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Computational Vision • Eye Movements & Visuomotor Control
ISSN 0042-6989
Volume 50
Issue 21
12 October 2010

Vision Research 50 (2010) 2127–2136

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Size and shape after-effects: Same or different mechanism?

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ARTICLE INFO

Article history:
Received 26 April 2010
Received in revised form 30 July 2010

Keywords:
Contour
Curvature
Size
Adaptation
Shape
After-effect

ABSTRACT

The shape-frequency and shape-amplitude after-effects, or SFAE and SAAE, are shifts in the perceived shape-frequency and perceived shape-amplitude of a sinusoidal test contour following adaptation to a similar-shaped contour. These shape-effects are the shape analogs of the well-known size after-effect discovered by Blakemore and Sutton (1969), so it is possible that they are mediated by a size-sensitive mechanism. We tested this possibility by comparing the magnitudes of SFAEs/SAAEs elicited by contour/edge adaptors with those from luminance grating and line-grating adaptors. The rationale was that if the shape after-effects using the two classes of adaptors were similar, then they would likely be mediated by the same mechanism. We found that the SFAE and SAAE were greatly reduced when using luminance and line grating adaptors, suggesting that the SFAE and SAAE are not mediated primarily by either first- or second-order size-sensitive mechanisms. Based on previous studies we conclude that SFAEs/SAAEs are mediated by mechanisms primarily sensitive to curvature.

1. Introduction

An important tool in the study of shape perception is the shape after-effect. In this phenomenon, the perceived shape of an object is altered following adaptation to an object of slightly different shape (Anderson, Habak, Wilkinson, & Wilson, 2007; Bell, Gheorghiu, & Kingdom, 2009; Bell & Kingdom, 2009; Blakemore & Over, 1974; Gheorghiu & Kingdom, 2007a, 2008, 2009; Gheorghiu, Kingdom, Thai, & Sampasivam, 2009; Regan & Hamstra, 1992; Suzuki, 2001, 2003; Suzuki & Cavanagh, 1998). Two shape after-effects, the shape-frequency and shape-amplitude after-effects, or SFAE and SAAE, have been recently employed to study various aspects of curvature coding in human vision. The SFAE and SAAE are the perceived shifts in respectively the shape-frequency and shape-amplitude of a sine-wave-shaped contour following adaptation to a sine-wave-shaped contour of slightly different shape-frequency or shape-amplitude. As with other spatial after-effects such as the tilt after-effect (Gibson, 1933; Magnussen & Kurtenbach, 1980a, 1980b; Wenderoth & Johnstone, 1988) and size after-effect (Blakemore & Campbell, 1969), the perceived shifts in the SFAE and SAAE are always in a direction away from that of the adaptation stimulus. Gheorghiu and Kingdom (2007b) provided evidence that both the SFAE and SAAE are mediated by curvature-sensitive mechanisms rather than by mechanisms sensitive to local orientation adaptation, periodicity or global shape. However, it is still possible that the shifts in shape-amplitude and shape-frequency observed in the SAAE and SFAE are not a result of curvature adaptation per se, but of a general size adaptation process that has the effect of stretching or shrinking parts of the sinusoidal contour in the direction of the shape modulation or in the direction orthogonal to it. Blakemore and Campbell (1969) showed that adaptation to a luminance grating caused a shift in the apparent spatial frequency of a test grating away from that of the adaption spatial frequency. The SFAE can be considered to be the shape analog of this version of the size after-effect. The question however is whether it is more than just an analog, but is mediated by the same mechanism. The aim of this communication is to determine whether or not this is the case.

It is widely accepted that the size after-effect reported by Blakemore and Campbell (1969) is mediated by cortical channels selective to luminance spatial-frequency (Blakemore & Nachmias, 1971; Blakemore, Nachmias, & Sutton, 1970; Blakemore & Sutton, 1969; Burton & Ruddock, 1978). Readers can experience both the shape and size after-effects in Fig. 1. If one moves ones' eyes back and forth along the horizontal markers between the pair of adapting stimuli (left), and then transfer one's gaze to the central spot on the right, the two test patterns will likely appear to have a different shape-frequency (Fig. 1a), shape-amplitude (Fig. 1b) and size (Fig. 1c). An important property of all these after-effects is that they survive phase randomization during adaptation.

Are there *a priori* reasons for supposing that the SFAE and SAAE are manifestations of size after-effects? If they are manifestations, they should, for example, have properties in common. The size after-effect is broadly selective for orientation (Blakemore & Nachmias, 1971; Blakemore et al., 1970; Burton & Ruddock,

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doi:10.1016/j.visres.2010.08.006

