Local and global components of texture-surround suppression of contour-shape coding

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Evidence that contour-shapes and texture-shapes are processed by different mechanisms included the finding that contour-shape aftereffects are reduced when the adaptation stimulus is a texture made of contours rather than a single contour. This phenomenon has been termed "texture-surround suppression of contour-shape," or TSSCS. How does TSSCS operate and over what spatial extent? We measured the postadaptation shift in the apparent shape frequency of a single sinusoidal-shaped contour as a function of the number of contours in the adaptor stimulus. Contours were Gabor strings in which the Gabor orientations were either tangential (snakes) or orthogonal (ladders) to the path of the contour. We found that for extended surrounds, the aftereffect was strongly reduced when the surround contours were the same as the central adaptor contour, but not when the Gabors making up the surround contours were opposite-in-orientation to those of the central adaptor. For near surrounds, the aftereffect in a snake contour was unaffected by same-orientation but strongly suppressed by opposite-orientation surrounds, whereas the aftereffect for a ladder-contour was suppressed equally by both same- and opposite-orientation near surrounds. Finally, the strength of surround suppression decreased gradually with increasing spatial separation between center and surround. These results indicate that there are two components to texture-surround suppression in our shape aftereffect: one that is sensitive to opposite-orientation texture surrounds, operates locally, and disrupts contour-processing; the other that is sensitive to same-orientation texture surrounds, is spatially extended, and prevents the shape of the contour from being processed as a contour. We also demonstrate that the observed shape aftereffects are not due to changes in the apparent shape-frequency of the adaptors or the precision with which their shape-frequency is encoded, indicating that TSSCS is not an instance of crowding.

Keywords: texture, contour, shape, surround-suppression, adaptation, aftereffect, crowding


Introduction

Psychophysical, computational, and brain imaging studies have converged on the idea that texture-shapes and contour-shapes are processed by different mechanisms (Grigorescu, Petkov, & Westenberg, 2003, 2004; Petkov & Westenberg, 2003) localized in distinct visual areas (Dumoulin, Dakin, & Hess, 2008). While single-unit recordings have shown that contour-shapes are processed in extra-striate visual areas such as V4 and infero-temporal cortex (IT) (Bricart & Connor, 2004; Ito, Fujita, Tamura, & Tanaka, 1994; Ito, Tamura, Fujita, & Tanaka, 1995; Pasupathy & Connor, 2001, 2002), functional magnetic resonance imaging (fMRI) studies have shown that sparse images of contours elicit the strongest response in the extrastriate visual cortex, whereas textured images elicit the strongest response in the primary visual area (V1) (Dumoulin et al., 2008).

Kingdom and Prins (2009) found that the shape-frequency aftereffect, or SFAE, in which the perceived shape frequency of a sinusoidal-shaped contour is altered by adaptation to a slightly different shape-frequency contour, was reduced when the adaptor contour was surrounded by a series of contours identical in shape and parallel to that of the adaptor. The remarkable aspect of this finding is that the aftereffect is reduced even though the contours surrounding the adaptor contributed additional potential adaptation. The effect was orientation-specific: if the orientations of the elements making up the surround contours were orthogonal rather than parallel to those of the adaptor contour, the aftereffect was reduced only minimally. Here, we term this effect "texture-surround suppression of contour-shape," or TSSCS. The importance of TSSCS is that it is the first expression of the effect of a texture surround on the encoding of the shape of a fully visible contour. Although subsequent studies have explored the selec-
tivity of TSSCS to attributes such as stereoscopic-depth, color, and motion (Gheorghiu, Kingdom, & Varshney, 2009a; Gheorghiu, Kingdom, Thai, & Sampasivam, 2009b; Gheorghiu & Kingdom, 2011), we still know very little about how TSSCS operates and over what spatial extent. In this communication we address these issues.

What might be the physiological basis of TSSCS? Many V1 neurons that are sensitive to oriented lines or grating patches are suppressed by stimuli falling outside of their classical receptive field (CRF), with maximal suppression when the surround orientations are the same and minimal when orthogonal to those preferred by the CRF (Blakemore & Tobin, 1972; Cavanaugh, Bair, & Movshon, 2002a; Jones, Grieve, Wang, & Sillito, 2001; Knierim & van Essen, 1992; Levitt & Lund, 1997; Nelson & Frost, 1985; Nothdurft, Gallant, & Van Essen, 1999; Yao & Li, 2002). These V1 neurons are said to exhibit iso-orientation surround suppression. Almost 90% of orientation-selective V1 neurons exhibit iso-orientation surround suppression. For some V1 neurons however, oriented lines placed outside of the CRF enhance its response, for example, when the surround orientations are collinear with the preferred CRF orientation, termed collinear facilitation (Brincat & Westheimer, 2000; Kapadia, Ito, Gilbert, & Westheimer, 1995), or when orthogonally-oriented to the preferred CRF orientation, termed cross-orientation facilitation (Bair, Cavanaugh, & Movshon, 2003; Cavanaugh, Bair, & Movshon, 2002b). These contextual interactions therefore depend not only on the relative orientations of the surround and CRF but also on their relative spatial positions (Albright & Stoner, 2002).

