Three-dimensional shape from second-order orientation flows

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A B S T R A C T
In images of textured surfaces, orientation flows formed by perspective convergence invariably convey 3D shape. We show that orientation flows formed by contrast-modulated (CM) and illusory contours (IC) convey 3D shape, and that both stimulus types induce 3D shape aftereffects on CM and IC test stimuli. Adaptation to luminance-modulated (LM) orientation flows induce robust 3D shape aftereffects on CM and IC tests, however, aftereffects using CM/IC adapting stimuli on LM tests were substantially weaker. These results can be explained by the adaptation of 3D shape-selective neurons that invariantly extract first- and second-order orientation flows from striate and extra-striate signals, which receive stronger input from neurons selective for first-order orientation flows.

1. Introduction

Little is known about the neural mechanisms that enable us to perceive 3D shape from 2D monocular texture cues. Psychophysical studies show that correct 3D shape perception hinges on the visibility of specific patterns of orientation flows formed by perspective convergence (Li & Zaidi, 2000, 2004). Orientation flows play a crucial role not just in the perception of 3D shape-from-texture (Knill, 2001), but also from specular reflections (Fleming, Torralba, & Adelson, 2004) and shaded surfaces (Ben-Shahar, Huggins, & Zucker, 2002; Fleming, Li, & Adelson, 2008). Understanding how these orientation flows are neurally extracted will greatly advance our knowledge of how 3D percepts are computed from retinal images. Although recent physiological and imaging studies have begun to isolate neurons in extra-striate areas that respond selectively to surface slant and curvature as defined by monocular texture and shading cues (Georgieva, Todd, Peeters, & Orban, 2008; Liu, Vogels, & Orban, 2004; Shikata et al., 2001; Tsutsui, Sakata, Naganuma, & Taira, 2002), if and how neurons in these areas respond specifically to orientation flow patterns has not been determined.

Evidence for mechanisms that extract orientation flows comes from a recent study in which selective adaptation was utilized to reveal 3D shape aftereffects from retinal images (Li, Tzen, Ydagyarova, & Zaidi, 2008). Results from this study showed that adaptation to images of concave and convex textured surfaces induced 3D shape aftereffects that showed invariance to the phase and spatial frequency of the surface texture. In addition, the same study showed that aftereffects on test stimuli in which orientation flows were defined by luminance were robust when 3D shape in the adapting stimuli was conveyed by orientation flows formed by illusory tilts (using an illusion presented in Kitao, Pinna, and Brelstaff (2004) as adaptation stimuli). The invariance of the aftereffects helped rule out the possibility that they were due solely to the adaptation of local orientation-selective neurons in V1. Rather, the results could be explained by the adaptation of 3D shape-selective neurons that receive input from orientation-selective neurons in both striate and extra-striate areas.

The goal of the current study is to further investigate the pattern invariance of 3D shape-selective mechanisms. Specifically, we are interested in determining whether 3D shape aftereffects can be obtained when orientation flows are defined by non-Fourier, or second-order contours, whether mechanisms that extract these orientation flows can be neurally adapted, and whether adaptation to second-order orientation flows can alter the perceived 3D shape of stimuli in which orientation flows are defined by luminance and/or vice versa. The transfer of aftereffects across first- and second-order orientation flows would further strengthen the evidence for pattern-invariant 3D shape-selective mechanisms (Li et al., 2008).

The motivation for choosing to examine second-order orientation flows stems from the growing body of work suggesting that neural responses to second-order contours generally increase in extra-striate cortical areas, suggesting that first- and second-order contours may be primarily processed by different neural populations. Examples of second-order contours are shown in Fig. 1. Unlike the contours in the left panel, the horizontal contours in the middle, and right panels are not defined by luminance, and thus should not yield substantial responses from most horizontally-
oriented simple cells. In the middle panel, a vertical luminance grating is contrast-modulated by a horizontal grating contrast envelope. In this type of stimulus, excitatory, and inhibitory regions within the simple cell receptive field would be equally activated, causing minimal response. For the same reason, the horizontal abutting grating illusion on the right (Soriano, Spillmann, & Bach, 1996), in which horizontal illusory contours are formed by the misaligned ends of vertical lines, also should not activate most horizontally-oriented simple cells.