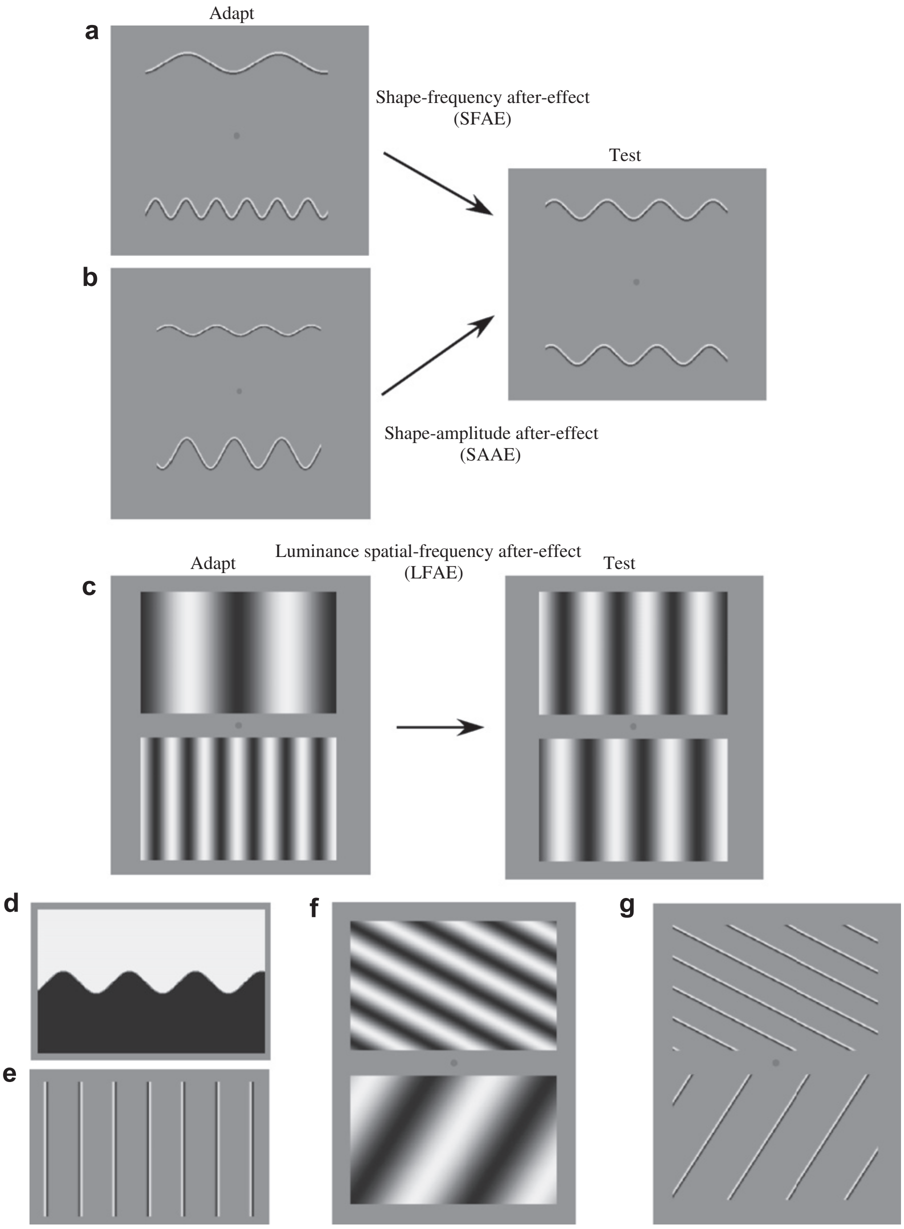

Fig. 1. Stimuli used in the experiments. One can experience: (a) the shape-frequency after-effect (SFAE) and (b) the shape-amplitude after-effect (SAAE) by moving one's eyes back and forth along the markers located midway between the pair of adapting contours (left) for about 90 s, and then shifting one's gaze to the middle of the test contours (right). (c) The size, or luminance spatial-frequency after-effect that is the apparent spatial frequency shift observed after adaptation to slightly different frequencies. (d–g) Example stimuli: sine-wave-shaped edge (d); line grating (e); oriented sine-wave luminance gratings adaptors (f), and line-grating adaptors. The sine-wave luminance and line gratings were oriented at 32 and 62° either to the right (+) or to the left (−) from the vertical.

1978; Heeley, 1979), spatial frequency (Blakemore & Nachmias, 1971; Blakemore et al., 1970; Nishida, Motoyoshi, & Takeuchi, 1999) and luminance-polarity or phase (DeValois, 1977). It increases with both adapting contrast and adapting duration (Blakemore et al., 1970). With regard to color selectivity, Virsu and Haapasalo (1973) reported a color-selective difference in the adaptation effect when using alternating adaptation to different colors and spatial frequencies. However, because they also found some transfer of the size after-effect between adaptor and test patterns that differ in color they concluded that the size after-effect was not color specific. More recent studies (Hardy & De Valois, 2002) have shown that both color-selective and color-non-selective mechanisms are involved in the size after-effect. The SFAE and SAAE are also selective for luminance polarity, luminance spatial-frequency and color direction (Gheorghiu & Kingdom, 2006, 2007a). On the other hand, the size after-effect shows an interocular transfer of about 60% (Bjorklund & Magnussen, 1981; Blake, Overton, & Lema-Stern, 1981) whereas the SFAE and SAAE shows an interocular transfer greater than 90% (Gheorghiu et al., 2009). The SFAE and SAAE are more-or-less contrast independent, though the largest after-effects are observed when adaptor and test contrasts are the same (Gheorghiu & Kingdom, 2006). Nishida et al. (1999) found that direction of motion had no influence on the magnitude of the size after-effect over a wide range of spatiotemporal frequencies, though there was a small degree of selectivity at low spatial and high temporal frequencies (0.5 c/deg, 8 Hz). Gheorghiu, Kingdom, and Varshney (2010) on the other hand found that both SFAEs and SAAEs were selective to global motion direction across a wide range of temporal frequencies though predominantly at high shape temporal frequencies. We also found that both shape after-effects were non-selective to local motion direction even at high luminance temporal frequencies. Taken together, although the size and shape-frequency/amplitude after-effects share some properties, they do not share all, so it is difficult to come to any firm conclusions as to whether they are mediated by the same mechanisms.

Are there *mechanistic* grounds for the idea that size and shape after-effects are mediated by a common mechanism? It is widely believed that the size after-effect, at least that measured by Blakemore and Sutton (1969), is mediated by narrowband luminance spatial-frequency channels in the cortex. How would such channels respond to our sinusoidal-shaped contour stimuli? The question is relevant also to the sinusoidal-shaped *edge* stimuli we have occasionally employed (Gheorghiu & Kingdom, 2006), as in Fig. 1d. Consider the Fourier decomposition of the stimuli shown in Fig. 2. Normalized-to-maximum 2D Fourier amplitude spectra are shown in Fig. 2a for sine-wave-shaped contours and Fig. 2b for sine-wave-shaped edges, at shape frequencies of 6 c/im (cycles per image) (left panels) and 2 c/im (right panels). These shape frequencies correspond to the 0.75 and 0.25 c/deg adaptation shape frequencies used in this study (which are used to elicit opposite-direction shifts in the apparent shape frequency of a 0.43 c/deg test contour). The plots reveal that most of the Fourier energy, and hence energy differences between the two adaptation shape frequencies, is found at orientations other than vertical or horizontal (vertical orientations are plotted along the horizontal meridians). The orientation dependency of peak Fourier amplitude is revealed more clearly when we select the Fourier components at just the two shape-frequencies (2 and 6 c/im) and plot these as a function of orientation, as in Fig. 3. The vertical dashed line in the plot indicates vertical (0°). Fourier amplitude peaks at about ±32° from vertical for contours/edges of 6 c/im and at about ±62° from vertical for contours/edges of 2 c/im. These angles are very close to the tangents of the shape modulation at the d.c. of the waveform.