From the standpoint of computer vision, model simulations of the responses of neurons exhibiting iso-orientation surround suppression reveal that they are sensitive to isolated contours, such as the edges of objects, but relatively unresponsive to lines or contours that form part of dense textures (Grigorescu et al., 2003, 2004; Petkov & Westenberg, 2003; Ursino & La Cara, 2004). The effect of iso-orientation surround suppression is thus to separate the processing of contours from that of textures. Huang, Jiao, and Jia (2008) have attempted to improve upon existing model simulations by combining iso-orientation surround suppression with collinear/cross-orientation facilitation. Thus contours that are iso-oriented with their surrounds are weakened via surround suppression, but those orthogonally-oriented with their surrounds are enhanced by cross-orientation facilitation. Kingdom and Prins (2009) hypothesized that neurons exhibiting iso-orientation surround suppression feed their responses into contour-shape-coding neurons located in higher visual areas, with the functional role of iso-orientation surround suppression being to separate isolated contours for the purpose of contour shape encoding. Although computational models suggest that contours that are orthogonally-oriented with their surrounds are enhanced by cross-orientation facilitation (Huang et al., 2008), none of our studies of TSSCS (Gheorghiu et al., 2009a; Gheorghiu et al., 2009b; Gheorghiu & Kingdom, 2011; Kingdom & Prins, 2009) have found evidence for facilitation.

In the Kingdom & Prins (2009) study as well as the other studies mentioned earlier, TSSCS manifested itself as a reduction in the changed appearance of a contour’s shape following adaptation. This does not imply any impairment in the detectability or discriminability of the shape of the contour caused by the surround texture. Rather, it implies that the shape of the surrounded contour is not processed as a contour but instead as part of a texture. This interpretation immediately raises the question of whether TSSCS is a manifestation of the phenomenon termed crowding. Crowding refers to the detrimental effect that nearby or flanking objects have on the spatial processing of a peripheral object, and is typically evidenced by a decline in the object’s discriminability or identifiability—for reviews see Levi (2008, 2011). Robol, Dakin, and Casco (2011) have suggested that crowding largely explains the orientation-dependent surround effects observed in contour detection and contour shape discrimination studies employing fragmented contours embedded in surround clutter (Dakin & Baruch, 2009; Schumacher, Quinn, & Olman, 2011).

In attempting to understand the relationship between TSSCS and crowding, it is important to bear in mind that crowding is a term for a set of phenomena not a mechanism; there is in fact no consensus at present as to what causes crowding. However, the exemplars of crowding are in most instances reductions in task performance, so TSSCS, which concerns the appearance of the shape of a fully-visible contour, would not at first sight appear to fall into the category of crowding. That said, some researchers have suggested that crowding is caused by a regularization process, i.e., a type of assimilation, in which the target object takes on the appearance of its flanks (Balas, Nakano, & Rosenholtz, 2009; Greenwood, Bex, & Dakin, 2010; Levi, 2011). This idea is not a far cry from our suggestion that the reduction in shape-aftereffect caused by surround contours occurs because the central contour adaptor becomes processed as part of the surround texture rather than as an isolated contour. But if TSSCS is an example of crowding via texture-regularization, why is the shape aftereffect reduced by the surround contours, given that the surround contours, which have the same shape-frequency as the target, are potentially additional adaptors (in classical crowding the surround consists of distracter elements that are ostensibly irrelevant to the detection of the
target)? An anonymous reviewer has suggested two possible reasons. First, if the surround were to have a different perceived shape-frequency from the central contour adaptor, the effect of texture regularization (i.e., crowding) would be to shift the apparent shape frequency of the central contour adaptor towards that of the surround. This shift might have the effect of reducing the aftereffect. Second, the surround contours might reduce the saliency of the central contour through crowding, that is, reduce the precision with which its shape frequency is encoded, and this could cause the reduction in after-effect. One of the aims of this study is to test both these possibilities.

In this study, we have investigated the spatial properties of TSSCS and interpreted our results in terms of iso-orientation surround suppression. We have measured the shape-frequency aftereffect, or SFAE, for contours comprised of strings of Gabor elements that were either tangential to the path of the contour, termed snakes, or orthogonal to the path of the contour, termed ladders. The adaptor contours were surrounded either by parallel-in-orientation or orthogonal-in-orientation contours and the SFAE was measured as a function of the number of surround contours as well as their separation from the adaptor contour. The results of this study have enabled us to refine our understanding of the mechanisms underlying TSSCS.

## General methods

### Subjects

Nine subjects participated in this study (five in each experiment), one of the two authors (EG) and eight subjects who 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 videographics card (Cambridge Research Systems) with 12-bit contrast resolution, presented on a calibrated, gamma-corrected monochromatic Siemens SMM 21,106 LS monitor with white phosphor (P-45), running at 130 Hz frame rate and with a spatial resolution of 996 × 777 pixels. The mean luminance of the monitor was 48 cd/m². Viewing distance was 100 cm.

Adapting stimuli consisted of pairs of sinusoidal-shaped textures or contours presented in the center of the monitor on the mean luminance background at 3.5° above and below the fixation marker, as shown in Figure 1a–c. The test stimuli were always pair of single contours. The adaptor pair consisted of textures or contours with shape frequencies of 0.2 and 0.6 c/deg, giving a geometric mean shape-frequency of 0.35 c/deg. The mean shape-frequency of the test contour pair was always kept constant at 0.35 c/deg. The shape-amplitude of the two adaptors and tests was fixed at 0.3°.