The neural encoding of second-order contours spans both striate and extra-striate areas. Although physiological and imaging work has focused on cortical area V2 and analogous areas (Leventhal, Wang, Schmolesky, & Zhou, 1998; Mareschal & Baker, 1998a, 1998b; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984; Zhan & Baker, 2006; Song & Baker, 2007), responses to second-order contours in V1 cannot be ruled out (Grosos, Shapley, & Hawken, 1993; Hirsch et al., 1995; Ramsden, Hung, & Roe, 2001; Sheth, Sharma, Rao, & Sur, 1996). However, signals tend to be relatively stronger in V2 (Sheth et al., 1996).

In human brains, second-order orientation-selective mechanisms have been revealed psychophysically by tilt aftereffects and the tilt illusion using second-order contours (Cruickshank & Schofield, 2005; Hawley & Keeble, 2006; Paradiso, Shimojo, & Nakayama, 1989; Smith, Clifford, & Wenderoth, 2001; van der Zwan & Wenderoth, 1995). The neural loci of these types of mechanisms have been examined in fMRI studies showing that second-order contours activate V1, V2, and an array of extra-striate areas beyond V2, but that this neural activity is stronger in extra-striate areas such as V3A, V4 V, V7, and V8 compared to early visual areas (Mendola, Dale, Fischl, Liu, & Tootell, 1999). Similarly, neural orientation adaptation to second-order contours is increasingly pronounced in extra-striate areas such as V01, and it has been suggested that the pattern of adaptation elicited from second-order stimuli may be due to responses of neurons in these areas that respond only to second-order, and not first-order, stimuli (Larsson, Landy, & Heeger, 2006; Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007).

In the current study, we measured 3D shape aftereffects from images of 3D surfaces containing first- or second-order orientation flows. Examples of the stimuli are shown in Fig. 2. Surfaces were corrugated in depth as a function of horizontal position. The critical orientation flows for these surfaces are formed by the horizontal contours in the surface texture. These contours form distinct flow patterns for concave and convex surfaces shapes (Li & Zaidi, 2001). The first-order orientation flows were luminance-modulated in a horizontal–vertical plaid. The second-order orientation flows were either contrast-modulated or formed by illusory contours. We determined the capacity with which all three stimulus types convey 3D shape, and used selective adaptation to determine whether 3D shape aftereffects were invariant to first- and second-order orientation flows.

![Image of Fig. 1](image1.png)

**Fig. 1.** Unlike luminance-modulated contours (left), both contrast-modulated (middle) and illusory contours (right) should elicit little or no response in simple cells.

![Image of Fig. 2](image2.png)

**Fig. 2.** Adaptation stimuli used in the current study. Surfaces were formed from carved sinusoidal corrugations. Concave and convex shapes were conveyed by luminance-modulated (LM), contrast-modulated (CM), or illusory contour (IC) orientation flows.
2. Experimental procedures

2.1. Apparatus and presentation

All stimuli were presented on a calibrated 22 in. Mitsubishi Diamond Pro 2070 flat screen CRT monitor with a 1024 × 768 pixel screen running at a refresh rate of 100 frames per second. The monitor was driven by a Cambridge Research Systems VSGe Visual Stimulus Generator controlled through a 3.2 GHz Pentium 4 PC. Experimental code was written using the CRS Toolbox for MatLab. A CRS CB6 infrared response box was used to record responses.