Fig. 4b shows the amplitudes of just the vertical component at the shape-frequency of the contours and edges, and compares these to that of a vertical luminance grating of 50% contrast (the same luminance-contrast as that of the shapes) at an equivalent spatial frequency. One can see that the sine-wave-shaped contour has zero amplitude at its shape frequency, whereas the sine-wave-shaped edge has about a quarter of the amplitude of the luminance grating. These differences can be understood intuitively by comparing the two adjacent half cycles (demarcated by dashed black lines) of each of the three waveforms in Fig. 4a.

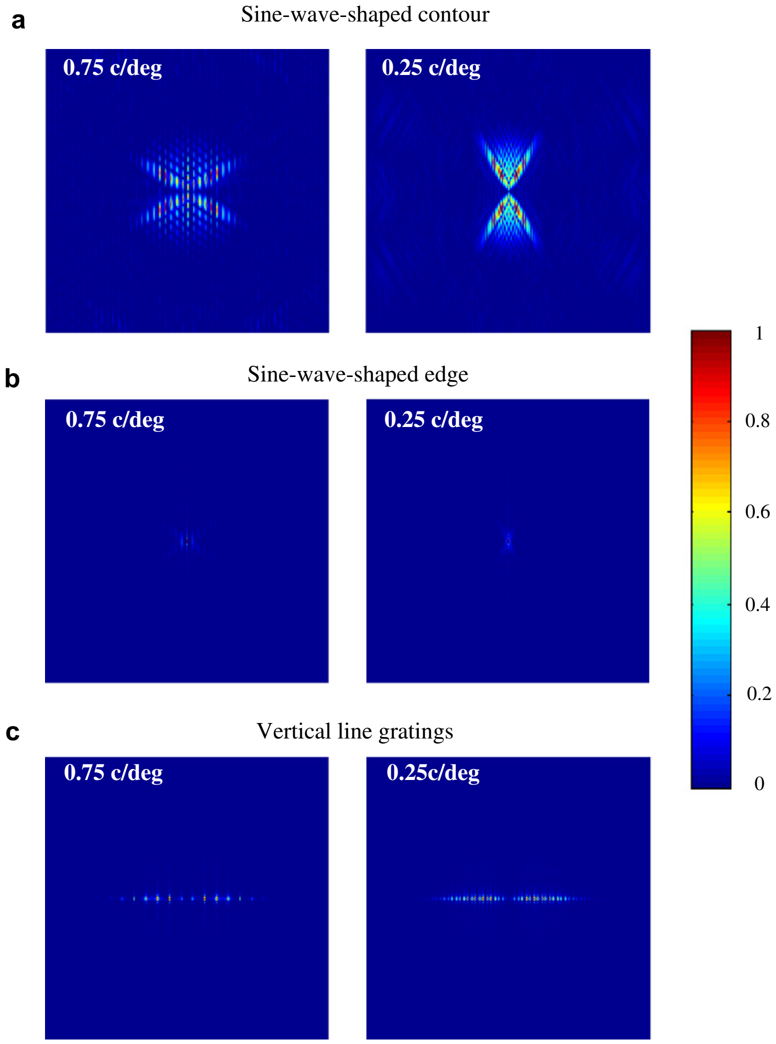

Fig. 2. Two-dimensional Fourier amplitude spectrum for: (a) sine-wave-shaped-contours, (b) sine-wave-shaped edges and (c) line gratings of shape-frequencies of 6 c/im (cycles per image) (left panels) and 2 c/im (right panels) normalized to the maximum Fourier amplitude of each spectrum. The 6 and 2 c/im frequencies correspond to the 0.75 and 0.25 c/deg shape-frequencies used in the experiments.

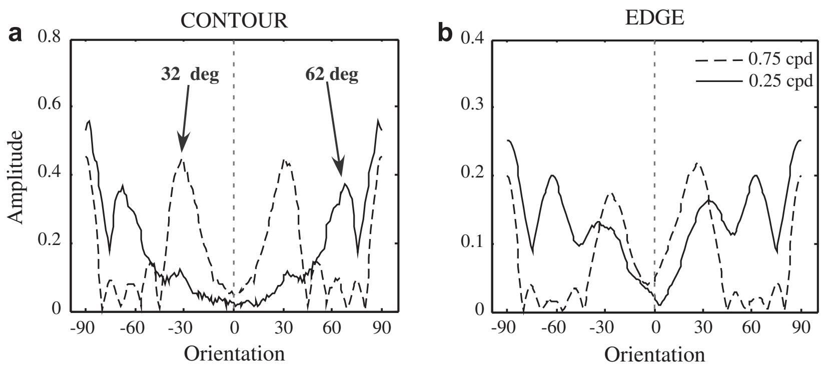

Fig. 3. Fourier amplitude at shape-frequency 0.25 c/deg (solid line) and 0.75 c/deg (dashed line) for sine-wave-shaped (a) contours and (b) edges, as a function of orientation. The vertical gray dashed line indicates the vertical orientation (0 deg).