All contours were constructed from strings of odd-symmetric (d.c. balanced) Gabor patches with a spatial bandwidth of 1.5 octaves, a center luminance spatial frequency of 4 c/deg, and a contrast of 85%. The Gabor patches were positioned along the sinusoidal-shaped profile and were oriented either tangential, termed snake, or perpendicular, termed ladder, to the path of the contour. The center-to-center spacing between adjacent Gabor patches along the contour was randomly selected from within the range ±0.15° around a mean of 0.4°. Because the Gabor-string contours were contained within a fixed width stimulus window of 8°, the number of Gabor patches differed by a factor of 1.22 between the two adaptors: the high shape-frequency contours had 27 Gabor and the low shape-frequency adaptors had 22 Gabor. The test contours averaged 24 Gabor.

The adaptor consisted of a central contour flanked by a surround made of a series of contours arranged in parallel. All contours were either snakes or ladders. For both types of central adaptor contour, snake and ladder, there were three conditions: no surround, central contour flanked by same-orientation surround (e.g., snake surrounded by snakes or ladder surrounded by ladders), and central contour flanked by opposite-orientation surround (e.g., snake surrounded by ladders or ladder surrounded by snakes) (Figure 1d–g). The test in all conditions was the same type of contour as the central adaptor contour (e.g., snake central-adaptor plus snake test; ladder central-adaptor plus ladder test). In Experiment 1, we varied the number of contours in the surround. We used adaptors that consisted of a total of 3, 5, 7, 9, 11, and 13 contours, the middle of which was the central adaptor.

### Procedure

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 to reinforce the initial adaptation. A schematic representation of the adapting and test procedure is shown in Figure 1d. During the adaptation period, the shape-phase of the contour 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 shape-phase of the test contour was also randomly

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**Figure 1a–c**. The test stimuli were always pair of single contours. The adaptor pair consisted of textures or contours with shape frequencies of 0.2 and 0.6 c/deg, giving a geometric mean shape-frequency of 0.35 c/deg. The mean shape-frequency of the test contour pair was always kept constant at 0.35 c/deg. The shape-amplitude of the two adaptors and tests was fixed at 0.3°.

**Figure 1d–g**. The test in all conditions was the same type of contour as the central adaptor contour (e.g., snake central-adaptor plus snake test; ladder central-adaptor plus ladder test). In Experiment 1, we varied the number of contours in the surround. We used adaptors that consisted of a total of 3, 5, 7, 9, 11, and 13 contours, the middle of which was the central adaptor.
Figure 1. Stimuli used in the experiments. One can experience the shape-frequency aftereffect (SFAE) obtained with single contour adaptors (a) and textures (b, c) by moving one’s eyes back and forth along the markers located midway between the pair of adapting contours (top) for about 90 s, and then shifting one’s gaze to the middle of the single test contours (bottom). The textures consisted of a central contour flanked by either (b) same or (c) orthogonal orientation surround contours. Example textures consisting of a (d) snake central contour flanked by snake surround contours; (e) ladder central contour flanked by ladder surround contours; (f) ladder central contour flanked by snake surround contours, and (g) snake central contour flanked by four (left), two (middle) and one (right) ladder surround contours.
assigned in every test period. The presentation of the test contour was signaled by a tone. Subjects were required to fixate on the marker placed between each pair of contours for the entire session. A head and chin rest helped to minimize head movements.

A staircase method was used to estimate the point of subjective equality, or PSE. The geometric mean shape-frequency of the two test contours was held constant at 0.35 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 0.7 and 1.44. 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. In order that the total amount of adaptation for each condition was the same, we used a staircase method that was terminated after a fixed number (25) of trials, rather than a fixed number of reversals. The shape-frequency ratio at the PSE was calculated as the geometric mean shape-frequency ratio of the test that followed the lower shape-frequency adaptor to the test that followed the higher shape-frequency adaptor, averaged across the last 20 trials. For each with-adaptor condition we 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 standard errors are the ones shown in the graphs. Note that the magnitude of the aftereffect is defined as the ratio of shape-frequencies at the PSE, and thus its units are dimensionless.

Experiment 1: Effect of number of surround contours on TSSCS

Figure 2a shows SFAEs obtained using a snake central-adaptor/test, in which the adaptor contour was flanked by same-orientation surround contours (dark symbols), opposite-orientation surround contours (white symbols) or no surround (dashed line), as a function of the number of surround contours. Figure 2b shows the corresponding results for the ladder central-adaptor/test conditions. The rightmost lower panel in Figure 2a and 2b shows the across-subjects average of these SFAE and also indicate the percent difference between the two test shape-frequencies at the PSE. The effect of the surround contours is clearly very different for same-orientation and opposite-orientation surrounds and the difference is most marked for the snake central-adaptor/test. Figure 2a shows that the effect of increasing the number of same-orientation surround contours is to increasingly reduce the SFAE from its no-surround baseline (dashed line). On the other hand, the addition of just two flanking, opposite-oriented surround contours reduces the SFAE significantly, but adding more opposite-oriented surround contours produces no further reduction in the SFAE (white symbols). The pattern of results for the ladder central-adaptor/test (Figure 2b) is similar except that the initial reduction of the SFAE with the addition of two flanking contours is pronounced, and similar in magnitude, for both same- and opposite-orientation surrounds.

