Why do shape aftereffects increase with eccentricity?

Elena Gheorghiu

Frederick A. A. Kingdom

Jason Bell

Rick Gurnsey

Laboratory of Experimental Psychology, University of Leuven, Leuven, Belgium

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

Department of Psychology, Australian National University, Canberra, ACT, Australia

Department of Psychology, Concordia University, Montreal, Quebec, Canada

Studies have shown that spatial aftereffects increase with eccentricity. Here, we demonstrate that the shape-frequency and shape-amplitude aftereffects, which describe the perceived shifts in the shape of a sinusoidal-shaped contour following adaptation to a slightly different sinusoidal-shaped contour, also increase with eccentricity. Why does this happen? We first demonstrate that the perceptual shift increases with eccentricity for stimuli of fixed sizes. These shifts are not attenuated by variations in stimulus size; in fact, at each eccentricity the degree of perceptual shift is scale-independent. This scale independence is specific to the aftereffect because basic discrimination thresholds (in the absence of adaptation) decrease as size increases. Structural aspects of the displays were found to have a modest effect on the degree of perceptual shift; the degree of adaptation depends modestly on distance between stimuli during adaptation and post-adaptation testing. There were similar temporal rates of decline of adaptation across the visual field and higher post-adaptation discrimination thresholds in the periphery than in the center. The observed results are consistent with greater sensitivity reduction in adapted mechanisms following adaptation in the periphery or an eccentricity-dependent increase in the bandwidth of the shape-frequency- and shape-amplitude-selective mechanisms.

Keywords: eccentricity, shape, curvature, adaptation, aftereffect


Introduction


However, when it comes to stimulus appearance, not everything “declines” with eccentricity. For example, motion-induced changes in perceived position (De Valois & De Valois, 1991), the tilt aftereffect (Harris & Calvert, 1985; Muir & Over, 1970; Over, Broerse, & Crassini, 1972), the aftereffect in which a briefly presented line causes a circle to appear elliptical (Suzuki & Cavanagh, 1998), and the perceived velocity of the motion aftereffect (Castet, Keelbe, & Verstraten, 2002; van de Grind, Koenderink, & van Doorn, 1986; Wright, 1986; Wright & Johnston, 1983, 1985a) all increase with eccentricity. In this communication, we show that two shape aftereffects also increase with eccentricity and examine possible reasons why. The two shape aftereffects are the shape-frequency and shape-amplitude aftereffects (SFAE and SAAE). They, respectively, refer to the perceived shifts in the apparent shape frequency and the shape amplitude of a sinusoidal-shaped contour following adaptation to a
Figure 1. Stimuli used in the experiments. One can experience (a) the shape-frequency aftereffect (SFAE) and (b) the shape-amplitude aftereffect (SAAE) by moving one’s eyes back and forth along the markers located midway between the pair of adapting contours (left) for about 90 s and then shifting one’s gaze to the middle of the test contours (right). Sample contours (c) presented at 2.5-, 5-, and 7.5-deg eccentricities and (d) scaled by a scaling factor $S$ of 1 (small), 2, 3, 4, and 5 (big).
slightly different-shaped sinusoidal contour (Gheorghiu & Kingdom, 2007, 2008, 2009). Both aftereffects can be experienced in Figure 1. We consider several possible explanations for the increase of these aftereffects with eccentricity: (i) scaling of contour-shape receptive fields with eccentricity (i.e., cortical magnification); (ii) unusual basic encoding of shape frequency and shape amplitude; (iii) reduced spatial interactions between the contour pairs when presented peripherally; (iv) less rapid decline of adaptation at test onset in the periphery; (v) greater adaptation gain in the periphery. To anticipate, we were able to rule out the first four of these explanations, leaving greater adaptation gain as a possibility.

### Experiment 1: Eccentricity dependence of shape aftereffects

We first demonstrate that adaptation to sinusoidal-shaped contours produces shape aftereffects that increase in magnitude with eccentricity. To do this, we used adaptor and test contours presented at three eccentricities: 2.5, 5, and 7.5 deg from the fixation marker (Figure 1c).

### Subjects

Twelve subjects participated in Experiment 1. Three of these were the authors (EG, FK, and JB) and the remaining nine were naive with regard to the experimental aims. All subjects had normal or corrected-to-normal visual acuity. Each subject gave informed consent prior to participation in accordance with the university guidelines.

### Stimuli

The stimuli were generated by a ViSaGe video-graphics card (Cambridge Research Systems) with 12-bit contrast resolution, presented on a calibrated, gamma-corrected Sony Trinitron monitor, running at 120-Hz frame rate and with a spatial resolution of 1024 × 768 pixels. The mean luminance of the monitor was 40 cd/m². Viewing distance was 100 cm.

Example stimuli are shown in Figure 1. Adaptation and test stimuli consisted of pairs of 2D sinusoidal-shaped contours. Each contour covered an area of 8 (width) × 4 (height) deg. The adaptor pair for the SFAE consisted of contours with a shape amplitude of 0.43 deg and shape frequencies of 0.25 and 0.75 c/deg, giving a geometric mean shape frequency of 0.43 c/deg. For the SAAE, the shape frequency of the adaptor pair was 0.43 c/deg, while the shape amplitudes were 0.25 and 0.75 deg (geometric mean of 0.43 deg). Unless otherwise stated, the two adaptors/tests were presented in the center of the monitor at 2.5 deg above and below the fixation marker. The cross-sectional luminance profile of the contours was odd-symmetric and was generated according to a first derivative of a Gaussian function:

\[
L(d) = L_b \pm L_h \cdot C \cdot \exp(0.5) \cdot (d/\sigma) \cdot \exp\left[-\left(d^2\right)/(2\sigma^2)\right],
\]

where \(d\) is the distance from the midpoint of the contour’s luminance profile along a line perpendicular to the tangent, \(L_b\) is background luminance of 40 cd/m², \(C\) is contrast, and \(\sigma\) is the space constant. The contrast \(C\) was set to 0.5 and \(\sigma\) was set to 0.044 deg. The ± sign determined the polarity of the contour. The contours have a constant cross-sectional width, as described previously in Gheorghiu and Kingdom (2006).

