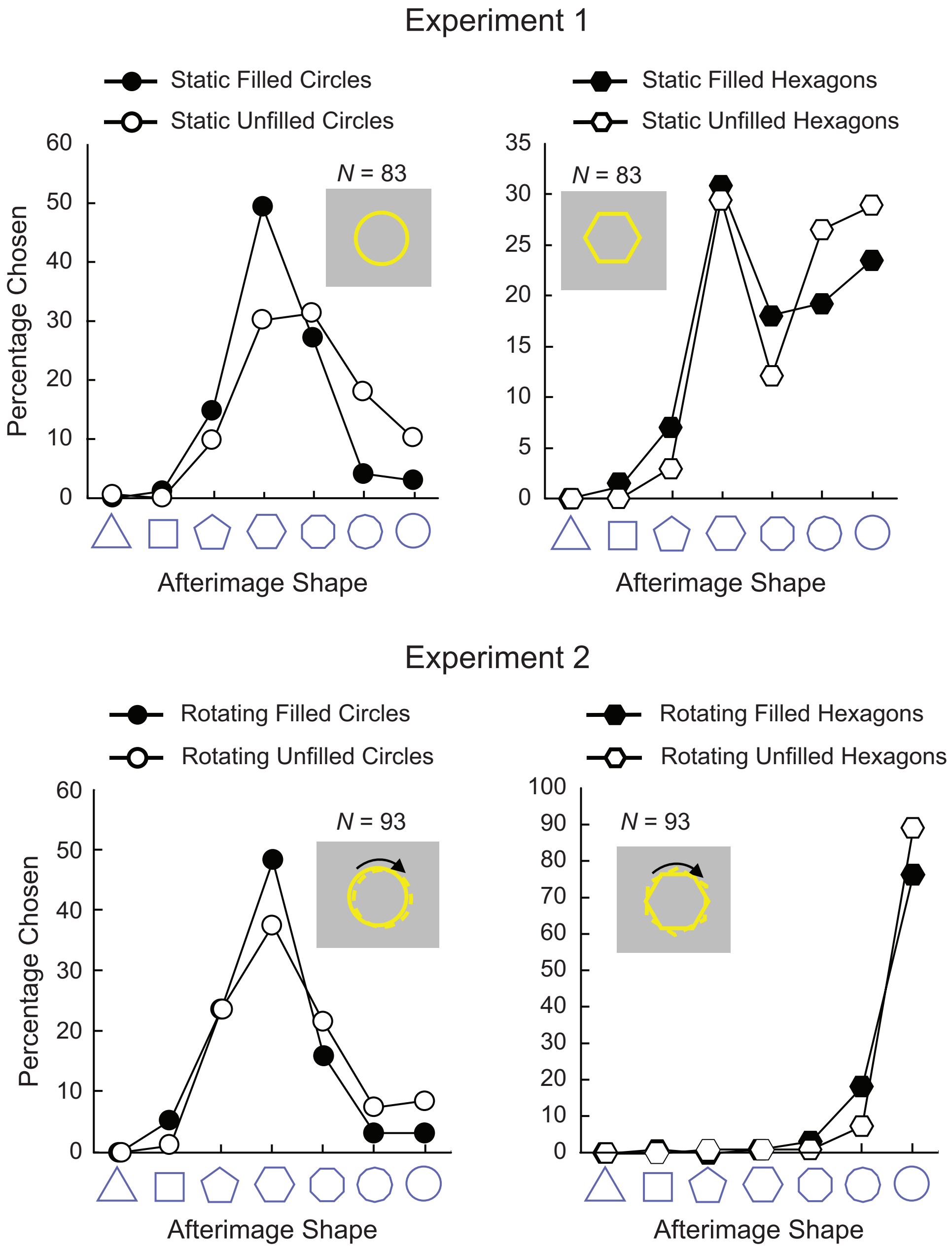

Fig. 2. Results from Experiment 1 (top row) and Experiment 2 (bottom row). Each graph shows the percentage distribution of the seven response options when the adaptation stimuli were filled and when they were unfilled. Adaptation stimuli consisted of either circles (left panels) or hexagons (right panels); the shapes in Experiment 1 were static, and the shapes in Experiment 2 were dynamic (see insets). After viewing each adaptation stimulus, observers selected which one of seven shapes most closely resembled the shape in the afterimage they saw.

present illusion is caused by adaptation to the circular contour itself.