Observers’ head positions were fixed with a chin-rest situated 1 m away from the stimulus monitor. All stimuli were presented centered on the screen such that the center of each image was level with the observer’s eye. Viewing was monocular; each observer patched the same eye for all sessions. The experiment took place in a dimly-lit room. The only feedback was an audio cue indicating that the observer’s response had been recorded. To minimize fatigue, observers typically ran no more than two sessions consecutively and took breaks as they felt necessary. Baseline sessions were conducted first in random order within and across observers, followed by adaptation sessions that were randomized within and across observers.

2.2. Stimuli

Three main sets of test stimuli were created using three different surface textures (Fig. 2): a full contrast 2.6 cpd luminance-modulated horizontal–vertical plaid (what we will subsequently refer to as the LM stimulus); a 2.6 cpd vertical full contrast grating contrast-modulated by a horizontal grating envelope (to be referred to as the CM stimulus); and an abutting grating illusory contour stimulus (the IC stimulus). The IC stimulus was created by overlaying one pixel white lines on the white or black regions of the CM stimulus in alternating high contrast bands (e.g. referring to Fig. 2, lines were overlaid onto the white regions within one high contrast band and black regions within the next high contrast band. The height of the white lines was determined by the distance between the centers of two adjacent zero contrast bands). To minimize effects of light adaptation, the contrast between the dark background and the white lines was chosen such that the mean luminance of the IC stimulus was equivalent to the mean luminance of the LM and CM stimuli. (Equating the IC stimuli for mean contrast, while concurrently maintaining equivalent mean luminance, would have been difficult since Michelson contrast assumes equal proportions of light and dark pixels which is clearly not the case for the IC stimuli.) When mapped onto these corruptions, both the CM and IC textures correctly convey concavities and convexities, as evidenced by our baseline data. As a control condition, we also generated a low (10%) contrast version of the LM stimulus.

All textures were mapped first by repeating the texture along the depth axis to form a volumetric solid, and then carving the solid sinusoidally in depth as a function of horizontal position (see constant-μ corrugations in Li and Zaidi (2004)). These textured carved corrugations were then projected in perspective into the image plane. Frequency modulations are minimized in this mapping since frequency is correlated almost entirely with surface depth and not with surface slant (see Fig. 11 of Li and Zaidi (2004)). We chose a texture mapping with minimal frequency modulations because we have shown previously that frequency modulations can be unreliable cues to depth, whereas for corru- gations varying in depth as a function of horizontal position, the orientation flows of the horizontal component of the texture unequivocally convey differences between concavities and convexities (Li & Zaidi, 2000, 2003, 2004).

Each stimulus image contained 1.5 cycles of the corrugation with either a central concavity or convexity. All stimuli were presented in circular apertures 6.5° in diameter. (Circular apertures were used to minimize the possibility that 3D shapes were perceived based on systematic orientation differences between the texture patterns and the straight sides of a rectangular aperture.) The mean luminance of all stimuli was 54 cd/m². A central fixation cross spanning 17 × 17 arc min was present on the monitor screen at all times.

There were nine distinct corrugations in each set of test stimuli, varying in peak-to-trough amplitude in 3.5 cm increments: −14, −10.5, −7, 3.5, 0, 3.5, 7, 10.5, and 14 cm (negative numbers reflect concave curvatures, and positive reflect convex curvatures). The two most curved stimuli (+14 and −14 cm, shown in Fig. 2) were used as the adaptation stimuli. For each session, the corrugation amplitude (and sign) of the adapting stimulus was different from eight of the nine test stimuli, thus orientation flows of the adapting and test stimuli were almost always retinally misaligned.

2.3. Procedure

Observers were verbally instructed about the experiment with the help of a document that included descriptions of the purpose of the study, the task they were being asked to perform, examples of the different stimuli, and a flow chart of how each trial in both the baseline and adaptation sessions would be presented. Prior to hearing about the task, observers were asked to describe the different stimuli in their own words to ensure that they were perceived as 3D.