### Procedure: Shape aftereffects

Each session started with an initial adaptation period of 90 s, followed by a repeated test of 0.5 s duration interspersed with top-up adaptation periods of 2.5 s. During the adaptation period, the shape phase of the contour changed randomly every 0.5 s in order to minimize the effects of local orientation adaptation and to prevent the occurrence of afterimages. The presence of the test contour was indicated by a tone. The shape phase of the test contour was also randomly assigned in every test period. For the entire session, subjects were required to fixate on the marker placed between each pair of contours.

A staircase method was used to estimate the PSE. For the SFAE, the geometric mean shape frequency of the two test contours was held constant at 0.43 c/deg while the computer varied the relative shape frequencies of the two tests in accordance with the subject’s response. At the start of the test period, the ratio of the two test shape frequencies was set to a random number between 0.71 and 1.4. On each trial, subjects indicated via a button press whether the upper or lower test contour had the higher perceived shape frequency. The computer then changed the ratio of test shape frequencies by a factor of 1.06 for the first five trials and 1.015 thereafter, in a direction opposite to that of the response, i.e., toward the point of subjective equality (PSE). The session was terminated after 25 trials. We found in previous studies (Gheorghiu & Kingdom, 2007, 2008, 2009) that a step size of 1.015 was sufficient to produce a visible change in the shape frequency on each trial while ensuring that the convergence is stable over the last 20 trials enabling an accurate estimate of the PSE to be obtained. The shape-frequency ratio at the PSE was calculated as the geometric mean shape-frequency ratio of the two tests averaged across the last 20 trials, with the ratio’s numerator the test that followed the lower shape-frequency adaptor and its denominator the test that followed the higher shape-frequency adaptor. For each with-adaptor condition, we...
Figure 2. Results for **Experiment 1**: SFAEs (white symbols) and SAAEs (black symbols) as a function of stimulus eccentricity for twelve subjects.
made six measurements, three in which the upper adaptor had the higher shape-frequency and three in which the lower adaptor had the higher shape-frequency. In addition, we measured for each condition the shape-frequency ratio at the PSE in the absence of the adapting stimulus (the no-adaptor condition). To obtain an estimate of the size of the SFAE, we first calculated the difference between the logarithm of each with-adaptor shape-frequency ratio at the PSE and the mean of the logarithms of the no-adaptor shape-frequency ratios at the PSE. We then calculated the mean and standard error of these differences across the six measurements. These are the values shown in the graphs. Note that the magnitude of the aftereffect (or shape-frequency ratio at PSE) is defined as a ratio of shape frequency, and thus, its units are dimensionless.

The procedure for measuring the SAAE followed the same principle as for the SFAE. The computer varied the relative shape amplitudes of the two tests in accordance with the subject’s response, while the geometric mean shape amplitude of the two test contours was held constant at 0.43 deg.

Results

Figure 2 shows SFAEs (white symbols) and SAAEs (black symbols) as a function of eccentricity for each of the twelve subjects. Both aftereffects increase with eccentricity in ten out of twelve subjects, the exceptions being SW and LS. One might suppose that the shape-frequency or shape-amplitude ratios at the PSE for the unadapted condition (i.e., the baseline) might change with eccentricity. However, the SFAE and SAAE are expressed as measures relative to their baselines, thus eliminating any baseline differences between center and periphery. In fact, however, the across-subjects average for both the shape-frequency and shape-amplitude baseline conditions is flat across eccentricity, as Figure 3a shows.

To obtain an overall picture of the effect of eccentricity, we normalized the aftereffects at each eccentricity to that of the 2.5 deg eccentricity condition for each subject. Figure 3b shows the average of these normalized values for the ten subjects that showed an effect of eccentricity. On average for these subjects, the increase in aftereffect is about \( \times1.63 \) for the 5 deg eccentricity and \( \times2.15 \) for the 7.5 deg eccentricity. In what follows, we consider five possible reasons for these increases in aftereffect with eccentricity.

Discussion

Why might the SFAE and SAAE increase with eccentricity? The first and perhaps most obvious possible reason is the same as that often advanced to explain the decline in eccentricity of performance tasks: cortical magnification. Cortical magnification refers to the reduc-

![Figure 3](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932790/)

Figure 3. Results for Experiment 1. (a) The average across ten subjects of the logarithm of the shape-frequency (white symbols) and shape-amplitude (black symbols) ratio at the PSE in the absence of the adapting stimulus (i.e., the baseline condition).

(b) Normalized average SFAE (white symbols) and SAAE (black symbols) across ten subjects. A value of 1 indicates that the magnitude of the aftereffects is obtained at 2.5 deg eccentricity.
orientation discrimination (Makela et al., 1993; Scobey, 1982), vernier acuity (Andrews, 1967; Andrews et al., 1973; Levi & Waugh, 1994; Whitaker, Rovamo, MacVeigh, & Makela, 1992), and structure from motion/structure from texture (Gurnsey et al., 2006). For face identification, a double scaling of both stimulus size and contrast is needed (Melmoth et al., 2000). Moreover, threshold elevation following luminance spatial frequency adaptation has been found to depend on eccentricity (Koenderink et al., 1978; Williams, Wilson, & Cowan, 1982) in a manner predictable from cortical magnification (Williams et al., 1982).