To summarize these results and express them in terms of TSSCS we calculated a surround suppression index (SSI) as follows: $SSI = 1 - \frac{SFAE_{texture}}{SFAE_{contour}}$, where $SFAE_{texture}$ and $SFAE_{contour}$ are the shape aftereffects obtained with the texture- and contour-adaptors. Thus, a surround suppression index of 1 indicates complete suppression while 0 indicates no suppression. Figure 3 plots the across-subjects average SSI for snake (Figure 3a) and ladder (Figure 3b) central-adaptor/test conditions. The amount of suppression for both snake and ladder central-adaptor/tests caused by same-orientation surrounds increases with the number of surround contours, reaching an SSI of 0.75 for adaptors consisting of 13 contours (black symbols). On the other hand the amount of suppression is constant for opposite-oriented surrounds (SSI = ~0.42; white symbols).

These findings suggest that for our aftereffect paradigm, TSSCS with same-orientation surrounds is spatially extensive, whereas for opposite-orientation surrounds it is only local, albeit pronounced. This suggests that the local component revealed using opposite-orientation surrounds is mediated by a different mechanism from that mediating the spatially-extensive effect found with same-orientation surrounds. In what follows we present two experiments that aim to determine the nature of the local and the spatially extensive component of TSSCS.

Experiment 2: The local component: Disruption of contour-shape processing?

Contour shape coding appears to involve a non-linear process that binds together local orientation
and/or position information into units such as curves (Bell, Gheorghiu, Hess, & Kingdom, 2011; Gheorghiu & Kingdom, 2009), with recent evidence suggesting that the non-linear process is multiplication, which is a form of AND-gating or its mathematical equivalent (Gheorghiu & Kingdom, 2009). The presence of orientations opposite to those that make up the curve could disrupt this process (see red line in Figure 1g), especially because during the adaptation period the neurons whose receptive fields fall within the rectangular window containing the adaptor contour will also be stimulated by the opposite surround orientations.

Figure 2. Results for Experiment 1: SFAEs obtained with (a) snake and (b) ladder central contour adaptor flanked by same-orientation surround (dark symbols), orthogonal-orientation surround (white symbols), and no surround (dashed line) as a function of the number of contours in the adapting texture. The rightmost lower panel in (a) and (b) show the across-subjects average of these SFAE and also indicate the percent difference between the two test shape-frequencies at the PSE.
due to the fact that the shape-phase of the contour, along with its surround, is randomly changed every second.

We decided to test this idea by interleaving opposite orientations into a single adaptor contour. Adaptation contours were either snakes (S), ladders (L), or strings of alternating orientations (A). The snake and ladder contours were either compact (left of Figure 4a) or sparse; in the sparse contours every other Gabor was missing—these are the SS and LS conditions on the right of Figure 4a. Test contours were either sparse snakes (SS) or sparse ladders (LS). We measured four adapting conditions for each of the two types of test contour: SS, A, S, and LS adaptors with an SS test contour, and SS, A, L, and LS adaptors with an LS test contour.

Results are shown in Figure 4b and the key result is that whereas the aftereffect is unaffected by removing every other Gabor from the adaptor (compare adaptors SS and S in the left panel or LS and L in the right panel), it is significantly reduced when the adaptor alternates in orientation (compare adaptors SS and A in the left panel or LS and A in the right panel). Figure 5 shows the average aftereffect across subjects with each subject's data normalized to the SS or LS adaptor conditions. On average across the two types of test contour (Ls, Ss), SFAEs were reduced by ~ 44% in the alternating (A) adaptor condition (red bar) and by ~ 67% in the opposite-orientation adaptor and test condition.

These results indicate that interleaving orthogonal orientations into the adaptor significantly disrupts the SFAE, but not because one is simply removing half of the relevant adaptor orientations.

**Experiment 3: Spatially extended component: Does it decline with distance?**

In Experiment 1 we concluded that texture-surround suppression had a spatially extended component sensitive to same-orientation surrounds (black symbols in Figure 3) since we found that the strength of the suppressive effect increased with the number of surround contours. However, the results of Experiment 1 do not tell us whether the suppressive effect is constant across space or declines with distance from the central adaptor contour. It likely declines, so to test whether it does we used same-orientation center-surround adaptors made of nine contours, either snakes or ladders. The surround and central contour were separated by a gap whose size varied between 0 and 2.1° in steps of 0.3°. Example snake (left panels) and ladder (right panels) stimuli are shown in Figure 6. The test was always a single contour of same orientation as the adaptor. Figure 7 shows the SFAEs obtained with snake (white symbols) and ladder (dark gray symbols) adaptors as a function of the gap size between center and surround. Again the dashed lines indicate SFAEs with no surround for snake (thin dashed line) and ladder (coarse dashed line) adaptors.

The across-subjects average SSI is shown in Figure 7b, which shows that there is a gradual decline in
surround suppression with increasing gap size for both snake and ladder contours. There is some variability between subjects as to the relative amount of suppression, but as the mean SSI data in Figure 7b shows, there is overall greater suppression in the ladder condition, especially for small gap sizes (compare dark and white symbols).