Each observer ran a total of 32 sessions (four baseline conditions for each of the LM, CM, IC, and low contrast LM test stimuli, eight adaptation conditions each for the LM, CM, and IC test stimuli, and four adaptation conditions for the low contrast LM test stimuli). The task in all the sessions was to judge whether the center of the test stimulus presented appeared convex or concave. Baseline sessions for each set of test stimuli were run prior to the adaptation sessions in order to determine shape percepts prior to adaptation. In the baseline sessions, each of the nine test stimuli were presented nine times in random order in single sessions that lasted approximately 10 min. The only difference between baseline and adaptation sessions was the presence of an adapting stimulus. Within each adaptation session, a single adapting stimulus (e.g. concave CM) and a single set of test stimuli (e.g. LM) were used.

All sessions began with a 60 s adaptation to a mean grey screen. In adaptation sessions (see Fig. 3), this was followed by a two-minute adaptation to one of eight adapting stimuli (four patterns × two shapes). Then, a 200 ms inter-stimulus interval of the grey background was followed by one of the nine test stimuli presented at 200 ms (for the LM, CM, and low contrast LM test stimuli) or 600 ms (for the IC stimuli). It was determined in preliminary trials that the extra time was necessary for observers to perceive the shapes of the IC stimuli. Similarly increased stimulus durations for judging orientations of subjective contours in tilt aftereffect paradigms have been previously reported (Hawley & Keeble, 2006). An audio cue coincided with the presentation of the test stimulus. A 400 ms Gaussian noise mask followed, which was included to reduce any afterimages from the test stimulus. The screen was then returned to the grey background until the observer responded. Once the observer responded, in all subsequent trials of the adaptation session, the adapting stimulus was presented for 5 s before each test stimulus to maintain the level of adaptation. Each adaptation session lasted approximately 15 min.
The perceived flat point was estimated from the fit for each data set as the amplitude of corrugation that yielded convex responses on half of the trials. If there was no effect of adaptation, then the perceived flat point in the adaptation conditions would not differ from the flat point extracted in the baseline condition. An aftereffect from adaptation to a convex surface (Fig. 4, square symbols) would cause a flat surface (amplitude = 0) to appear concave, and the entire psychometric function to shift away from the baseline curve towards the right. In this case, a physically convex test stimulus is perceived as flat, and thus the perceived flat point would be negative.

Data averaged across the five observers are shown in Fig. 5. (It is worth noting that although data from the two experienced and three naïve observers are averaged together, aftereffects were generally stronger for the naïve observers.) Each panel plots the averaged perceived flat points for each test stimulus class (LM, CM, and IC) as affected by each of the adapting stimuli. Error bars represent 95% confidence intervals. Asterisks indicate which conditions exhibit significant deviations of the perceived flat point away from zero. The first bar in each graph represents the perceived flat point in the baseline condition. Despite a slight bias towards convexity for LM tests, the perceived flat points in the baseline conditions did not vary significantly from physically flat (perceived flat point = 0) indicating that observers perceived the 3D shapes accurately for all stimulus classes.

Shape aftereffects in the expected directions were obtained in all adaptation conditions: adaptation to convex stimuli resulted in a shift of the averaged perceived flat point towards positive (convex) values and adaptation to concave stimuli produced a shift of the averaged perceived flat point towards negative (concave) values.

If the adapted mechanisms were highly pattern-selective, we would expect to see strongest aftereffects when the adapting and test stimuli were of the same pattern type. This was the case only for LM tests (Fig. 5A, black bars). Results for CM tests (Fig. 5B) followed the same trends as the LM tests: the LM adapting stimuli elicited the greatest aftereffects, followed by CM stimuli, and the IC stimuli induced the weakest aftereffects. Although IC adapting stimuli generally induced the weakest aftereffects on test stimuli of other classes (Fig. 5A and B), when used as tests, they were strongly affected by adapting stimuli of all types (Fig. 5C). Within the two second-order stimulus classes, CM and IC adapting stimuli induced aftereffects of about the same magnitude on tests of the same or the other stimulus class (Fig. 5B and C).