If cortical magnification is responsible for the increase in aftereffects with eccentricity, then this suggests that the peripheral stimuli are better matched to the underlying receptive fields than are the central stimuli, since the gain changes caused by adaptation are presumably biggest when stimuli and receptive field are matched. It follows that either an upwards and downwards scaling of the peripheral stimuli will result in a decline in the aftereffect. Harris and Calvert (1985) found that the tilt aftereffect in peripheral vision was reduced to the level of that in central vision when the stimuli were scaled upwards by a suitable amount, consistent with the cortical magnification explanation. However, a stronger test of whether cortical magnification is responsible for the increase in aftereffects with eccentricity would be to measure the aftereffect across a range of different stimulus scales in both central and peripheral vision, with the prediction that there would be a scale in central and a scale in peripheral vision for which the aftereffects were both maximal and equal. We have adopted this method for our test of cortical magnification.

At the smallest scale (scale 1), the cross-sectional luminance profile of the contours had a $\sigma$ of 0.024 deg and an overall stimulus width of 1.6 deg. For the SFAE at this scale, the adaptor pair consisted of contours with a shape amplitude of 0.176 deg and shape frequencies of 1.25 and 3.75 c/deg, giving a geometric mean shape frequency of 2.15 c/deg. For the SAAE at this scale, the adaptor pair consisted of contours with a shape frequency of 2.15 c/deg and shape amplitudes of 0.1 and 0.3 deg, giving a geometric mean shape amplitude of 0.173 deg. For the remaining scales, the stimuli were magnified by 2, 3, 4, or 5 times. Four subjects participated in this experiment, all of which had participated in Experiment 1.

### Results

Figures 4a and 4b shows SFAEs and SAAEs, respectively, as a function of scale for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricities. The average across subjects for SFAE and SAAE is shown in Figures 4c and 4d, respectively. As in Experiment 1, the aftereffects are larger at 7.5 deg compared to 2.5 deg. However, they are similar in magnitude across scale at each eccentricity. Although there is some intersubject variability in the absolute magnitude of aftereffects, the average across subjects for the SFAE and SAAE (Figures 4c–4d) indicates a general tendency for the strength of the aftereffects to be constant across scales.

The data for the SFAE were submitted to a 2 (eccentricities) by 4 (scales) repeated measures ANOVA. (Note that only four levels of scale were used because we were unable to obtain data for scale 1 at 2.5°.) The $p$-values associated with this and subsequent analyses were those associated with the Greenhouse–Geisser correction for violations of sphericity. For clarity, the original degrees of freedom are reported. The ANOVA showed a statistically significant main effect of eccentricity, $F(1, 3) = 196.34, p = 0.001$, $\eta_p^2 = 0.985$, indicating that the aftereffect increased with eccentricity. The main effect of scale was not statistically significant, $F(3, 9) = 0.62, p = 0.62$, $\eta_p^2 = 0.171$, indicating that the aftereffect was not affected by scale when averaged over eccentricity. Finally, there was a statistically significant interaction of eccentricity and scale, $F(3, 9) = 11.71, p = 0.007$, $\eta_p^2 = 0.796$, indicating that the effect of scale changed as a function of eccentricity.

To investigate this interaction, we computed the slope of the linear regression line that relates aftereffect magnitude to scale for each eccentricity and subject. We used a one-group $t$-test to determine whether these means were different from zero. The analysis revealed that for the SFAE, the slopes were not statistically significant, $t(3) = -1.275, p = 0.292$ and $t(3) = 0.158, p = 0.885$, for 2.5 and 7.5 deg, respectively. Although neither slope is statistically significantly different from 0, the slopes tend in

### Experiment 2: Scaling of contour-shape receptive fields with eccentricity?

#### Stimuli, subjects, and methods

To test the idea that the eccentricity dependence of the SAAE and SFAEs are related to a mismatch between the scales of the stimuli and the relevant mechanisms, we used adaptor and test contours that varied in scale by factors of 1 (smallest), 2, 3, 4, and 5 (biggest). Example contours are shown in Figure 1d. The contours were presented at eccentricities of 2.5 and 7.5 deg and viewed at a distance of 100 cm. If receptive field scaling is the reason for the increase in aftereffect with eccentricity, we would expect the largest aftereffects at a smaller scale for the 2.5 deg eccentricity compared to 7.5 deg eccentricity and similar-sized aftereffects at the optimum scales at each eccentricity.
Figure 4. Results for Experiment 2: (a) SFAEs and (b) SAAEs as a function of stimulus scale for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricity conditions for each subject. The average across subjects for the (c) SFAE and (d) SAAE.
Figure 5. Results for Experiment 2 for the unadapted or baseline condition. The logarithm of the (a) shape-frequency and (b) shape-amplitude ratio at the PSE as a function of stimulus scale for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricity conditions for each subject. The average across subjects for the (c) shape-frequency and (d) shape-amplitude ratio at the PSE.
opposite directions at the two eccentricities, thus explaining the interaction of eccentricity and scale.

The data for the SAAE were submitted to a 2 (eccentricities) by 5 (scales) repeated measures ANOVA. The ANOVA showed a statistically significant main effect of eccentricity, \( F(1, 3) = 26.05, p = 0.015, \eta_p^2 = 0.90 \), indicating that the aftereffect increased with eccentricity. The main effect of scale was not statistically significant, \( F(4, 12) = 3.77, p = 0.121, \eta_p^2 = 0.557 \), indicating that the aftereffect was not affected by scale when averaged over eccentricity. Finally, there was a statistically significant interaction of eccentricity and scale, \( F(4, 12) = 4.67, p = 0.059, \eta_p^2 = 0.609 \), indicating that the effect of scale changed as a function of eccentricity.