The present results demonstrate the possibility that afterimage formation is determined by cortical shape adaptation and not by simple retinal bleaching. To examine the importance of the shape of the adaptation stimulus independently of the shape of retinal bleaching, I used a dynamic adaptation stimulus in Experiment 2.

Experiment 2

Method

Four conditions were used in Experiment 2, one for each type of adaptation stimulus: unfilled rotating circles, filled rotating circles, unfilled rotating hexagons, and filled rotating hexagons. Circles rotated at 1.0 revolutions per second, and hexagons rotated at 0.2 revolutions per second. The center of rotation of the circles was 14.0 min of arc apart from the center of the circle. The dynamic hexagon and circle stimuli produced similar circular retinal paintings (i.e., circular retinal bleaching). The method was the same as in Experiment 1. The author and 92 observers (including all observers in Experiment 1) completed one trial for each condition. All observers except the author were naive to the purpose of the experiment and provided written consent.

Results and discussion

As Figure 2 shows, adaptation to circle stimuli typically produced hexagonal afterimages. Few observers selected a circle shape, despite the circular retinal painting generated by the stimulus. However, the circular retinal paintings produced by rotating hexagons yielded circular afterimages for the majority of observers. The two distributions of afterimages produced by rotating circles and rotating hexagons were almost completely dissociated. This tendency was equivalent for filled and unfilled shapes.

These results demonstrate that the shape of the adaptation stimulus is critical for afterimage formation, independently of the shape of the retinal paintings they create. The results cannot be considered an artifact from employing an LCD screen. If the observers had viewed some traces of the moving figures remaining on the screen, they would have seen circular shapes after viewing all four types of stimuli.

Unlike the results of Experiment 1, the findings of Experiment 2 indicate that although the shape of the retinal painting produced by a rotating hexagon was circular, it did not yield a hexagonal afterimage. The corners of the rotating hexagons were exhibited equally along the circular path, so adaptation to a corner occurred equally along the circle, resulting in an afterimage of a perfect circle. However, responses to rotating circles were essentially the same as to stationary circles; that is, the shape adaptation arose only to a curvature along the circular path, typically resulting in a hexagonal afterimage. Thus, curves and corners could have a competing relationship in cortical shape processing. When one shape produces fatigue through adaptation, the other shape possibility dominantly appears.

Experiment 3

In Experiment 3, I tested whether the effect observed in the first two experiments would also arise through interocular transfer. Generally, a phenomenon in which adaptation in one eye affects the other eye's perception may be considered as evidence that a cortical process based on binocular input contributes to the effect (e.g., Nishida, Ashida, & Sato, 1994; Paradiso, Shimojo, & Nakayama, 1989). It is well known that no interocular transfer of the afterimage itself arises; this indicates that the afterimage primarily arises as a result of retinal bleaching. However, it is also known that afterimages sometimes reflect cortical activity (e.g., representation of a filled-in surface; Shimojo et al., 2001), suppression as a result of binocular rivalry (Tsuchiya & Koch, 2005), and attentional modulation (Suzuki & Grabowecky, 2003; van Boxtel, Tsuchiya, & Koch, 2010).

Method

Forty-four observers participated in Experiment 3. All participants were naive to the purpose of the experiment and provided written consent. Using a mirror stereoscope and an LCD screen (Mitsubishi RDT204WM) with a resolution of 1,376 × 768 pixels, I presented different adaptation stimuli to participants' left and right eyes using the left and right halves of the screen (see Fig. S1 in the Supplemental Material). All stimuli were presented against a pair of gray backgrounds (27.1 cd/m^2 each), one of which appeared above and one of which appeared below a central fixation cross. The cross and the backgrounds were embedded within a dotted texture.