**Experiment 4: Is TSSCS caused by crowding?**

As discussed in the Introduction, one theory of crowding posits that crowding is texture regularization. Therefore the reduction in the shape aftereffect by surround contours observed here might be caused by a shift in the apparent shape frequency of the central contour adaptor towards that of the surround contours and towards shape-frequencies less optimal for the SFAE. If so, then one would predict that adapting to a single contour (i.e., no-surround) whose apparent shape-frequency had been matched to a contour with a surround should produce the same-size reduction in aftereffect caused by the presence of the surround. To test this prediction, subjects performed two experiments. The first was a shape-frequency matching experiment in which we determined the apparent shape-frequency of 0.2 and 0.6 c/deg contours in the presence of either same or opposite-orientation surround contours, as a function of the numbers of surround contours. The second experiment measured SFAEs using single contours (i.e., no surround) whose shape-frequencies were set to the apparent shape-frequency of the central contour.
frequency of contours in the presence of same- and opposite-orientation surrounds, as determined from the first experiment.

Another possibility that arises from considering TSSCS as crowding is that the surround reduces the saliency of the central adaptor contour, that is, the precision with which its shape frequency is encoded, causing a reduction in aftereffect. In order to test this we wanted to keep the task as similar as possible to that employed to measure the aftereffect, so we measured saliency in terms of the precision of the PSEs, where precision is defined as the inverse of the standard deviation, or SD of the PSEs. If reduced saliency is the cause of the reduced SFAEs then we would expect precision to vary with the number of surround contours in a comparable way to that of the reduction in SFAE found in Experiment 1.

Stimuli and procedure

We used a pair of contours consisting of a test contour of fixed shape-frequency and a comparison contour whose shape frequency was adjusted from trial to trial. Both comparison contour and central contour test were snakes only. In the conditions in which the test contour was flanked by surround contours, the center and surround contours were of fixed, same shape-frequency, as in the aftereffect experiments. There were three conditions: no surround (Figure 8a), snake central-contour surrounded by snakes (Figure 8b), and snake central-contour surrounded by ladders (Figure 8c). For all these three test conditions the comparison contour was always a single snake contour. In order to avoid that subjects base their shape-frequency judgments on the sinusoidal-shaped edge of the textures (i.e., on the contour on the outer sides of the surround) instead of the central-contour test, we placed the texture stimuli in a rectangular window (Figure 8b and c). As in Experiment 1, the test and comparison contours were presented at 3° above and below the fixation marker (see Figure 8). Again, as in all previous experiments (Experiments 1–3) the shape-amplitude of both test and comparison stimuli was fixed to 0.3° and the duration of each stimulus presentation was 0.5 s. We used two values for the shape-frequencies of the snake test-contours, 0.2 and 0.6 c/deg, respectively, values that correspond to the shape-frequencies of the two adaptors used in Experiment 1. The comparison snake-contour was of adjustable shape-frequency. In separate experimental sessions, for each shape-frequency of the test contour (i.e., 0.2 and 0.6 c/deg) we determined its apparent shape-frequency in the presence of either same or opposite-orientation surround contours as a function of the numbers of surround contours. On each trial the subject decided whether the comparison or the test snake contour had the higher shape-frequency. Since all the contours in the snake surround condition had the same shape-frequency as the central contour (as in the aftereffect studies) the subject presumably judged the apparent shape-frequency of the texture as a whole.

The PSE was obtained using the same staircase procedure as used with the aftereffects (see General Methods). We used 3, 5, 7, 9, 11, and 13 contours as in Experiment 1. For each condition we made eight measurements. The shape-frequency ratio at the PSE was calculated as the mean geometric ratio of the comparison (single contour) to test (contour in the presence or absence of surround) shape-frequencies over the last 20 trials of the staircase. We then calculated the mean and standard error of these differences across the eight measurements. To obtain an estimate of the precision with which the shape frequency is encoded for each condition, we calculated the standard deviation (SD) across the eight measurements of the logarithms of the shape-frequency ratios at the PSE. Four subjects participated in the 0.2 c/deg condition and three subjects in the 0.6 c/deg condition, all of which had participated in Experiment 1.

Because the apparent shape-frequencies of the 0.2 and 0.6 c/deg test contours in the presence of surrounds (i.e., the crowded conditions) were determined in separate experimental sessions, an anonymous reviewer raised the possibility that the observers might be able to build an internal template and identify the unchanging shape-frequency of the test contours. In addition, although the observers were instructed to fixate on
the marker placed between the test and comparison contours, it was suggested that a stimulus duration of 0.5 s is long enough for the observers to make eye movements to the comparison contour or to both test and comparison contours. Thus, to bypass the fact that observers can identify the unchanging in shape-frequency test contour from the comparison contour in all crowded conditions, we measured again the apparent shape-frequency of the two test contours of 0.2 and 0.6 c/deg using a shorter stimulus duration of 0.2 s and mixing randomly the shape-frequencies within the same session by using two randomly interleaved staircases. To avoid possible eye movements, we used a stimulus duration of 0.2 s. Three subjects participated in this experiment, two of which had participated in Experiment 1.