To investigate this interaction, we again computed the slope of the linear regression line that relates aftereffect magnitude to scale for each eccentricity and subject and used a one-group \( t \)-test to determine whether these means were different from zero. There was a statistically significant decrease with scale at 2.5 deg (\( t(3) = -7.727, p = 0.005 \)) and a statistically significant increase with scale at 7.5 deg (\( t(3) = 3.643, p = 0.036 \)). Again, the interaction is explained by a different eccentricity dependence of the aftereffect at 2.5 and 7.5 deg. Importantly, the aftereffect does not decrease with scale at 7.5, and therefore, we find no evidence that SFAE and SAAE decrease in the periphery with increasing stimulus size.

The SFAE and SAAE shown in Figure 4 are expressed as relative measures between the adapted and unadapted baseline conditions, thus eliminating any possible effect of baseline differences between center and periphery and between different scales. To confirm that baseline measures are stable and do not vary with eccentricity or scale, Figure 5 shows the logarithm of the shape-frequency (Figure 5a) and shape-amplitude (Figure 5b) ratio at the PSE obtained in the absence of the adaptor as a function of the scaling factor for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricities. Note that in these conditions the expected value should be zero. The average across observers is shown in Figures 5c and 5d. Figure 5 indicates that the baseline measures do not change with either scale or eccentricity.

The shape-frequency baseline data were submitted to 2 (eccentricities) by 4 (scales) repeated measures ANOVA. There was no statistically significant effect of eccentricity, \( F(1, 3) = 2.75, p = 0.196, \eta_p^2 = 0.478 \), no statistically significant effect of scale, \( F(3, 9) = 1.49, p = 0.283, \eta_p^2 = 0.331 \), and no statistically significant interaction of eccentricity and scale, \( F(3, 9) = 5.32, p = 0.099, \eta_p^2 = 0.640 \).

The shape-amplitude baseline data were submitted to 2 (eccentricities) by 5 (scales) repeated measures ANOVA. There was no statistically significant effect of eccentricity, \( F(1, 3) = 0.001, p = 0.974, \eta_p^2 = 0.00 \), no statistically significant effect of scale, \( F(4, 12) = 66, p = 0.518, \eta_p^2 = 0.18 \), and no statistically significant interaction of eccentricity and scale, \( F(4, 12) = 0.216, p = 0.817, \eta_p^2 = 0.067 \).

In conclusion, the results in Figure 4 show that, at a given eccentricity, aftereffect magnitude is stimulus scale-invariant and do not support the idea that the scaling of contour-shape receptive fields with eccentricity is the cause of the larger aftereffects in the periphery.

### Experiment 3: Shape-frequency/shape-amplitude discrimination thresholds

The scale independence of the SAAE and SFAE is interesting because it contrasts with the expectation that basic discrimination thresholds will be scale-dependent at each eccentricity. This then raises the question of whether or not shape-frequency and shape-amplitude discrimination thresholds are scale-dependent across the visual field. Therefore, we measured these thresholds at a range of sizes (the same scales 1, … 5 as those used in Experiment 2) at both 2.5 and 7.5 deg.

#### Subjects and methods

There were four subjects in the experiment, two of which had participated in Experiments 1 and 2. Discrimination thresholds were measured using a two-alternative forced-choice (2AFC) procedure in the absence of the adapting stimulus (the no-adaptor condition). For shape-frequency discrimination, we used pairs of sine-waved shaped test contours in which one was a pedestal-alone contour with fixed shape frequency of 0.43 c/deg and the other was a pedestal-plus-increment with an adjustable increment shape frequency. The shape amplitude of the stimuli was fixed at 0.43 deg. The pedestal-alone and pedestal-plus-increment were simultaneously presented to the subject above and below fixation for 0.25 s.

An adaptive staircase method (2 up/1 down) was used to estimate the threshold at the level of 70.7% correct. On each trial, subjects indicated via a button press whether the upper or lower test contour had the higher perceived shape frequency. Feedback was provided after each trial by means of a tone following an incorrect response. The computer changed the ratio of pedestal-plus-increment to pedestal-alone (0.43 c/deg) test shape frequencies by a factor of 1.06 for the first five trials and 1.015 thereafter, in a direction opposite to that of the response. The staircase was terminated after 11 reversals. The threshold estimate was calculated as the mean shape-frequency ratio of the pedestal-plus-increment to pedestal-alone averaged across trials for the last 9 reversals. For each eccentricity condition, we made five threshold measurements. We then calculated the mean and standard error of the logarithms of the no-adaptor shape-frequency discrimination thresh-
Figure 6. Results for Experiment 3: (a) Shape-frequency and (b) shape-amplitude discrimination thresholds as a function of stimulus scale for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricity conditions for each subject. The average across subjects for the (c) shape-frequency and (d) shape-amplitude discrimination thresholds.
olds across the five measurements. These are the shape-frequency discrimination threshold values shown in the graphs.

The procedure for measuring shape-amplitude discrimination thresholds followed the same principle. The shape amplitude of the pedestal-alone contour was fixed at 0.43 deg and the computer varied the shape amplitude of the pedestal-plus-increment contour in accordance with the subject’s response. The shape frequency of both pedestal-alone and pedestal-plus-increment contours was fixed at 0.43 c/deg.

**Results**

Figure 6a shows shape frequency and Figure 6b shows shape-amplitude discrimination thresholds as a function of stimulus scale for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricity conditions. The average across subjects for the shape-frequency and shape-amplitude discrimination thresholds is shown in Figures 6c and 6d, respectively. The results show that both shape-frequency and shape-amplitude discrimination thresholds are higher in the periphery than in the center and decrease with increasing stimulus scale, more prominently in the periphery than in the center, as is typically seen in the size scaling literature. Both central and peripheral thresholds reach comparable values at stimulus scale 5. On the other hand, both shape aftereffects are prominently larger in the periphery than in the center at stimulus scale 5 (see Figure 4).