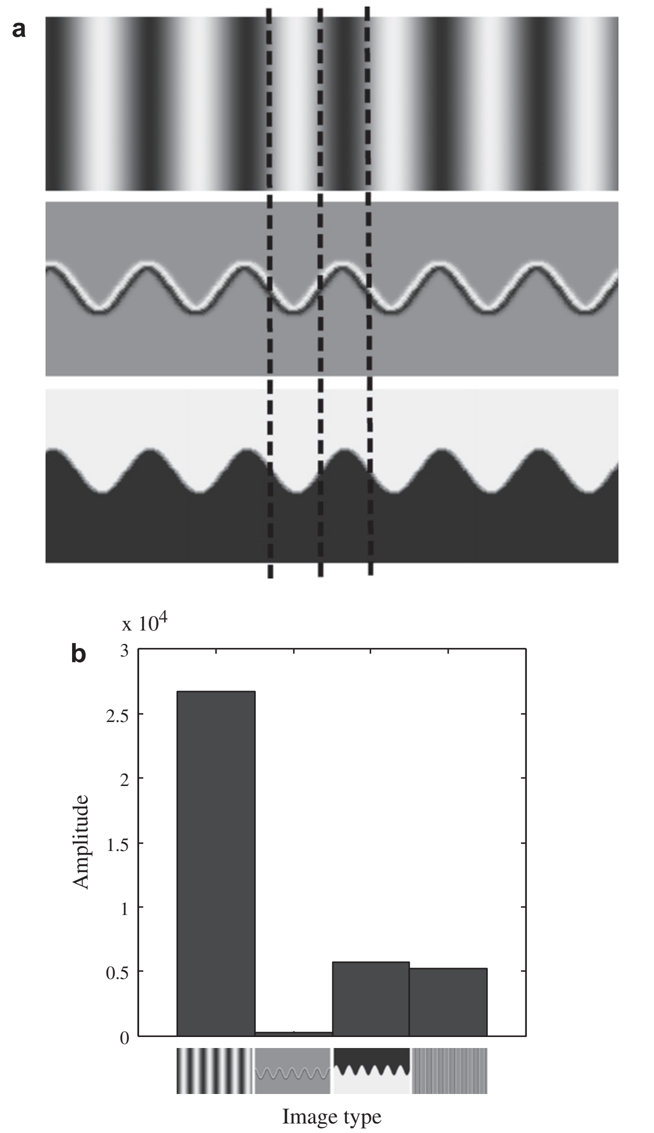

Fig. 4. (a) Stimulus images used to explain how vertical energy in sine-wave-shape stimuli and sine-wave luminance grating is different (see text for details). Dashed line delineates half-cycles of the shape and luminance stimuli. (b) Absolute value of the vertical component of Fourier amplitude spectra at the shape-frequency of 0.75 c/deg for luminance gratings, sine-wave-shaped contours and edges, and line gratings.

In the case of the edge for example, one half cycle has more white than black whereas the adjacent half-cycle has more black than white, hence having non-zero Fourier amplitude.

Fourier analysis therefore reveals that horizontally modulated sine-wave-shaped *edges* have significant amounts of vertical energy at their shape-frequencies, whereas horizontally modulated sine-wave-shaped *contours* have little or no vertical energy at their shape frequency. Fourier analysis also reveals that *both* sine-wave-shaped contours *and* sine-wave-shaped edges have significant amounts of energy at ± orientations close to the tangent of the contour/edge at the waveform's d.c. Therefore, assuming that the size after-effect is mediated by narrowband spatial-frequency channels, it *is* possible that the SFAE is mediated by the same spatial-frequency channels as the size after-effect. For sine-wave-shaped edges, the channels would either be vertically and/or obliquely oriented, while for sine-wave-shaped contours the channels would be obliquely oriented.

In the rest of this communication we describe experiments aimed at testing these possibilities by considering whether the SFAE/SAAE can be induced by *luminance, or first-order* size adaptation. A size adaptation mechanism that mediated, for example, the SFAE would have the effect of perceptually stretching or shrinking parts of the sinusoidal contour in the direction of the shape modulation.

We also consider whether the contour-based SFAEs and SAAEs are mediated by *contrast, or second-order* size adaptation. A second-order size after-effect would not result from adaptation to luminance variations, but from adaptation to luminance-contrast variations. The mechanisms mediating second-order size adaptation are presumably tuned to two stimulus properties: the coarse-scale 'envelope' of contrast change over space and the finer-scale 'carrier' luminance-contrasts that they detect. To test whether contour-based SFAEs/SAAEs are mediated by a second-order size after-effect we have used adaptors constructed from lines that have the same cross-sectional luminance profile as that of the sine-wave-shaped contours and spaced at the same periodicity. Example stimuli are shown in Fig. 1e and g.

To summarize: we aim to test whether the SFAE and SAAE are mediated by the same mechanisms as the size after-effect, that is mediated by luminance spatial-frequency-selective channels. To do this, we have measured both the size after-effect and the SFAE/SAAE using two classes of stimuli: sine-wave-shaped contours/edges and vertical/horizontal/oriented sine-wave luminance/line gratings. We have compared shape after-effects for adaptor-and-test combinations of the same class with those of a different class. The amount of transfer between the different class adaptor-and-test conditions (i.e. luminance-based adaptor and shape-based test) and same class adaptor-and-test conditions is indicative of the contribution of size mechanisms to the SFAE/SAAE. Thus if the size of the SFAE/SAAE obtained with luminance and/or line-grating adaptors is similar in magnitude to that obtained from sine-wave-shaped contour/edge adaptors, then we may conclude that the SFAE and SAAE are mediated by the same luminance spatial-frequency channels as the size after-effect.

2. Methods

2.1. Observers

Four subjects participated in different experiments. Two subjects were two of the authors (FK and EW) and two subjects (AB and BM) were naive with regard to the experimental aim. All subjects had normal or corrected-to-normal visual acuity. Each subject gave informed consent prior to participation in accordance with the university guidelines.

2.2. Stimuli

The stimuli were generated by a ViSaGe video-graphics card (Cambridge Research Systems) with 12-bits contrast resolution, presented on a calibrated, gamma-corrected Sony Trinitron monitor (120 Hz frame rate, 1024 × 768 pixels spatial resolution). The mean luminance of the monitor was 40 cd/m^2.

Adaptor and test stimuli consisted of pairs of 2D contours or luminance gratings. The two adaptors and tests were presented at 3.5° above and below the fixation marker. Each contour/grating filled an area of 8 (width) × 4 (height) deg. The cross-sectional luminance profile of the contours/gratings was odd-symmetric and was generated according to a first derivative of a Gaussian function:

$$L(d) = L_b \pm L_b \cdot C \cdot \exp \cdot (0.5) \cdot (d/\sigma) \cdot \exp[-(d^2)/(2\sigma^2)] \quad (1)$$

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/m^2, C contrast and σ the space-constant. C was set to 0.5 and σ to 0.044° for all experiments. The ± -sign determined the polarity of the contour. Our contours were designed to have a constant cross-sectional width, as described elsewhere (Gheorghiu & Kingdom, 2006). Edge luminance profiles were constructed according to the same equation, with the constraint that the profile remained asymptotic at the peak of the function (see Fig. 1d).