Although the CM stimuli were designed to tap neurons that respond to differences in contrast, these plaids could still elicit responses from neurons that respond to luminance differences if there were luminance artifacts in the stimulus. While we made every effort to ensure that our monitor output was carefully calibrated to minimize such artifacts, it is difficult to guarantee their absence. Specifically, a luminance artifact in the CM adapting stimulus could adapt simple cells and thus explain aftereffects induced on LM tests (Fig. 5A, darkest grey bars). Similarly, if a luminance artifact in the CM test stimulus activates simple cells, adaptation to both LM and CM stimuli could result in aftereffects (Fig. 5b, black and darkest grey bars). For comparison, we included the low contrast (10%) LM stimuli to see whether luminance artifacts could explain these results. The 10% contrast was chosen as a control comparison with the CM stimulus because we believe, given

2.4. Observers

The two authors and three naïve observers participated in the experiment. All observers had normal or corrected-to-normal visual acuity.

3. Results

For each of the 32 data sets per observer, the percentage of trials reported as convex was plotted vs. the curvature amplitude of the test stimulus quantified in centimeters. A least-squares procedure was used to fit Weibull functions to each data set. As an example, Fig. 4 depicts data for one observer for the baseline and two adaptation sessions for a single test set.

The perceived flat point was estimated from the fit for each data set as the amplitude of corrugation that yielded convex responses on half of the trials. If there was no effect of adaptation, then the perceived flat point in the adaptation conditions would not differ from the flat point extracted in the baseline condition. An aftereffect from adaptation to a convex surface (Fig. 4, square symbols) would cause a flat surface (amplitude = 0) to appear concave, and the entire psychometric function to shift away from the baseline curve towards the right. In this case, a physically convex test stimulus is perceived as flat and the perceived flat point would be positive. The greater the convexity required for perceived flatness, the greater the aftereffect. An aftereffect elicited by adaptation to a concave surface (Fig. 4, triangle symbols) would cause the opposite effect: a shift of the psychometric curve to the left. In this case, a physically concave test stimulus is perceived as flat, and thus the perceived flat point would be negative.

Data averaged across the five observers are shown in Fig. 5. (It is worth noting that although data from the two experienced and three naïve observers are averaged together, aftereffects were generally stronger for the naïve observers.) Each panel plots the averaged perceived flat points for each test stimulus class (LM, CM, and IC) as affected by each of the adapting stimuli. Error bars represent 95% confidence intervals. Asterisks indicate which conditions exhibit significant deviations of the perceived flat point away from zero. The first bar in each graph represents the perceived flat point in the baseline condition. Despite a slight bias towards convexity for LM tests, the perceived flat points in the baseline conditions did not vary significantly from physically flat (perceived flat point = 0) indicating that observers perceived the 3D shapes accurately for all stimulus classes.

Shape aftereffects in the expected directions were obtained in all adaptation conditions: adaptation to convex stimuli resulted in a shift of the averaged perceived flat point towards positive (convex) values and adaptation to concave stimuli produced a shift of the averaged perceived flat point towards negative (concave) values.

If the adapted mechanisms were highly pattern-selective, we would expect to see strongest aftereffects when the adapting and test stimuli were of the same pattern type. This was the case only for LM tests (Fig. 5A, black bars). Results for CM tests (Fig. 5B) followed the same trends as the LM tests: the LM adapting stimuli elicited the greatest aftereffects, followed by CM stimuli, and the IC stimuli induced the weakest aftereffects. Although IC adapting stimuli generally induced the weakest aftereffects on test stimuli of other classes (Fig. 5A and B), when used as tests, they were strongly affected by adapting stimuli of all types (Fig. 5C). Within the two second-order stimulus classes, CM and IC adapting stimuli induced aftereffects of about the same magnitude on tests of the same or the other stimulus class (Fig. 5B and C).