To confirm the effect of scale at each eccentricity, we computed the slope that relates shape-frequency and shape-amplitude discrimination thresholds to scale for each eccentricity and subject, then calculated the mean for each condition and eccentricity. We used a one-group t-test analysis to test whether these means were statistically different from zero. The analysis revealed that the slopes were statistically significant for both shape-frequency ($t = -4.602, p = 0.02$ for 2.5 deg; $t = -12.774, p = 0.002$ for 7.5 deg) and shape-amplitude ($t = -4.022, p = 0.027$ for 2.5 deg; $t = -3.284, p = 0.046$ for 7.5 deg) discrimination thresholds.

These results confirm the general rule that basic discrimination thresholds are scale-dependent across the visual field. The results contrast starkly with those of Experiment 2 (see Figure 5) in which the strength of the aftereffect was size independent at each eccentricity. Therefore, we may conclude that the scale invariance for the aftereffects seen in Experiment 2 is not a consequence of unusual, low-level encoding of the stimuli. The size independence of the SFAE and SAAE is different than the size dependence of the shape-frequency and shape-amplitude discrimination thresholds. This indicates that shape aftereffects and shape discrimination thresholds are likely mediated by different mechanisms. We now examine three other possible explanations for the eccentricity dependence and size independence of the SAAE and SFAE.

**Experiment 4: Between-adaptor spatial interactions?**

The increase in SFAE and SAAE with eccentricity may have to do with the change in both adaptor and test separation with eccentricity. That is, the two test stimuli are closer together at 2.5 deg than 7.5 deg. The smaller adaptor separation at 2.5 deg might result in less adaptation because the adaptors engage overlapping receptive fields. On the other hand, the smaller target separation at 2.5 deg might make it easier to make veridical judgments about their properties; perhaps it is easier to deploy attentional strategies.

To test this possibility, we dissociated eccentricity from adaptor separation by placing the fixation marker to one side of the contour pairs as in Figure 7a. We used two values for contour separation, 3 and 9 deg, and two values for eccentricity, 5 and 15 deg. Three subjects participated in this experiment.

Figure 7b shows the SFAE and Figure 7c shows the SAAE as a function of contour separation for 5 deg (black symbols) and 15 deg (white symbols) eccentricity. The results show a prominent increase in the size of both aftereffects with eccentricity when adaptor separation was held constant (compare white and dark symbols), and a small increase in both aftereffects with adaptor separation when eccentricity was held constant (compare white symbols between them and dark symbols between them). In order to obtain an overall picture of the relative contribution of stimulus separation and eccentricity, we calculated the difference in aftereffect between the two stimulus separations expressed as a proportion of the differences in the aftereffect between the two eccentricities.

On average, stimulus separation contributed ~12% (9.74% for SFAE and 14.59% for SAAE) to the increase in the size of aftereffects with eccentricity. Therefore, we may conclude that adaptor separation is not the main factor for the increase in the aftereffects with eccentricity.

**Experiment 5: Temporal decay differences between center and periphery?**

The standard account of aftereffects is the cross-fiber model (Frisby & Stone, 2010) in which adaptation biases the distribution of activity across channels resulting in a
Figure 7. Results for Experiment 4: (a) Contour-shape stimuli presented at different eccentricity (5 and 15 deg) and contour separation (3 and 9 deg) combinations. (b) SFAEs and (c) SAAEs as a function of contour separation for 5 deg (white symbols) and 15 deg (dark symbols) eccentricities.
Figure 8. Results for Experiment 5: (a) SFAE and (b) SAAE as a function of interstimulus interval (ISI) for contours presented at 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricities. ISI is defined as the time interval between the offset of the adaptor and onset of test.
displacement of the perceived property of the test stimulus (e.g., shape frequency or shape amplitude) away from that of the adaptor. If this was the case, then we might have expected size scaling to reveal identical aftereffects once differences in the scale of the encoding mechanisms and stimuli have been controlled. **Experiment 2** shows this clearly not to be the case. It may be, however, that there is a change in the rate of recovery from adaptation across the visual field. For example, if the adapted channels at fixation recover more quickly than those in the periphery, then the time-averaged activity of the adapted channels will be lower in the periphery than at fixation. The prediction from this view would be that the initial adaptation both at fixation and in the periphery should be similar, but the recovery should be faster at fixation.

To examine whether the increase in the aftereffects with eccentricity is due to shorter temporal decay times in the periphery, we used adaptor and test contours that were separated in time by interstimulus intervals (ISIs) of 0, 0.5, 1, 2, 4, 6, and 8 s. **Experiment 3** shows the SFAE and SAAE were measured for adaptor/test contours at 2.5 and 7.5 deg eccentricity. Two subjects participated in this experiment; both had participated in all previous experiments.

**Figure 8a** shows the SFAE and **Figure 8b** shows the SAAE as a function of ISI for the 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricities. The results show that for both eccentricities, the aftereffects decrease with increasing ISI. Both aftereffects reach the non-adapted baseline value (dashed line) at 8 s ISI. To facilitate the comparison between the two eccentricity conditions, we normalized the aftereffects obtained for each ISI to their mean magnitude, for each eccentricity and subject. **Figures 8c and 8d** show the normalized results. The data do not support the prediction that adaptation is matched at 2.5 and 7.5 deg at short ISIs and declines more quickly with ISI at 2.5 deg. The normalized data (**Figures 8c and 8d**) show that the temporal decline of adaptation is similar for center and periphery. The two results strongly suggest that the increase in SFAE and SAAE with eccentricity is not caused by differences in the temporal decay of adaptation.