We used two classes of adapting and test stimuli: (a) shape stimuli that were sine-wave-shaped contours and edges, and (b) luminance stimuli that were sine-wave luminance and line gratings. Example stimuli are shown in Fig. 1. There were two conditions: (i) both adaptor and test of the same class, either shape (contours and edges) or luminance (sine-wave luminance and line gratings), and (ii) adaptor and test of different class: luminance-based adaptor (sine-wave luminance and line gratings) and shape-based test (sine-wave-shaped contours and edges). This resulted in four combinations: luminance grating adaptor and shaped-contour test, luminance grating adaptor and shaped-edge test, line grating adaptor and shaped-contour test, and line grating adaptor and shaped-edge test. The luminance and line grating adaptors were either vertical, horizontal or oriented at 32° (for spatial frequency 0.75 c/deg) and at 62° (for spatial frequency 0.25 c/deg). Example oriented grating adaptors are shown in Fig. 1f–g. The gratings were oriented at 32 and 62° either to the right (+) or to the left (−) from the vertical. During the adaptation period the grating orientation alternated between right and left every 0.5 s in order to adapt both orientations equally. For example, the low spatial frequency grating (0.25 c/deg) alternated between +62 and −62° orientations whereas the high spatial frequency grating alternated between +32 and −32°. We choose to alternate between the left and right orientations and not present them together, as a plaid, in order to avoid the formation of angles or curves at the intersection of the gratings, which would then stimulate curvature mechanisms. The vertical and oriented luminance and line gratings were used only in the experiment in which we measured SFAEs, and horizontal luminance gratings were used only in the experiment in which we measured SAAEs. Subject BM did not participate in the measurement of SFAEs with oriented grating adaptor and shaped-contour/shaped-edge test.

In what follows, shape after-effects, i.e. SFAEs and SAAEs, are always measured in sine-wave-shaped contour/edge tests, while size after-effects are always measured in luminance/line grating tests. We used pairs of adaptors that differed by a factor of three in shape-frequency/shape-amplitude for the SFAE/SAAE, and by a factor of three in spatial frequency for the size after-effect (see Fig. 1). The adaptor pair for the SFAE consisted of contours with a shape-amplitude of 0.43° 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°, giving a geometric mean of 0.43°. The mean shape-frequency and mean shape-amplitude of the test contour pair were always maintained constant at 0.43 c/deg and 0.43°, respectively.

The size after-effect was measured with vertical and horizontal gratings adaptors and tests. The size after-effect measured with vertical gratings is analogous to the SFAE in that the perceived shift in spatial frequency is along the horizontal dimension. Similarly the size after-effect measured with horizontal gratings is analogous to the SAAE in that the perceived shift in spatial frequency is along the vertical dimension. For the size after-effect, the adaptor pair consisted of vertical (or oriented) luminance gratings with a spatial frequency of 0.25 and 0.75 c/deg, giving a geometric mean spatial frequency of 0.43 c/deg. The mean spatial frequency of the vertical (or oriented) grating test pair was always maintained constant at 0.43 c/deg. For the horizontal grating adaptors, grating cycle width was matched to twice the amplitude of the contour-shape adaptors used in the SAAEs, resulting in spatial frequencies of 0.333 and 0.85 c/deg and a geometric mean spatial frequency of 0.53 c/deg.

2.3. Procedure

Each session began 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 waveform-phase of the adaptors was randomly changed every 0.5 s in order to prevent the formation of afterimages and to minimize the effects of local orientation adaptation. The presentation of the test was signaled by a tone. The waveform-phase of the test stimulus was also randomly assigned in every test period. The display was viewed in a dimly lit room at a viewing distance of 100 cm. Subjects were required to fixate on the marker placed between each pair of stimuli for the entire session.

A staircase method was used to estimate the point of subjective equality (or PSE). For the SFAE the geometric mean frequency of the two test stimuli 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. towards the PSE. The session was terminated after 25 trials. Six measurements were made for each *with-adaptor* condition, three in which the upper adaptor had the higher shape-frequency and three in which the lower adaptor had the higher shape-frequency. 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 nominator the test that followed the lower shape-frequency adaptor and its denominator the test that followed the higher shape-frequency adaptor.

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 or magnitude 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 ratio 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 after-effect is defined as a *ratio* of either shape-frequency (for the SFAE), shape-amplitude (for the SAAE) or luminance spatial-frequency (for the size after-effect) and thus its units are dimensionless.

The procedure for measuring the magnitude of SAAE and the size after-effect followed the same principle as for the SFAE. For the SAAE, 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°. For the size after-effect, the computer varied the relative spatial frequencies of the two test gratings in accordance with the subject's response, while the geometric mean spatial frequency of the two test gratings was held constant at 0.43 c/deg in the experiment with vertical gratings and at 0.56 c/deg in the experiment with horizontal gratings.

3. Results

Consider Fig. 5. To facilitate comparison, the 'same' adaptor/test condition SFAEs are shown as the leftmost pair of columns in *both* Fig. 5a and b. Fig. 5a in addition shows all the conditions using luminance grating adaptors, while Fig. 5b shows all the conditions using line grating adaptors. 'Same' adaptor-test combinations are shown as white and light gray bars, whereas 'different' adaptor-test combinations are shown as dark gray and black bars. The white bars are for shaped-contours/edges while the light gray bars are for luminance/line gratings. The dark gray bars are for the vertical luminance grating/line adaptors and shaped-contour/edge tests, while the black bars are for the oriented luminance gratings/line adaptors and shaped-contour/edge tests. Thus size after-effects are shown as light gray bars while all other bar colors indicate shape after-effects. Fig. 6 shows the analogous results with SAAEs obtained with horizontal gratings/line adaptors and shaped-contour/edge tests.

The 'same' results in Figs. 5 and 6 reveal similar magnitudes of shape and size after-effect (compare white and light gray bars in Fig. 5a; also in Fig. 6a). A one-way within-subjects ANOVA (analysis of variance) with factor 'Same condition' (shaped-contour vs. shaped-edge vs. luminance gratings) showed not significant difference between these conditions: $F(2, 6) = 0.705$, $p > 0.05$ for SFAE and $F(2, 6) = 2.276$, $p > 0.05$ for SAAE. The results however show prominently reduced second-order size after-effects obtained with line gratings, with the exception of BM's vertical line-grating condition and EW's horizontal line-grating condition.

A one-way within-subjects ANOVA with factor 'Same condition' (shaped-contour vs. shaped-edge vs. line gratings) showed a significant difference between these conditions for the SAAE ($F(2, 6) = 5.3$, $p < 0.05$) but not for the SFAE ($F(2, 6) = 4.627$, $p > 0.05$). The probable reason why the second-order size after-effects were not significantly different from the SFAEs is the large variability between observers in the former. We also tested whether first- and second-order size after-effects were significantly different from each other. The analysis revealed that the second-order size after-effects were not significantly different from the first-order size after-effects obtained with vertical luminance gratings ($F(1, 6) = 1.99$, $p > 0.05$) but were significantly different from those obtained with horizontal luminance gratings ($F(1, 6) = 26.56$, $p < 0.05$).