Although the CM stimuli were designed to tap neurons that respond to differences in contrast, these plaids could still elicit responses from neurons that respond to luminance differences if there were luminance artifacts in the stimulus. While we made every effort to ensure that our monitor output was carefully calibrated to minimize such artifacts, it is difficult to guarantee their absence. Specifically, a luminance artifact in the CM adapting stimulus could adapt simple cells and thus explain aftereffects induced on LM tests (Fig. 5A, darkest grey bars). Similarly, if a luminance artifact in the CM test stimulus activates simple cells, adaptation to both LM and CM stimuli could result in aftereffects (Fig. 5b, black and darkest grey bars). For comparison, we included the low contrast (10%) LM stimuli to see whether luminance artifacts could explain these results. The 10% contrast was chosen as a control comparison with the CM stimulus because we believe, given
the contrast levels used in the CM stimuli, any luminance artifacts resulting either from the monitor or from early neural transduction should be substantially less than 10% contrast. Indeed, the luminance artifacts found in Zhou and Baker (1994) for comparable displays were estimated to be no greater than 0.6%. If the CM stimuli were encoded purely on the basis of luminance artifacts, we would expect substantially larger effects of the low contrast LM stimulus compared to the CM stimulus.

This trend was not seen in the data. For the LM test stimuli (Fig. 5a), both CM and low contrast LM adapting stimuli elicited aftereffects of about the same magnitude. Similarly, for CM tests (Fig. 5b), CM and low contrast LM adapting stimuli elicited aftereffects of similar magnitude. Thus aftereffects elicited by the CM stimuli were substantially greater than what would be expected based on luminance artifacts alone, and thus it is unlikely that luminance artifacts are solely responsible for these results. It is worth noting that adaptation to CM and high contrast LM stimuli rendered low contrast LM tests invisible so data were not collected in these conditions. Low contrast LM tests were visible with IC adapts, however no shape aftereffects were obtained in this condition.

Although the results in the baseline conditions indicate that observers accurately judged concavities and convexities of all LM, CM, and IC stimuli, casual observations suggest that the LM stimuli appear more curved than the CM stimuli, and the CM stimuli appear more curved than the IC stimuli. To examine whether the strongest aftereffects from LM adapting stimuli on LM and CM test stimuli (Fig. 5A and B) could be attributed to the superior ability of these patterns to convey 3D shape, we ran a control experiment in which observers compared the relative curvatures of stimuli across texture types. Observers viewed side-by-side pairs of the most concave or most convex (−14 or +14 cm curvature amplitude) stimuli of two texture types, and judged in a 2AFC task which of the pair appeared more curved in 3D. As in the original experiment, stimuli spanned 6.5°, and were separated by a gap of 1°. All possible combinations of LM/CM, CM/IC, and LM/IC pairs were presented in a set of 12 stimuli (four in each category). Two stimuli were generated for each paired set of concave or convex stimuli, transposing the positions of the paired images. Five observers (two of three original naïve observers along with another naïve observer and the two authors) ran one session in which the 12 stimuli were each presented six times in random order. At the start of the session, each observer adapted for 1 min to a mean grey screen, then each stimulus was presented for 2 s before the screen returned to grey until the observer responded. A beep alerted the observer to the stimulus presentation and a second beep alerted the observer that the response had been registered.

Fig. 6 shows results averaged across the five observers. Error bars represent 95% confidence intervals. The percentage of responses in which the first of each stimulus pairing (indicated on the abscissa) appeared more curved is plotted for each of the three paired conditions. The black bar indicates, somewhat surprisingly, that LM and CM stimuli were judged to be about equally curved across observers. The next two bars indicate, not surprisingly, that LM and CM stimuli were judged to be more curved than IC stimuli.