**Apparent shape-frequency results**

Figure 9 shows shape-frequency matching results averaged across subjects for snake-contour tests of 0.2 c/deg (left panel) and 0.6 c/deg (right panel) flanked by snake-surrounds (dark symbols) and ladder-surrounds (white symbols), as a function of the number of
surround contours. Figure 9a shows the results obtained with stimulus durations of 0.5 s and a single staircase procedure (as in the adaptation experiments). Figure 9b shows the results for 0.2 s duration and a two randomly interleaved staircase procedure. The results indicate that the apparent shape-frequency of the test is similar for same-orientation and opposite-orientation surrounds and remains approximately constant with increasing number of surround contours (compare dark and white symbols) for both 0.2 and 0.6 c/deg test contours. Figure 9a shows that all conditions give comparable results irrespective of the type and the number of surround contours with no hint of a similar pattern to the SFAEs shown in Figure 2. To obtain a measure of the overall shifts in perceived shape-frequency caused by the surround, we averaged the matches across...
different number of contours and across subject for each type of surround. For the snake-surrounds the apparent shape-frequencies of the 0.2 and 0.6 c/deg textures were respectively 0.198 and 0.556 c/deg, corresponding to 1.05% and 7.23% decreases in perceived shape-frequency. For the ladder-surround condition, the apparent shape-frequencies of the 0.2 and 0.6 c/deg central contours were respectively 0.1984 and 0.5639 c/deg, corresponding to decreases of 0.8% and 6.01%. A two-way repeated measure ANOVA with factors Surround-Type (snake vs. ladder) and Number of Surround Contours (3, 5, ..., 13) on the data shown in Figure 9 revealed no significant difference between the snake- and ladder-surround ($F(1, 18) = 0.21, p > 0.05$ for 0.2 c/deg and $F(1, 12) = 1.68, p > 0.05$ for 0.6 c/deg test). The main effect of number of surround contours was not significant ($F(5, 18) = 2.74, p > 0.05$ for 0.2 c/deg and $F(5, 12) = 0.56, p > 0.05$ for 0.6 c/deg snake contours test).

Similarly, the apparent shape-frequency matching results obtained with 0.2 s stimulus duration using two randomly interleaved staircases (Figure 9b) showed that all conditions give comparable results irrespective of the type and the number of surround contours. A two-way repeated measure ANOVA with factors Surround-Type (snake vs. ladder) and Number of Surround Contours (3, 5, ..., 13) showed no significant difference between the snake- and ladder-surround ($F(1, 12) = 0.0014, p > 0.05$ for 0.2 c/deg and $F(1, 12) = 0.909, p > 0.05$ for 0.6 c/deg test). The main effect of number of surround contours was also not significant ($F(5, 12) = 2.066, p > 0.05$ for 0.2 c/deg and $F(5, 12) = 0.117, p > 0.05$ for 0.6 c/deg snake contours test).

Again, to obtain a measure of the overall shifts in perceived shape-frequency caused by the surround, we averaged the matches across different number of contours and across subject for each type of surround. For the snake-surrounds the apparent shape-frequencies of the 0.2 and 0.6 c/deg textures were respectively 0.2066 and 0.5358 c/deg, corresponding to 3.3% increase and 10.7% decrease in perceived shape-frequency. For the ladder-surround condition, the apparent shape-frequencies of the 0.2 and 0.6 c/deg central contours were respectively 0.2068 and 0.5459 c/deg, corresponding to an increase of 3.39% and 9.01%.

As a further test, new aftereffects were measured using single contour adaptors (no surround) set to the apparent shape-frequencies of the contours calculated above for stimulus durations of 0.5 s only, since this was the test duration used in Experiment 1. The test contours were set to the geometric mean shape-frequency of the two adaptors. Only one subject (EG) participated in this experiment. Figure 9c compares SFAEs obtained using the conventional 0.2 and 0.6 c/deg adaptor pairs with the lower-in-shape-frequency pairs from the matching experiment. The SFAEs are almost identical, ruling out the possibility that the reduction in SFAE with the increasing number of surround contours obtained in Experiment 1 is the result of a shift in the apparent shape frequency of the central contour adaptor towards that of the surround.

**Precision results**

Figure 10a shows the across-subjects average of the SD of the PSEs obtained with snake-contour tests of...
Figure 9. Results for Experiment 4: (a) Shape-frequency matching results obtained with snake-contour test of 0.2 c/deg (left panel) and 0.6 c/deg (right panel), flanked by snake-surround (black symbols), ladder-surround (white symbols), and no surround (red dashed line), as a function of the number of surround contours for 0.5 s duration and a single staircase procedure. (b) Shape-frequency matching results for 0.2 s duration and a two randomly interleaved staircase procedure (see text for details). (c) SFAEs obtained with single contours whose
shape-frequencies were matched to the apparent shape-frequency of the snake central contour flanked by snake-surround (dark gray bar labeled S) and ladder-surround (light gray bar labeled O). For comparison, we also show the SFAEs obtained with single contour adaptors (no surround) with 0.2 and 0.6 c/deg (black bar labeled C).