The more important findings concern the amount of transfer of after-effect in the 'different' conditions, as these indicate the contribution of size-sensitive mechanisms to the SFAE/SAAE. Figs. 5 and 6 show that SFAEs/SAAEs are significantly reduced when the adaptors are vertical (dark gray bars in Fig. 5), oblique (black bars in Fig. 5) and horizontal (dark gray bars in Fig. 6) luminance and line gratings, compared to those obtained using shaped-contour/edges adaptors (white bars). A one-factor within-subjects ANOVA for the factor adapt-test condition (same vs. different) reveals that the difference between the 'same' and 'different' conditions for the SFAE is significant for all conditions, that is for vertical luminance grating adaptors ($F(1, 14) = 23.12$, $p < 0.05$), vertical line grating adaptors ($F(1, 14) = 27.92$, $p < 0.05$), oriented luminance grating adaptors ($F(1, 10) = 22.22$, $p < 0.05$) and oriented line grating adaptors ($F(1, 10) = 20.83$, $p < 0.05$). For the SAAE the difference is also significant for all conditions, that is for horizontal luminance grating adaptors ($F(1, 14) = 50.25$, $p < 0.05$) and line grating adaptors ($F(1, 14) = 50.99$, $p < 0.05$).

Finally, we wanted to test whether the after-effects in the 'different' conditions were significantly different from the non-adapted condition, represented on the graphs as the zero baseline. ANOVAs showed that none of the SAAEs in the 'different' condition were significantly different from the non-adapted baseline, that is for horizontal luminance adaptors ($F(1, 14) = 0.32$, $p > 0.05$) and line grating adaptors ($F(1, 14) = 1.64$, $p > 0.05$). However, all SFAEs in the 'different' condition *were* significantly different from the non-adapted baseline condition, that is for vertical luminance grating adaptors ($F(1, 14) = 24.57$, $p < 0.05$), vertical line gratings adaptors ($F(1, 14) = 17.74$, $p < 0.05$), oriented luminance grating adaptors ($F(1, 10) = 10.26$, $p < 0.05$) and oriented line grating adaptors ($F(1, 10) = 10.54$, $p < 0.05$).

4. Discussion

We investigated whether two shape after-effects, the SFAE and SAAE, and the size after-effect were mediated by a common mechanism sensitive to either the size of luminance or the size of contrast variations. First, we found little or no shape after-effect in either contour or edge test shapes following adaptation to vertical, horizontal or oblique luminance gratings. This suggests that luminance, or first-order size channels do not mediate SFAEs/SAAEs. Second we found little or no shape after-effect in contour test shapes following adaptation to vertical, horizontal or oblique line gratings that were matched to the test in both local luminance scale and periodicity. This suggests that contrast, or second-order size channels also do not mediate SFAEs/SAAEs. In short, we have found no evidence that SFAEs/SAAEs are mediated by either first- or second-order size channels.

In order to obtain an overall picture of the difference between the 'same' and 'different' adaptor-and-test conditions, we normalized the after-effect obtained for each 'different' adaptor-and-test condition to the after-effect obtained using the 'same' adaptor-and-test condition, for each observer. One can think of this measure as the amount of transfer of the after-effect in the 'different' condition. Fig. 7 shows the average, across-observers transfer of SFAE (Fig. 7a) and SAAE (Fig. 7b) in the 'different' condition for luminance (dark gray bars) and line (black bars) grating stimuli.