There were five conditions, which were defined by the stimulus presented to the left eye. In each condition, the right eye viewed six static yellow circles (108 cd/m^2). In four of the conditions, the left eye viewed six blue shapes (13.1 cd/m^2), which varied per condition: static circles, slowly rotating circles (1.0 revolutions per second), rotating stars (0.2 revolutions per second), and rotating hexagons (0.2 revolutions per second). In an additional condition, no stimuli were presented to the left eye (which saw the gray background only). The rotating stars consisted of eight lines of equal length (122% of the circle diameter). Images were presented to both eyes in corresponding retinal positions. Yellow and blue figures are difficult to fuse binocularly because their luminance polarities against a gray background are opposite.

To ensure that observers viewed stimuli binocularly, I embedded two random-dot stereograms in the dotted texture on both the left and right sides of the central fixation cross. These two stereograms instantiated two small rectangles. Before testing, subjects acknowledged that they could perceive the rectangles floating in front of the dotted texture, which confirmed that they were viewing the stimulus display binocularly.

After a 10-s adaptation period, a blank field was presented to each eye for 2 s. The blank field for the left eye was colored black (0.45 cd/m^2) to diminish the left-eye afterimage, and the blank field for the right eye was colored white (112 cd/m^2) to suppress visibility of the left-eye afterimage. All observers confirmed that they saw only a blue or purple afterimage in the bright test field, which suggests that the origin of the afterimage was in the right eye. After the blank fields were presented for 2 s (with a click sound at 1 s to prompt observers to attend to the afterimages), observers saw a 1-s mask, as in the previous two experiments. All observers were then asked to rate the roundness of the right-eye afterimages four times for each condition. Twenty-two of the observers also rated the plain-background condition (in which only the right eye saw a stimulus; see Fig. 3). Ratings were made on a scale ranging from 0

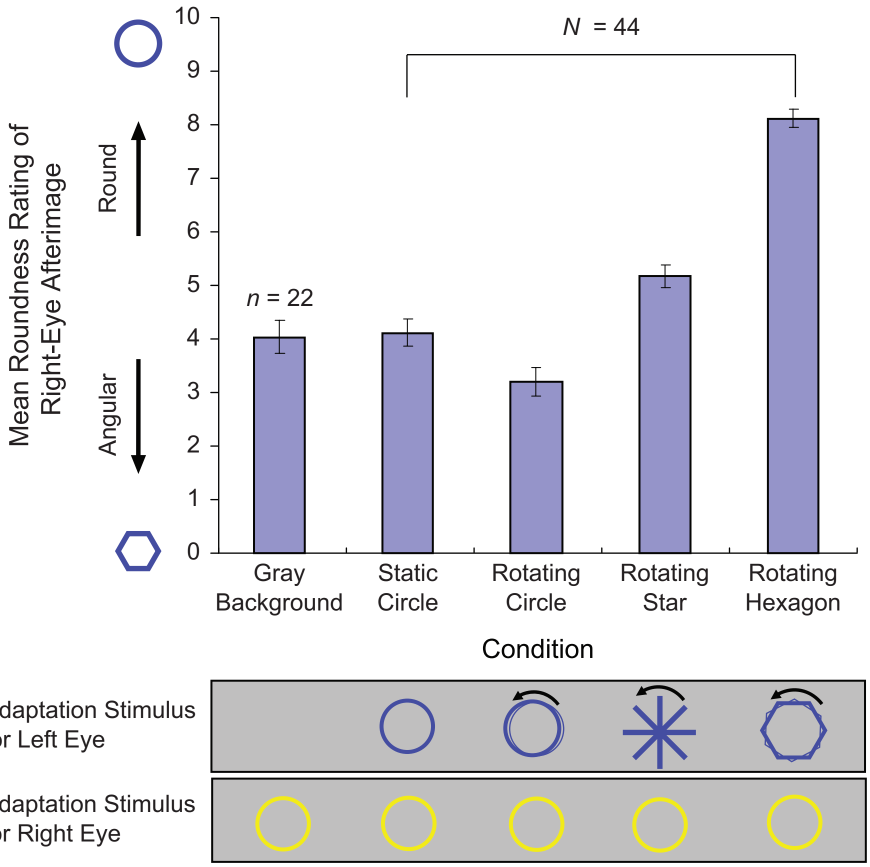

Fig. 3. Results from Experiment 3: mean rating of the roundness of right-eye afterimages as a function of condition. Conditions were defined by the stimulus presented to the left eye; the right eye viewed static yellow circles in all conditions. Error bars show ±1 *SE*.