**Experiment 6: Differences in adaptation gain between center and periphery?**

The simplest explanation for the increased SAAE and SFAE in the periphery is that the sensitivities of the coding mechanisms are more strongly suppressed by adaptation in the periphery than at fixation; we call this adaptation gain. To test this possibility, we compared pre- and post-adaptation shape-frequency and shape-amplitude discrimination thresholds at two eccentricities, 2.5 and 7.5 deg. The effects of adaptation on subsequent discrimination thresholds can be quite complex. Model predictions of these adaptation effects depend on the number of filters involved, their bandwidths, and specific definition of threshold. Nevertheless, any model predicts higher post-adaptation thresholds if there is greater suppression of filter sensitivity following adaptation. Therefore, if the magnitude of the post-adaptation shift in perceived shape amplitude and shape frequency (**Experiment 1**) reflects greater adaptation gain, then the effect of adaptation on discrimination thresholds should increase with eccentricity.

**Subjects and methods**

Discrimination thresholds were measured using a two-alternative forced-choice (2AFC) procedure in the absence of the adapting stimulus (the **no-adaptor condition**) as well as after adaptation to sine-wave-shaped contours (the **with-adaptor condition**). For the **with-adaptor condition**, within each session, subjects first adapted to a pair of contours for 90 s followed by repeated pair of test contours of 0.25 s interspersed with top-up adaptation periods of 2.5 s. During the adaptation and test periods, the shape phase of the contours changed randomly every 0.5 s in order to minimize the effects of local orientation adaptation and to prevent the occurrence of afterimages. For shape-frequency discrimination, we used pairs of sine-wave-shaped test contours in which one was a pedestal-alone contour with fixed shape frequency of 0.43 c/deg and the other was a pedestal-plus-increment with an adjustable increment shape frequency. The shape-amplitude of the stimuli was fixed at 0.43 deg. The pedestal-alone and pedestal-plus-increment were simultaneously presented to the subject above and below fixation for 0.25 s.

Threshold elevation was measured using a two-alternative forced-choice (2AFC) procedure and a 2-up/1-down staircase method that homes in at 70.7% correct, as described in **Experiment 3**, subjects and methods section. To obtain an estimate of threshold elevation, we first calculated the **difference** between the logarithm of each **with-adaptor** shape-frequency threshold estimate and the mean of the logarithms of the **no-adaptor** shape-frequency threshold. This is mathematically equivalent with calculating the logarithm of the ratio of each **with-adaptor** to **no-adaptor** shape-frequency threshold estimates (log(W/N) = log(W) − log(N)). We then calculated the mean and standard error of these log thresholds difference across the five measurements. These are the threshold elevation values shown in the graphs.

For the shape-frequency discrimination experiment, the shape frequency of the adaptor pair was set to one of the eleven values: 0.2, 0.243, 0.295, 0.358, 0.43, 0.53, 0.642, 0.78, 0.95, 1.15, and 1.4 c/deg. We used pairs of test contours in which one was a pedestal-alone contour with fixed shape frequency of 0.43 c/deg and the other was a pedestal-plus-increment with adjustable increment shape frequency. The shape-amplitude of both the adaptor and test stimuli was fixed at 0.43 deg. For each eccentricity,
Figure 9. Results for Experiment 6: (a) Shape-frequency threshold elevation as a function of adaptor shape frequency and (b) shape-amplitude threshold elevation as a function of adaptor shape amplitude obtained for 2.5 deg (dark symbols) and 7.5 deg (white symbols) eccentricities.
the shape-frequency threshold elevations for each of the eleven values of shape frequency of the adaptor pair were measured in separate blocks of trials, four times in random order for each subject. For the shape-amplitude discrimination thresholds, the shape amplitude of the adaptor pair was set to one of eleven values: 0.2, 0.243, 0.295, 0.358, 0.43, 0.53, 0.642, 0.78, 0.95, 1.15, and 1.4 deg, while the shape frequency of the adaptor and test contours was fixed to 0.43 c/deg. We used pairs of test contours in which one was a pedestal-alone contour with fixed shape amplitude of 0.43 deg and the other was a pedestal-plus-increment with adjustable increment shape amplitude. For each eccentricity, the shape-amplitude threshold elevations for each of the eleven values of shape amplitude of the adaptor pair were measured in separate block of trials, four times in random order for each subject. Four subjects participated in the shape-frequency discrimination experiment and three subjects in the shape-amplitude discrimination experiment, all of which had participated in Experiment 1.

Results

Figure 9a shows shape-frequency discrimination threshold elevations and Figure 9b shows shape-amplitude discrimination threshold elevations for 2.5-deg (dark symbols) and 7.5-deg (white symbols) eccentricities. The light gray arrows indicate the shape frequency/shape amplitude of the pedestal-alone contour. The results clearly show greater threshold elevation in the periphery than in the center (compare white and dark symbols), except subject JB in the shape-frequency discrimination condition. These results, combined with those of Experiments 1, 2, and 4, suggest that peripheral mechanisms are simply more strongly adaptable.