Figure 10. (a) The across-subjects average of the SD of PSEs obtained with snake-contour tests of 0.2 c/deg (left panel) and 0.6 c/deg (right panel) flanked by snake-surrounds (dark symbols) and ladder-surrounds (white symbols), as a function of the number of surround contours for stimulus duration of 0.5 s. The red-dashed line indicates SD of PSEs for the no surround condition. (b) Same as (a) but for 0.2 s duration and a two randomly interleaved staircase procedure.
contour is encoded is similar for snake and ladder
surrounds and is constant with the number of surround
contours (compare dark and white symbols), for both
0.2 and 0.6 c/deg test contours. All SDs of PSEs were
higher in the presence of the surround, however. This is
probably because texture-shape mechanisms are less
precise than contour-shape mechanisms. To test this
possibility we also measured the SD of PSEs using a
pair of textures consisting of a snake test-texture of
fixed shape-frequency and a snake comparison-texture
whose shape frequency was adjusted from trial to trial
(Figure 11a). Each pair of textures was presented for
0.5 s. We compared these results with those obtained
with snake comparison-contour and snake test-contour
flanked by snake surround (Figure 11b, black symbols
in Figure 10a). Figure 11c shows the across-subjects
average of the SD of PSEs obtained with snake textures
(blue symbols) as a function of the number of contours
in the texture for 0.2 and 0.6 c/deg test texture. The
results indicate that the SDs of PSEs obtained when
both test and comparison are textures are comparable
or greater to those obtained when the test is a texture
and the comparison a contour.

To conclude: for both 0.5 and 0.2 s stimulus
durations, neither the apparent shape-frequency of
the central contour nor the precision with which its
shape-frequency is encoded varies significantly with the
number of surround contours and the type of surround.
This is quite unlike the strong dependency of the SFAE
in Experiment 1 on the number of surround contours.
Thus our findings are not consistent with the idea that
TSSCS is an instance of crowding, even if crowding is
cased by texture-regularization.

Discussion

To our knowledge this is the first study to investigate
parametrically the effect of texture-surround suppres-
sion on the perceived shape of both snake and ladder
contours. Our results show that (a) for extended
texture-surrounds the SFAE is strongly suppressed by
same-orientation but not opposite-orientation texture
surrounds; (b) for near texture-surrounds the SFAE is
strongly suppressed by opposite- but not same-orien-
tation texture surrounds; (c) there is a gradual decrease
in the magnitude of same-orientation surround sup-
pression with increasing spatial separation between
center and surround for both ladder and snake
textures; (d) orthogonally-interleaved orientations dis-
rupt the SFAE more than one would expect from
simply removing half the orientations. In addition, we
demonstrated that the observed shape aftereffects
results are not due to changes in the apparent shape-
frequency of the adaptors or the precision with which
their shape-frequency is encoded because both these
measures were invariant with the type and the number
of surround contours. Taken together, these results
reveal that in our shape aftereffect paradigm, texture-
surround suppression has two components: one that is
sensitive to opposite-orientation texture surrounds,
operates locally, and disrupts contour-processing, and
the other that is sensitive to same-orientation texture
surrounds, is spatially extended, and prevents the shape
of the contour from being processed as a contour.

It is worth reiterating the significance of the main
finding of Experiment 1. We found that the shape-
frequency aftereffect for both snake and ladder adaptor
contours was reduced when the central adaptor was
surrounded by identically-shaped same-orientation
contours, with a surround suppression index (SSI) of
0.75 (see Figure 3) for 12 surround contours. These
surrounds were packed with identically-shaped con-
tours that were all potential adaptors, yet they not only
failed to contribute additional adaptive power but did
the exact opposite and reduced the aftereffect. This is a
very different scenario from that of most contextual
surround studies, where the surround is irrelevant in
the sense of not providing information about the center
signal.

What of crowding? First, the contours in these
surrounds did not occlude each other, and therefore
our results cannot be explained by overlay masking.
Second, Experiment 4 showed that the apparent shape-
frequency of the central contour, as well as the
precision with which it was encoded and whether
presented for 0.5 s or 0.2 s, was invariant to the number
of surround contours, unlike the reduction in afteref-
flect. This suggests that the particular manifestation
of TSSCS studied here is not caused by crowding.

Additional indirect evidence that TSSCS is not
cased by crowding comes from recent studies investi-
gating the chromatic selectivity of the two phenom-
ena. Kennedy and Whitaker (2010) found that
crowding was strongest when target and flanker had
the same chromaticity and almost absent when they
differed in chromaticity, implying that crowding is
strongly selective for color direction. We recently found
on the other hand that TSSCS is only weakly selective
for color direction (Gheorghiu & Kingdom, 2011);
surround suppression obtained with center-surround
contours of the same cardinal directions (i.e., both red-
green or blue-yellow) was only about 25% stronger
than with orthogonal cardinal directions (red-green vs.
blue-yellow). Moreover, with a luminance central-
contour adaptor/test, surround suppression was non-
selective to color direction.

One might suppose that a contour adaptor flanked
by an opposite-orientation surround would ungroup
and as result pop-out. If this was the case, then the
central-contour adaptor would be resistant to surround
suppression. Instead, the addition of a single pair of flanking opposite-orientation surround contours reduced the SFAE significantly, and in the case of a snake adaptor/test, more so than a pair of flanking same-orientation surround contours (Figure 2a). We suggest that the opposite-orientation surrounds disrupt the non-linear process that integrates the local orientations/positions of the central adaptor contour in order to encode its shape. In support of this idea we showed that interleaving opposite orientations into a single contour adaptor disrupted the shape aftereffect more so than if one simply removed half the orientations (Experiment 2). But why are the opposite-orientation surrounds so disruptive if they are not actually part of