![Fig. 5](image-url)

**Fig. 5.** Perceived flat points averaged across five observers for each of the three test stimulus conditions. Each bar represents the perceived flat point as affected by each of the adaptation stimuli. Error bars represent 95% confidence intervals. Asterisks indicate which conditions exhibit significant deviations of the perceived flat point away from zero.

![Fig. 6](image-url)

**Fig. 6.** Percentage of times stimuli of one texture type appeared more curved than stimuli of another texture type. Data are averaged across five observers and error bars represent 95% confidence intervals. The first bar represents the percentage of times LM stimuli appeared more curved than CM stimuli, the second bar, CM stimuli more curved than IC stimuli, and the third bar, LM stimuli more curved than IC stimuli.
These results suggest that the strong aftereffects induced by LM adapting stimuli on LM and CM test stimuli cannot be attributed to LM stimuli appearing more curved. The results do suggest, however, that weak aftereffects of IC adapting stimuli on LM and CM test stimuli may be correlated with the inferior ability of the IC stimuli to convey 3D shape.

4. Discussion

Our results show that contrast-modulated and illusory contour orientation flows convey 3D shape, and that the mechanisms that extract these orientation flows are neurally adaptable. In addition, the 3D shape aftereffects show pattern invariance across stimuli in which orientation flows are defined by first-order (LM) vs. second-order (CM and IC) cues, with strong aftereffects induced by first-order orientation flows and substantially weaker aftereffects induced by second-order orientation flows.

We have shown in previous work that when orientation flows from perspective convergence are visible, 3D shape is invariably perceived. Since it is impossible to separate the 2D pattern and the 3D percept, we assume that any mechanism that responds selectively to one of the 2D orientation flow patterns automatically signals the 3D shape associated with it. To isolate mechanisms that extract orientation flows in this study, we chose a texture mapping that minimizes frequency modulations in the image (Li & Zaidi, 2004). Substantial frequency modulations arise in other texture mappings such as those used for developable or folded surfaces, in which frequency in the image is correlated with surface slant. However, we have shown that in developable surface mappings, frequency modulations can lead to incorrect shape percepts, since the visual system perceptually correlates frequency with surface depth rather than slant (Li & Zaidi, 2000, 2003, 2004). To rule out the contributions of adaptation to frequency modulations in our study, we tested an additional control condition in which the vertical grating of the LM adapting stimulus was uniform in frequency. This stimulus still yielded robust aftereffects on LM and IC test stimuli, confirming that the aftereffects quantified in this study were due to adaptation of mechanisms that specifically extract orientation flows.

Although the aftereffects obtained using LM adapting and test stimuli could result from the adaptation of arrays of orientation-selective simple cells that respond selectively to LM contours, their responses alone cannot easily account for the transfer of aftereffects across pattern types found in this study or in Li et al. (2008). Simple cells as a population are phase- and frequency-selective, respond minimally to contrast-modulated and illusory contours, and would not directly respond to the illusory tilts used in Li et al. (2008). Thus adapting to LM orientation flows would only affect the responses of orientation-selective simple cells that respond to LM contours and, as a result, the CM and IC test stimuli should not appear altered by adaptation. However, our results clearly showed robust aftereffects of LM adapting stimuli on CM and IC test stimuli (Fig. 5B and C).