General discussion

We have shown that two shape aftereffects, the shape-frequency and shape-amplitude aftereffects (SFAE and SAAE), increase with eccentricity. Eccentricity-dependent changes in two other aftereffects, the tilt and motion aftereffects, have been reported before (Harris & Calvert, 1985; Muir & Over, 1970; Over et al., 1972; Wright, 1986; Wright & Johnston, 1985a, 1985b). Similarly, for the aftereffect in which a briefly presented line causes a circle to appear elliptical (Suzuki & Cavanagh, 1998), Muir and Over (1970) found a 35% increase in the tilt aftereffect when going from central vision to 7 deg eccentricity, whereas we found that the SFAE and SAAE increased by an average of 115% when going from 2.5 to 7.5 deg (see Figure 3). Although Harris and Calvert (1985) found that the increase in tilt aftereffect with eccentricity was abolished when the peripheral stimuli were increased in size to compensate for differences in cortical magnification, we found that with our aftereffects, changes in stimulus scale had no significant effect on aftereffect magnitude. This indicates that scaling or magnification of curvature receptive fields with eccentricity does not explain the larger peripheral SFAEs and SAAEs.

The SFAEs and SAAEs are evoked by stimuli that are somewhat novel and so the failure of size scaling to compensate for the eccentricity-dependent increase in the aftereffects might reflect undocumented peculiarities associated with them. The SFAEs and SAAEs are induced by stimuli that are sinusoidal modulations of a contour about a horizontal straight line. One might think that a better stimulus configuration to study eccentricity effects is to use stimuli that are sinusoidal modulations about an arc rather than a line. However, this configuration would distort the stimulus and introduce a factor not present in previous studies. Specifically, if the stimuli were defined on an arc, then as stimulus size increases the ends of each pair of contour adaptors/tests would eventually abut (e.g., for size 5 at 2.5 deg). This would limit the sizes we can test and introduce a possible confound because proximity of the upper and lower contours would be correlated with size. For this reason, we used contours that are sinusoidal modulations about a straight line. Irrespective of whether the contour stimuli are modulated about a line or arc, the mechanisms implicated in both shape aftereffect and shape discrimination must integrate information over space when spatially extended stimuli are used. Our question is whether this entire process scales with eccentricity. Indeed, this is implicit in the vast majority of size scaling studies, although there are a few notable exceptions (Whitaker, Makela et al., 1992). In the size scaling literature, there is the unavoidable fact that all stimuli become poorly localized as stimulus size increases. Eccentricity is nominally defined as the center of the stimulus, but it is clear that larger stimuli extend across space, by definition. This is not typically a serious issue for size scaling experiments such as those we have described in Experiments 2 and 3. The question addressed in the size scaling literature is one of local scale. Essentially, is the effect of changing stimulus size the same at each eccentricity except for a shift along the log size axis? On this view, the visual system is sensitive to stimuli of different sizes. At any given nominal eccentricity, mechanisms of various sizes exist. Mechanisms engaged by larger stimuli must integrate information across larger areas than those engaged by smaller stimuli. The question is whether the size dependence is qualitatively similar at all eccentricities. Our stimuli are designed to answer this question.

The failure of size scaling to compensate for the eccentricity-dependent increase in the SFAE and SAAE might reflect undocumented peculiarities associated with
our stimuli. Therefore, in Experiment 3, we examined scale-dependent changes in discrimination thresholds at 2.5 and 7.5 deg eccentricity. Unlike the associated aftereffects, discrimination thresholds showed the expected scale dependence at both eccentricities: discrimination thresholds decreased as stimulus size increased. Therefore, the changes in aftereffect strength with eccentricity appear to be specific to adaptation. This leaves the question of how to explain the eccentricity-dependent increases in the aftereffects. Experiment 4 showed that part of this increase can be explained by configurational aspects of the stimuli; we...
found a small increase (∼12%) in the aftereffects with increased spatial separation between the pair of contours when eccentricity was held constant. Experiment 5 tested whether differences in the rate of recovery from adaptation might explain the bulk of the eccentricity-dependent changes in the aftereffects, but we found no evidence in support of the idea. Finally, we found in Experiment 6 that the eccentricity-dependent changes in the aftereffects were mirrored by eccentricity-dependent changes in post-adaptation discrimination thresholds. The evidence thus suggests that adaptation gain simply increases with eccentricity, that is, post-adaptation sensitivity suppression increases with eccentricity.

There is, however, another possibility. An explanation that is prima facie consistent with the data is that the eccentricity-dependent change in aftereffect strength is due to eccentricity-dependent changes in the bandwidths of the coding mechanisms. Figure 10 demonstrates the idea. In all panels, the x-axis represents stimulus values (0.1 to 10) on an unspecified stimulus dimension; this could be shape frequency or shape amplitude. Figure 10a shows banks of nine (columns 1 and 3) or fifteen (columns 2 and 4) filters that have full bandwidths at half-height of 2 or 4 octaves. We model adaptation to a stimulus value of 0.3 by reducing each filter’s sensitivity in proportion (50%) to its response (R) to the adapting stimulus. Since maximum sensitivity is 1, the adapted sensitivity is $1 - 0.5R$. These post-adaptation sensitivities are shown in Figure 10b. The effects of adaptation on the magnitude of the aftereffect was examined by finding the stimulus value that elicited a pattern of responses in the unadapted filters that best matches the pattern elicited by a test stimulus from the adapted filters, using a stimulus with a higher value than the adapting stimulus. The measure used to find the best match was the simple correlation between filter responses to adaptor or unadapted stimuli. The test stimulus was set to 0.77 (vertical blue line). Figure 10c shows the unadapted (blue symbols) and adapted (green symbols) filter responses to the test stimulus of 0.77 (vertical blue line). The stimulus value that produces a distribution of responses in the unadapted filters that best matches the distribution of responses to the test stimulus in the adapted filters is indicated by the vertical green line. The perceived shifts between the unadapted and adapted conditions are expressed as percentages and roughly match the perceived shifts in shape frequency and shape amplitude obtained in Experiment 1.