Figure 11. (a) Example of a pair of textures consisting of a snake test-texture of fixed shape-frequency and a snake comparison-texture whose shape frequency was adjusted from trial to trial. (b) Pair of snake comparison-contour and snake test contour flanked by snake surround. (c) The across-subjects average of the SD of PSEs obtained with snake textures test and comparison (blue symbols) and with snake comparison-contour and snake test contour flanked by snake surround (dark symbols) as a function of the number of contours in the texture for 0.2 (left panel) and 0.6 c/deg (right panel) test texture.
the central adaptor contour? The least exotic but most likely explanation is that the opposite surround orientations get **mixed up** with the central adaptor orientations during the adaptation period. A curvature-sensitive neuron whose receptive field is positioned somewhere within the rectangular window containing the adaptor contour would be stimulated by both the adaptor and opposite-orientation surround contours during the adaptation period because the shape-phase of the contour was changed every half second. Even if the shape-phase had not been changed during adaptation, eye movements would likely have sufficed to ensure that the curvature-sensitive neurons were stimulated by both adaptor and surround orientations. If this explanation is correct, then we have to conclude that the apparently strong local component of suppression from opposite surround orientations found in our aftereffect paradigm is a quirk of procedure rather than an indication of the neuronal organization of surround suppression. What the results with opposite-orientation surrounds do nevertheless tell us is that the suppressive effects of these surrounds are not spatially extensive.

Why do interleaved opposite orientations disrupt the SFAE? We have previously suggested that the curvature-sensitive neurons underpinning the SFAE combine responses from orientation sub-units via a process of multiplication or its mathematical equivalent (Gheorghiu & Kingdom, 2009). A natural extension of this idea is to suppose that opposite interleaved orientations have the opposite non-linear effect to multiplication: divisive inhibition.

Experiment 2 also showed that SFAEs obtained using sparse-sampled contour adaptors (L<sub>S</sub>, S<sub>S</sub>) were ~ 67% lower for opposite- compared to same-orientation tests (compare black and white bars), a reduction comparable to that found in a previous study using compact snake and ladder contours (Gheorghiu & Kingdom, 2008). We also found comparable sized aftereffects with adaptors/tests with the same local orientation of elements, whether collinear or orthogonal-to-path (compare white bars labeled S<sub>S</sub> with L<sub>S</sub>). The results of Experiment 2, together with those from Gheorghiu and Kingdom (2008), indicate that contour-shape coding mechanisms exhibit a degree of selectivity for local orientation defined in relation to the tangent of the curve (i.e., collinear and orthogonal) as well as for the absolute local orientation (vertical and horizontal) of microelements. The fact that the aftereffects obtained with sparse-sampled contour adaptors were ~ 67% lower for opposite compared to same-orientation tests (compare black and white bars) rules out the possibility that curvature coding is non-selective for orientation. The small aftereffects obtained with adaptors and tests of opposite-orientation (black bars) are likely explained by the facts that curvature encoders are selective for local orientation, but have relatively broad local-orientation tuning.

In previous studies we have shown that SFAEs are mediated by mechanisms selective for local curvature, i.e., sinusoidal half-cycles in cosine phase (Gheorghiu & Kingdom, 2007, 2009). Neurophysiological studies have found neurons in area V4 that are selective for parts of shapes with constant sign of curvature (Pasupathy & Connor, 1999, 2001, 2002). Therefore, the best candidate area for these shape aftereffects is V4. As suggested by our present and earlier studies (Gheorghiu et al., 2009b; Kingdom & Prins, 2009), it seems likely that V1 neurons exhibiting iso-orientation surround suppression feed their responses into high-level visual areas, such as V4, that are directly involved in processing contour shape. It is possible however that iso-orientation surround suppression operates in the higher visual areas. Behavioral support for this idea comes from our earlier finding that texture-surround suppression is stereo-depth selective (Gheorghiu et al., 2009b). The near-complete restoration of the SFAE when the central adaptor contour and same-orientation surround were positioned in different depth planes implies that the disparities of the inhibitory extra-receptive field surrounds are the same as those of their classical receptive-field centers. There is some neurophysiological evidence that in area V4 neurons sensitive to oriented bars have a pronounced near-disparity bias (Hinkle & Connor, 2001, 2005; Watanabe, Tanaka, Uka, & Fujita, 2002), which Hinkle and Connor (2001, 2005) suggest might reflect their involvement in figure-ground segregation. It is also possible that these neurons might be subject to iso-orientation surround suppression and hence mediate the selectivity to stereo-depth found by Gheorghiu et al. (2009b).

With regard to the spatial extent of TSSCS, our results show that there is a gradual decrease in the strength of surround suppression with increasing spatial separation between center contour and surround texture for both snake and ladder textures (Experiment 3). Although the surround suppressive effect produced by ladder textures is stronger than that for snake textures (SSI = ~0.8 for ladder and ~ 0.55 for snake textures in Figure 7b) at small gap sizes, for larger separations the suppression effects decline and are of similar magnitude (SSI = ~0.45), implying that for very large gap sizes the suppression would be abolished altogether.

To conclude: the results from the current study have extended our understanding of TSSCS. We have shown that there are two components to TSSCS in our aftereffect paradigm: one that is sensitive to opposite-orientation texture surrounds, operates locally, and disrupts contour-processing and the other that is sensitive to same-orientation texture surrounds, is
spatially extended, and prevents the shape of the contour from being processed as a contour.

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