(perfectly angular; i.e., a polygon) to 10 (perfectly round; i.e., a circle).

Results and discussion

As Figure 3 shows, despite the right eye being always adapted to circles, the perceived afterimage shapes changed depending on the adaptation stimulus presented to the left eye. A one-way analysis of variance revealed a significant difference between conditions, $F(3, 129) = 167.38$, $p = 2.73 \times 10^{-44}$. Multiple comparisons using Ryan's (1959) method revealed significant differences between all conditions ($p < .001$), except for the plain-background and static-circle conditions, $t(21) = 0.31$, $p = .76$, two-tailed.

The right-eye afterimage exhibited the most angular shapes when the left eye was adapted to rotating circles. This result was expected because each eye image should produce a polygon afterimage, as was the case in Experiments 1 and 2. However, after the left eye viewed rotating hexagons, the shapes perceived in the right-eye afterimage were almost circular. This demonstrates that adaptation to a polygon in the left eye suppressed adaption to a circle in the right eye to produce a polygonal afterimage (i.e., adaptation to circles should have produced a polygonal afterimage, as in Experiment 1). In the rotating-star condition, the ratings were in the middle of the scale. This may be because the image presented to the left eye was neither round nor angular. The right-eye afterimage was affected by left-eye adaptation, although the right eye adapted to circles in all cases. Thus, the adaptation process that forms afterimages appears to exist in the cortex, where it collects shape information from input from both eyes.

These results could be interpreted as reflecting the amount of exposure to curves and corners after binocular rivalry. In the static- and rotating-circle conditions, both eyes viewed a circle, even though there was binocular rivalry. In the rotating-star and rotating-hexagon conditions, only the right eye input was a circle. In addition, in the rotating-hexagon condition, the left-eye input included corners. The rated roundness seems to reflect these differences in exposure to curves and corners. Although whether or not binocular rivalry actually precedes shape processing in adaptation remains to be investigated, it appears that the shape-processing mechanisms collect information from both eyes.

General Discussion

The study reported here is the first to investigate shape changes in afterimages. The afterimage illusion clearly shows the contribution of a cortical process to afterimage formation. A complementary afterimage (MacKay, 1957) has some resemblance to the present effect because it also suggests rivalry in cortical processing.

The mechanism that detects curves has been debated (Blakemore & Over, 1974; Dobbins, Zucker, & Cynader, 1987; Wilson & Richards, 1989). Detecting corners and curves may require information from at least two local areas signaling differently oriented contours, which are possibly detected in V1 (Levi & Klein, 2000). The areas V2, V3/VP, and V4 are known to respond to corner or circular patterns (Dumoulin & Hess, 2007; Ito & Komatsu, 2004). Pasupathy and Connor (1999) demonstrated the existence of V4 cells that respond to corners and curves. Some cells responded differently to corners and curves, and other cells responded with equal strength. These findings indicate the possibility of balancing between curve and corner detection in V4.

However, Hegdé and Van Essen (2007), who showed that V2 cells of an awake monkey responded to both quarter-arc and obtuse-angle stimuli, identified a V1 cell that exhibited a similar response. Thus, the hierarchical model positing that after detection of local contour orientation and spatial frequency in V1 (Wilson, Mcfarlane, & Phillips, 1983), analysis of a combination of adjacent local contour information leads to detecting shape primitives in V2 through V4 may be too simple.

However, the effect observed here may arise within the ventral pathway starting at V1 because the observed interocular transfer indicates that the effect arises at the cortical level. Investigating the effect of stimulus size and eccentricity may provide a clue with regard to exploring the responsible cortical site in relation to the receptive field sizes.

The present effect may demonstrate rivalry in detecting corners and curves in cortical areas. If one of the corner- and curvature-detection processes is adapted or fatigued, activity in the other process may become relatively stronger. This may cause the perceptual shape switch in the afterimages between a circle and a polygon. The present effect can also be used as a psychophysical tool to explore shape representation in neural processing.

Declaration of Conflicting Interests

The author declared that he had no conflicts of interest with respect to his authorship or the publication of this article.