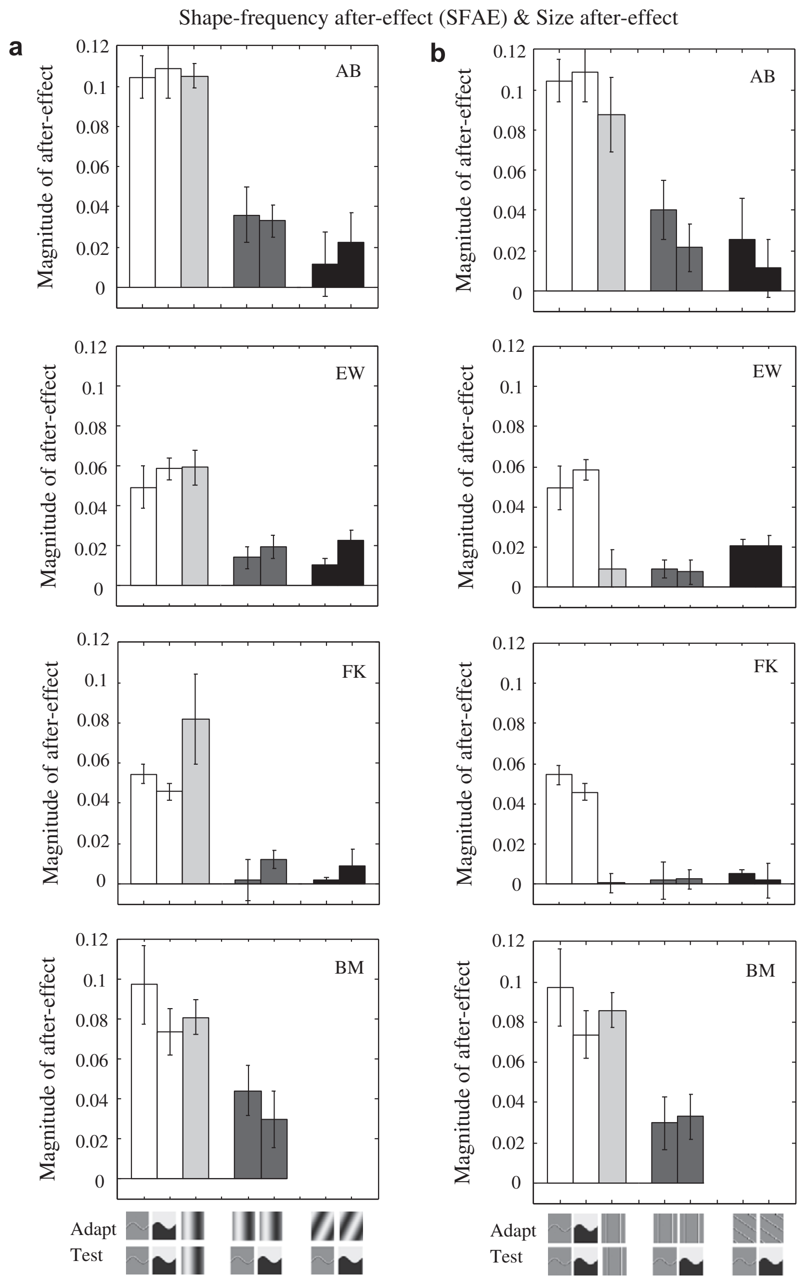

Fig. 5. (a) The SFAEs and size after-effects obtained with shaped-contour/edge and luminance grating stimuli. (b) The SFAEs and size after-effects obtained with contour/edge-shape and line grating stimuli. Note that the two white bars in (a) and (b) are the same conditions for shape-class stimuli. 'Same' adaptor-test combinations are shown as white (shape-class stimuli) and light gray (luminance-class stimuli) bars, whereas 'different' adaptor-test combinations are shown as dark gray and black bars. The dark gray bars are for the vertical luminance and line-grating adaptors and the shaped-contour/edge tests, whereas the black bars are for the oblique luminance and line-grating adaptors and shaped-contour/edge tests. Size after-effects are shown as light gray bars while all other bar colors indicate shape after-effects.

A value of 1 (dashed lines) indicates complete transfer. Fig. 7 reveals the substantially reduced transfer of the SFAE and SAAE in the 'different' compared to 'same' conditions for both first- and second-order luminance spatial-frequency stimuli (compare dark gray and black bars with the dashed line). Across conditions, the amount of transfer was 23.13% for SFAE and 3.71% for SAAE.

The fact however that in the 'different' conditions there was a degree of transfer of after-effect raises the question as to whether the size and shape after-effects are fundamentally different classes of after-effect or whether they are the same class but selective for the particular dimensions of size. The analogy here is with the way for example that size after-effects are partially selective for orientation (Blakemore & Nachmias, 1971; Blakemore et al., 1970): one would not wish to conclude from this fact that size after-effects for different oriented stimuli are fundamentally different classes of after-effect. The data from this study are not sufficient however to allow us to decide between the two aforementioned possibilities, and therefore it remains the possibility that there is indeed a generic class of size-sensitive mechanism that 'takes all-comers', but is nevertheless selective for the different dimensions of size, e.g. the sag of a curve, cord of a curve, bar width of a grating, length of a line, width of a line etc. What we can certainly say however is that the shape after-effects described here are not a straightforward manifestation of the size after-effect observed in luminance gratings.

As an aside, we demonstrated a second-order size after-effect obtained using line gratings that while smaller than the first-order size after-effect obtained using luminance gratings was neverthe-

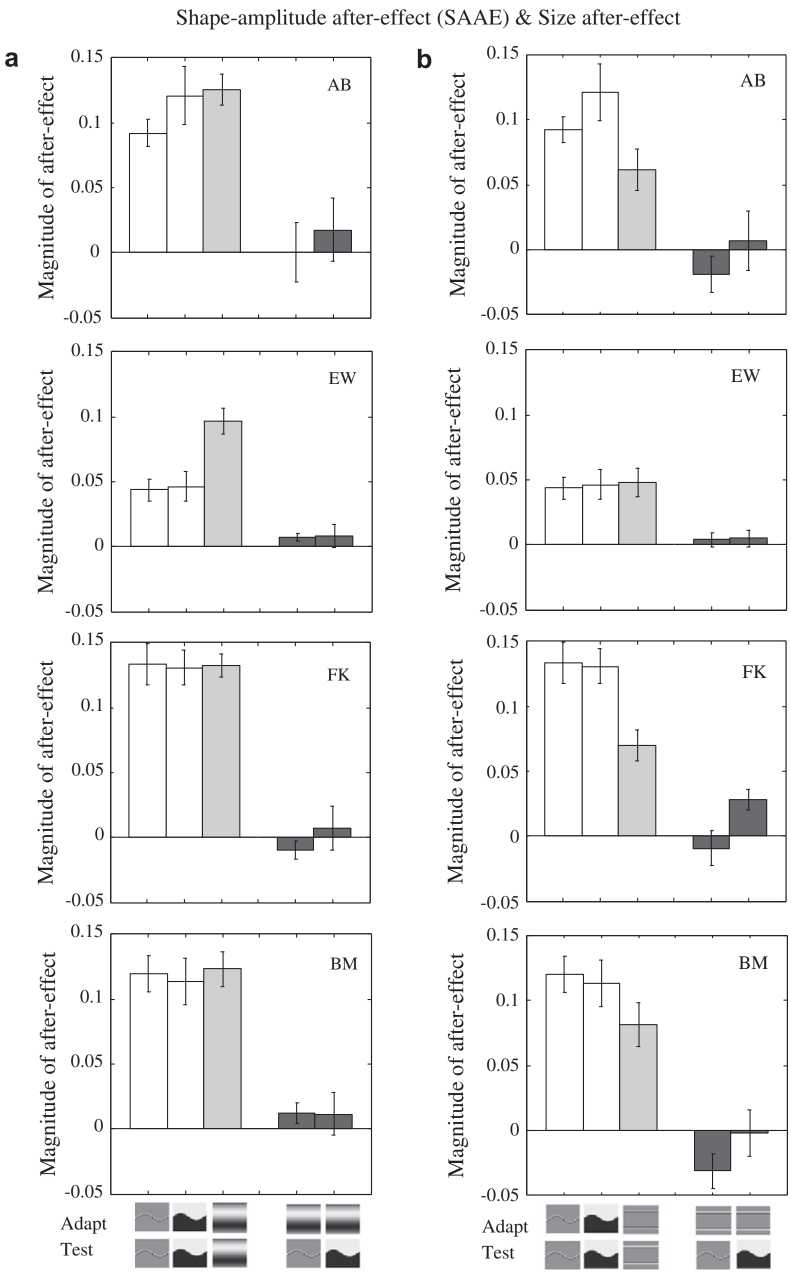

Fig. 6. (a) The SAAEs and size after-effects obtained with shaped-contour/edge and horizontal luminance grating stimuli. (b) The SAAEs and size after-effects obtained with shaped-contour/edge and horizontal line grating stimuli. Note that the two white bars in (a) and (b) are the same conditions for shape-class stimuli. 'Same' adaptor-test combinations are shown as white (shape-class stimuli) and light gray (luminance-class stimuli) bars, whereas 'different' adaptor-test combinations (i.e. horizontal luminance/line-grating adaptor and shaped-contour/edge test) are shown as dark gray bars. Size after-effects are shown as light gray bars while all other bar colors indicate shape after-effects.

less substantial. On average, the second-order size after-effect was about half (∼54.3%) of the magnitude of the first-order size after-effect obtained with horizontal gratings. With vertical gratings, while two subjects showed little or no second-order size after-effect (∼8.25%) of the magnitude of the first-order size after-effect the other two subjects showed considerable second-order size after-effect (∼94.7%).