One possibility is to consider the role of neurons that respond to both first- and second-order contours which are reported to exist in V1 (Grosen, 1993; Hirsch et al., 1995; Sheth et al., 1996), and in and beyond V2 (Leventhal et al., 1998; Mareschal & Baker, 1998b; Song & Baker, 2007; Zhan & Baker, 2006). We cannot rule out the possibility that adaptation of arrays of these cue-invariant orientation-selective neurons is contributing to the transfer of aftereffects found in this study. However, to explain the weaker aftereffects induced by second-order adapting stimuli, these neurons would have to exhibit substantially weaker responses to second-order contours compared to first-order contours. Previous work suggests that the relative strength of responses to first- and second-order stimuli depends on the cortical locus. For example, physiological results in V1 show weaker responses to second-order stimuli compared to first-order stimuli (Chaudhuri & Albright, 1997) but neurons in IT respond in a cue-invariant form to both types of stimuli (Brow, Vogels, Kovacs, & Orban, 1995). FMRI studies consistently show that neural adaptation to second-order contours increases in magnitude as we move up the visual pathway (Larsson et al., 2006; Montaser-Koushari et al., 2007), suggesting that in higher cortical areas, neural responses to second-order stimuli may be equal in strength or even exceed the strength of responses to first-order stimuli. If our results are due to adaptation of cue-invariant orientation-selective neurons in these higher areas, the asymmetry of aftereffect transfer we found cannot be easily explained.

The most parsimonious explanation for the transfer of aftereffects is the adaptation of populations of 3D shape-selective neurons, each of which responds to a specific pattern of orientation flows signifying a particular 3D shape. Such neurons would receive inputs from orientation-selective neurons in striate and extra-striate areas that respond to first- and second-order contours, and thus would respond invariantly to orientation flows defined by these different cues. Adaptation to LM orientation flows consistent with a convexity would thus activate and fatigue a convex-selective neuron. Subsequently, neurons tuned to concavities, which respond to orientation flows signifying concavities, would be left relatively more sensitive resulting in a perceptual bias towards concave shapes (and thus convex shape aftereffects). Since these neurons would be invariant to how the orientation flows are defined, this concave bias would alter the perceived shapes of subsequently presented LM, CM, and IC tests alike.

The stronger aftereffects induced by LM orientation flows on second-order tests compared to second-order adapting on LM tests is consistent with what others have found in the transfer of tilt aftereffects and tilt illusion between first- and second-order stimuli (Cruickshank & Schofield, 2005; Paradiso et al., 1989; Smith et al., 2001; van der Zwan & Wenderoth, 1995). In addition, although CM and IC orientation flows conveyed correct 3D shape, our observers anecdotaly reported that the 3D shapes were perceptually less compelling than the shapes conveyed by the LM stimuli. Indeed the reduced apparent curvature of the IC stimuli was demonstrated in the results of a control experiment (Fig. 6). One way to account for the asymmetry of aftereffect transfer and weaker shape percepts of second-order stimuli would be to stipulate weaker inputs to each shape-selective neuron from neurons that extract second-order contours. The weaker input could result simply from smaller numbers of second-order selective neurons, as was suggested by Paradiso et al. (1989). Smaller numbers of these neurons would explain why the IC adapting stimuli did not elicit strong aftereffects on LM tests (Fig. 5A), while still accounting for the robust aftereffects obtained with IC adapting and test stimuli (Fig. 5C). Additionally, the orientation-selectivity of these second-order neurons may be reduced relative to the orientation-selectivity of simple cells. This has been found for cue-invariant neurons in extra-striate areas (Leventhal, Thompson, Liu, Zhou, & Ault, 1995), and may explain reduced orientation discrimination thresholds for illusory contours (Vogels & Orban, 1987; Westheimer & Li, 1996) in addition to the overall weak shape percepts elicited by our second-order stimuli.

Recent studies have also used selective adaptation to identify 2D form-selective mechanisms (Anderson, Habak, Wilkinson, & Wilson, 2007; Clifford & Weston, 2005; Suzuki, 2001). The aftereffects obtained in these studies are also difficult to explain solely by the adaptation of low-level orientation-selective neurons in V1, and are explained instead by the adaptation of extra-striate 2D shape-selective mechanisms. Although orientation flows that convey 3D shape are inherently 2D patterns, they are patterns formed...
specifically by perspective convergence along 3D surfaces. Thus it is likely that the mechanisms underlying the aftereffects found in our study are distinct from those suggested for encoding cue-invariant 2D form. However, it does appear that cue invariance plays an important role in the processing of both 2D and 3D shapes.

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