Funding

Parts of this study were supported by Grants-in-Aid for Scientific Research (KAKENHI; 19103003, 23243076, and 22653092) and Grants for Promising Research Projects, Department of Design, Kyushu University.

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

References

Anstis, S., Rogers, B., & Henry, J. (1978). Interactions between simultaneous contrast and coloured afterimages. *Vision Research*, *18*, 899–911.

Blakemore, C., & Over, R. (1974). Curvature detectors in human vision? *Perception*, *3*, 3–7.

Brindley, G. S. (1962). Two new properties of foveal after-images and a photochemical hypothesis to explain them. *Journal of Physiology*, *164*, 168–179.

Craik, K. J. W. (1940). Origin of visual after-images. *Nature*, *145*, 512.

Davis, P. (1973). The role of central processes in the perception of visual after-images. *British Journal of Psychology*, *64*, 325–338.

Dobbins, A., Zucker, S. W., & Cynader, M. S. (1987). Endstopping in the visual cortex as a substrate for calculating curvature. *Nature*, *329*, 438–441.

Dumoulin, S. O., & Hess, R. F. (2007). Cortical specialization for concentric shape processing. *Vision Research*, *47*, 1608–1613.

Ellemberg, D., Allen, H. A., & Hess, R. F. (2006). Second-order spatial frequency and orientation channels in human vision. *Vision Research*, *46*, 2798–2803.

Hegdé, J., & Van Essen, D. C. (2007). A comparative study of shape representation in macaque visual areas V2 and V4. *Cerebral Cortex*, *17*, 1100–1116.

Hofstoetter, C., Koch, C., & Kiper, D. C. (2004). Motion-induced blindness does not affect the formation of negative afterimages. *Consciousness and Cognition*, *13*, 691–708.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology*, *148*, 574–591.

Ito, M., & Komatsu, H. (2004). Representation of angles embedded within contour stimuli in area V2 of macaque monkeys. *The Journal of Neuroscience*, *24*, 3313–3324.

Kelly, D., & Martinez-Uriegas, E. H. (1993). Measurements of chromatic and achromatic afterimages. *Journal of the Optical Society of America A*, *10*, 29–37.

Levi, D. M., & Klein, S. A. (2000). Seeing circles: What limits shape perception? *Vision Research*, *40*, 2329–2339.

Loomis, J. (1972). The photopigment bleaching hypothesis of complementary afterimages: A psychophysical test. *Vision Research*, *12*, 1587–1594.

Loomis, J. (1978). Complementary afterimages and the unequal adapting effects of steady and flickering light. *Journal of the Optical Society of America A*, *68*, 411–416.

MacKay, D. (1957). Moving visual images produced by regular stationary patterns. *Nature*, *180*, 849–850.

Nishida, S., Ashida, H., & Sato, T. (1994). Complete interocular transfer of motion aftereffect with flickering test. *Vision Research*, *34*, 2707–2716.

Paradiso, M., Shimojo, S. A., & Nakayama, K. (1989). Subjective contours, tilt aftereffects and visual cortical organization. *Vision Research*, *29*, 1205–1213.

Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology*, *82*, 2490–2502.

Pinna, B. (1991). Anomalous contours and illusion of angularity: Phenomenal and theoretical comparisons. *Perception*, *20*, 207–218.

Pritchard, R. M. (1961). Stabilized images on the retina. *Scientific American*, *204*, 72–78.

Riggs, L. A., Ratliff, F., Cornsweet, C., & Cornsweet, T. N. (1953). The disappearance of steadily fixated visual test objects. *Journal of the Optical Society of America A*, *43*, 495–501.

Ryan, T. A. (1959). Multiple comparisons in psychological research. *Psychological Bulletin*, *56*, 26–47.

Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science*, *293*, 1677–1680.

Suzuki, S., & Grabowecky, M. (2003). Attention during adaptation weakens negative afterimages. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 793–807.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*, 1096–1101.

van Boxtel, J. J. A., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences, USA*, *107*, 8883–8888.

Wilson, H. R., Mcfarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, *23*, 873–882.

Wilson, H. R., & Richards, W. A. (1989). Mechanisms of contour curvature discrimination. *Journal of the Optical Society of America A*, *6*, 106–115.