The findings of this study reinforce the claim made by Gheorghiu and Kingdom (2007b, 2008) that the SFAE and SAAE are mediated by mechanisms sensitive to *local curvature*. Gheorghiu and Kingdom (2007b) however pitched local curvature as the causal feature not against size, but against local orientation, average unsigned curvature, periodicity/density (SFAE only), shape amplitude (SAAE only) and global shape. Their evidence against orientation adaptation as the cause was that the after-effect elicited by sinusoidal-shaped adaptor contours was the same in magnitude for both square-wave-shaped and sine-wave-shaped test contours. On geometric grounds this is difficult to explain on the basis of local orientation adaptation. Specifically, if one considers the straight-vertical portions of the square-wave-shaped contour, equal and opposite magnitude tilt after-effects would be expected from a sine-wave-shaped adaptor in its two phase-quadrature positions (Gheorghiu & Kingdom, 2007b). Further evidence against local orientation adaptation as the causal feature of the SFAE and SAAE comes from the present study. One might consider that by using vertically and/or ± oriented spatial frequency channels, local orientation adaptation might also contribute to SFAE and SAAE by producing distortions in the perceived shape of the contour.

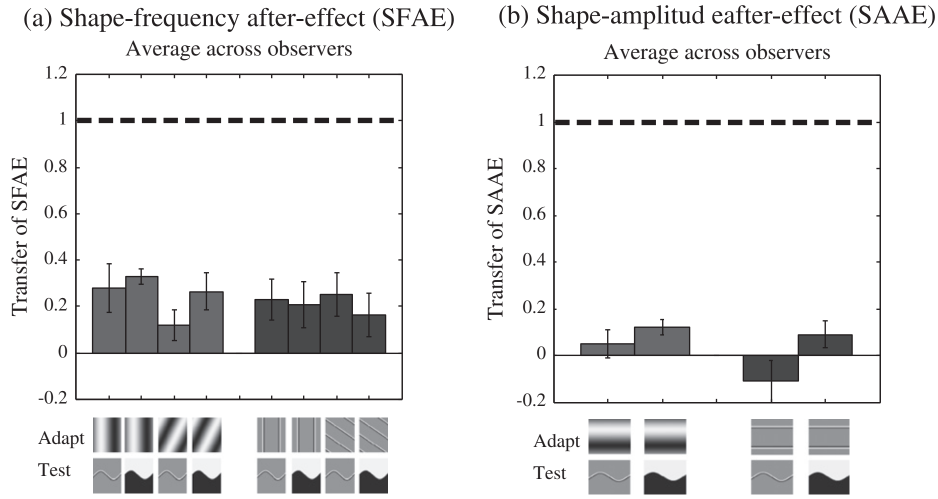

Fig. 7. Transfer of SFAE (a) and SAAE (b) in the 'different' condition for luminance (dark gray bars) and line (black bars) grating stimuli. The amount of transfer was calculated as the magnitude of SFAE/SAAE under the 'different' adaptor-and-test condition divided by the magnitude of SFAE/SAAE obtained under the corresponding 'same' adaptor-test condition. A value of 1 (dashed lines) indicates complete transfer. Across conditions, the amount of transfer was 23.13% for SFAE and 3.71% for SAAE.

The ± orientations are similar to the tangent of the sine-wave contours at the waveform's d.c. Thus, if local orientation adaptation would contribute to the shape after-effects, we would expect that the SFAE and SAAE obtained with sine-wave-shaped contour adaptors and ± orientated luminance/line gratings would produce similar magnitude of SFAE in shaped-contour tests. However, we found that prominently reduced SFAE/SAAE were obtained with luminance and line grating adaptors.

Additional evidence against local orientation was the degree of independence of the SFAE and SAAE; it was found that adapting to shape-frequency produced little or no after-effect in shape-amplitude, and adapting to shape-amplitude produced little or no after-effect in shape-frequency (Gheorghiu & Kingdom, 2008). This indicates that the sag and cord of a curve are independently processed, which is difficult to explain on the basis of orientation adaptation, since this would be expected to impact both the sag and the cord. Furthermore, we have recently shown that the motion-direction selectivity of orientation adaptation is not a factor in the motion-direction selectivity of the SFAE/SAAE (Gheorghiu et al., 2010). In short, two of the most studied types of spatial after-effect, luminance size (or spatial frequency) after-effect and the tilt after-effect (TAE), do not appear to be mediating either the shape-frequency or shape-amplitude after-effects.

The main evidence *in favor* of local curvature mediating the shape after-effects is that when using full sine-wave adaptors, both after-effects are maximal (i.e. asymptoted) when the test contour is only half a cycle of the shape waveform and in ± cosine phase (Gheorghiu & Kingdom, 2007b). Half-cycle cosine segments are the longest segments in the shape-waveform for which the sign of curvature is constant, consistent with curvature being the adaptable feature. Additional pieces of evidence in favor of local curvature are that both shape after-effects are selective to curvature polarity (Gheorghiu & Kingdom, 2008) and that the SAAE is tuned to shape-frequency (Gheorghiu & Kingdom, 2007b). Remember that the SAAE is an after-effect of shape-*amplitude* and there would be no reason to expect it to be maximal when adaptor and test were of the same shape-frequency if it was mediated by something other than curvature. In brief, SFAE and SAAE are mediated by adaptation to local curvature. Curvature receptive-fields have various sags and cords and these are independently combined to encode the perceived sag and cord. Thus curvature might be encoded via two sub-populations of neurons, both selective along a number of photometric (e.g. luminance polarity, luminance scale, chromaticity, etc.) and geometric (curvature polarity, curvature orientation, etc.) dimensions, but with one population tuned to curves of various sags and the other tuned to curves of various cords.

Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Grant # OGP01217130 given to F.K. and by a Research Foundation Flanders (Fonds Wetenschappelijk Onderzoek–Vlaanderen) postdoctoral fellowship given to E.G.

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