As would be expected from the standard, cross-fiber account of aftereffects, the perceived magnitude of the stimulus shifts upwards (i.e., towards higher stimulus values) following adaptation. In the model, the degree of the perceived shift in stimulus value (elevation) depends on the filters’ bandwidth (threshold elevation is greater in columns 3 and 4 than in columns 1 and 2), and this is little affected by the number of filters, i.e., nine or fifteen filters. Therefore, it may be that the eccentricity-dependent increases in the SFAE and SAAE may reflect an eccentricity-dependent increase in the bandwidth of the filters that encode shape frequency and shape amplitude.

This account is pleasing in its simplicity but may not be consistent with other existing evidence. First, several studies have examined eccentricity-dependent changes in the bandwidths of orientation and scale-selective filters (Mullen & Losada, 1999; Swanson & Wilson, 1985) and none of these supports the idea developed above. Mullen and Losada (1999) measured sensitivity to sine-wave gratings of 0.5 cpd at eccentricities of 0 to 30°. Sensitivity was measured in the presence of notch-filtered broadband noise. They found measures of critical bandwidth to be essentially independent of eccentricity.

Wilson, McFarlane, and Phillips (1983) showed that the bandwidth of frequency tuning at the fovea increased as grating frequency decreased, and Phillips and Wilson (1984) drew similar conclusions about orientation tuning. These foveal results are consistent with physiological studies by De Valois, Albrecht, and Thorell (1982). Swanson and Wilson (1985) argued that each of these filters scale with eccentricity, meaning that the bandwidth of spatial filters is inversely related to their peak frequency at each eccentricity, but for any given filter, its cohorts across eccentricity have the same bandwidth. This view presents two problems for our bandwidth account. If bandwidth increases as peak frequency decreases, this means we might have expected the size of the SAAE and SFAE to increase as stimulus size increases at both 2.5 and 7.5 deg eccentricities. Figure 4 shows no evidence of this. Swanson and Wilson’s claim that any given mechanism scales with eccentricity means that size scaling should have led to matched aftereffects at 2.5 and 7.5 deg eccentricities. Again, Figure 4 shows this not to be the case. The above-mentioned studies deal with detection and discrimination of sine-wave gratings and thus may not apply to the SAAE and SFAE that are mediated by mechanisms sensitive to local curvature (Gheorghiu & Kingdom, 2007, 2009). The eccentricity-dependent changes in the mechanisms that code shape frequency and shape amplitude may not be the same as the eccentricity-dependent changes in the mechanisms that code for luminance spatial frequency and orientation. For example, we recently showed evidence that first- and second-order luminance spatial frequency and the two shape aftereffects (SFAE and SAAE) are mediated by different mechanisms (Gheorghiu, Kingdom, & Witney, 2010). Therefore, the bandwidth model shown in Figure 10 has elegance and promise but needs further study.

The effects of adaptation on subsequent discrimination thresholds differ from the effects of adaptation on detection thresholds. In the case of orientation adaptation (or luminance spatial frequency adaptation), it is generally assumed that “orientation channels” whose tuning curves are steepest at the reference orientation contribute most to orientation discrimination. Thus, orientation adaptation tends to elevate discrimination thresholds at 10–20 deg off the adapting orientation (Wilson & Regan, 1984). If shape
frequency and shape amplitude were coded by “channels” tuned to different values of these features, one would expect the maximum threshold elevations to occur slightly off the value of the adapting shape frequency or shape amplitude. However, the data in Figure 9 do not show this pattern. This discrepancy is difficult to explain. However, it may be that the eccentricity-dependent changes in the mechanisms that code shape frequency and shape amplitude are not the same as the eccentricity-dependent changes in the mechanisms that code for luminance spatial frequency and orientation. For example, we recently showed evidence that local orientation adaptation (Gheorghiu & Kingdom, 2007), first- and second-order luminance spatial frequency adaptation, and the two shape aftereffects (SFAE and SAAE) are mediated by different mechanisms (Gheorghiu et al., 2010).

The size independence of the shape aftereffects is different than the size dependence of the shape-frequency and shape-amplitude discrimination thresholds, indicating that shape aftereffects described here are not mediated by the same mechanisms as those employed in the shape-frequency and shape-amplitude discrimination. We have previously shown that the SFAE/SAAE are likely mediated by mechanisms sensitive to local curvature (Gheorghiu & Kingdom, 2007) which represent curvature via a population response of curvature detectors that multiply their first-order afferent inputs (Gheorghiu & Kingdom, 2009). On the other hand, curvature detection and discrimination is probably accomplished with a minimum of neural machinery such as end-stopped cells (Dobbins, Zucker, & Cynader, 1987, 1989) or comparison of responses from pairs of orientation-selective V1 simple cells positioned at different points along the curve (Kramer & Fahle, 1996; Wilson, 1985; Wilson & Richards, 1989). Thus, curvature detection and discrimination do not necessarily provide an account of how curvature is represented in the brain. As typically seen in the size scaling literature but unlike the associated aftereffects, discrimination thresholds showed the expected scale dependence at both eccentricities: discrimination thresholds decreased as stimulus size increased. Therefore, the changes in aftereffect strength with eccentricity appear to be specific to adaptation.

Acknowledgments

This research was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Grant OGP01217130 given to F.K., by an Australian Research Council (ARC) Discovery Project (Grant DP110101511) given to J.B., and by a research grant “Krediet aan Navorsers” (KAN) and a Research Foundation Flanders (Fonds Wetenschappelijk Onderzoek—Vlaanderen) fellowship given to E.G.

Commercial relationships: none.
Corresponding author: Elena Gheorghiu.
Email: elena.gheorghiu@psy.kuleuven.be.
Address: Laboratory of Experimental Psychology, University of Leuven, Tiensestraat 102, Leuven B-3000, Belgium.

References


