Neural Mechanisms Underlying the Perception of Three-Dimensional Shape from Texture: Adaptation and Aftereffects

Carole Filangieri

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Neural Mechanisms Underlying the Perception of Three-Dimensional Shape from Texture:

Adaptation and Aftereffects

by

Carole M. Filangieri

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

2015
This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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THE CITY UNIVERSITY OF NEW YORK
Abstract

Neural Mechanisms Underlying the Perception of Three-Dimensional Shape from Texture: Adaptation and Aftereffects

by

Carole M. Filangieri

Advisor: Andrea Li, PhD

Input into the visual system is two-dimensional (2D) and yet we effortlessly perceive the world around us as three-dimensional (3D). How we are able to accurately extract 3D shape information from the 2D representations that fall on the retina remains largely unknown. Although much research has been conducted that investigates higher levels of form processing (i.e. face recognition), less is known about the mechanisms that underlie the perception of simple 3D shape. Previous studies in our lab have shown that our ability to perceive 3D shape from texture cues relies on the visibility of orientation flows -- patterns that run parallel to the surface curvature of a 3D shape. Using the psychophysical technique of selective adaptation, we have further characterized the neural mechanisms that underlie the accurate perception of 3D shape. In Experiment One, we examined whether orientation flows that are defined by second order contours convey 3D shape, whether they induce 3D shape aftereffects, and whether these aftereffects are invariant to the patterns that define the orientation flows. Aftereffects were obtained and 3D shape was conveyed using stimuli in which orientation flows were defined by two classes of second order contours, and adapting to second order stimuli caused 3D shape aftereffects in first order stimuli. These results can be explained by the adaptation of 3D shape-
selective neurons in extrastriate regions that invariently extract first- and second order orientation flows from striate and extrastriate signals. In Experiment Two, we were interested in determining to what extent these neural mechanisms are invariant to differences in spatial frequency. We chose adapting/test stimuli that differed in spatial frequency by a factor of three, consistent with documented frequency bandwidths of V1 and V2 neurons. Shape aftereffects were obtained, indicating that these neural mechanisms are invariant to differences in spatial frequency by a factor of 3. Furthermore, these neural mechanisms are invariant to the patterns in which spatial frequency was varied (i.e., stimuli in which the orientation flows were created by first- or second order properties). Both of these properties are indicative of neurons that are located in extrastriate cortex. In Experiment Three, we were interested in testing to what extent these neural mechanisms were selective for retinal position by misaligning adapting and test stimuli by 2º, which corresponded to a single convexity or concavity in our corrugated surfaces. Our results suggest that 3D shape-selective mechanisms that respond to luminance modulated orientation flows appear to be sensitive to shifts in position of 2º. Overall, our results indicate that there are 3D shape mechanisms that are pattern invariant, invariant to differences in spatial frequencies by a factor of 3, and that exhibit position selectivity to shifts in retinal position of 2º. Taken together, these results implicate 3D shape mechanisms that are located in extrastriate cortex.
Acknowledgements

I am most grateful to my advisor, Dr. Andrea Li, who accepted me into her lab without any substantial research experience and guided me throughout my graduate career. Andrea’s support, her deep knowledge of visual perception, and her concise and insightful feedback has helped me to become a better scientist. I also owe a great deal of thanks to Dr. Joan Borod for all of her help in navigating the administrative details of the dissertation process and for offering me encouragement and support when I was feeling unsure of my path. Thanks go to Dr. James Gordon, Dr. Carolynn Pytte, and Dr. Justin Storbeck as well, for generously agreeing to sit on my committee and for the feedback they provided.

I would also like to thank Danny Tam, Chellie Fowler, and Kristine Bonacchi for commiseration and camaraderie; I couldn’t ask for better colleagues. Thank you too, to Cathryn Burge, Melanie Stokes, and Kim Matthews, who, at times, were sounding boards, editors, sympathetic ears, and always good friends. There were many volunteers who served as “lab rats” for my experiments; my gratitude goes out to each of them for graciously volunteering their time. Last (but never least), thank you to my family: Jim, Ash, and Niall. I never could have accomplished this without your love, support, and encouragement.
Dedication

This dissertation is dedicated to the memory of my father, Joseph T. Filangieri, who always believed that I should become a doctor.
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CHAPTER ONE

Introduction

In normal vision, we perceive the three-dimensionality of the world around us effortlessly; however, the scenes that are projected on to the retina are two-dimensional (2D) images. The process by which these flat, 2D projections come to be perceived as accurate, three-dimensional (3D) representations of our environment is still largely a mystery. In particular, many questions remain with regard to the characteristics of the neural mechanisms that underlie the detection of 3D shape. What information do these mechanisms extract from the 2D retinal images? What similarities, if any, do these 3D shape mechanisms share with 2D shape mechanisms? Where do these neural mechanisms sensitive to 3D shape reside in the visual pathway, and what techniques can be used to help scientists understand their nature and learn how they communicate with other areas of the visual pathway and regions of the brain? These, and similar questions have engaged vision scientists for the better part of a century.

It is believed that Leonardo DaVinci first observed that it was easier to perceive depth, which is required for the perception of 3D shape, in a natural scene than when that scene was interpreted as a 2D painting. He proposed that this was because the image projected into each eye in a natural scene is slightly different, due to the differing locations of our eyes, and that this phenomenon was impossible to recreate artistically (Puerta, 1989). Later, Wheatstone would show that two slightly different pictures presented to each eye do produce the sensation of depth (Wheatstone, 1838). He invented the stereoscope, which many Americans came to know as the GAF View-Master, an ubiquitous toy in the latter half of the 20th century.
However, 3D shape can be conveyed by both binocular and monocular cues. Binocular cues include binocular disparity (Julesz, 1971), convergence, and shadow stereopsis (Puerta, 1989). Monocular cues include tilt, shading, and texture (Gibson, 1950).

Although some researchers have begun to employ neuroimaging techniques to help identify cortical regions that may be responsible for coding 3D shape (Georgieva, Todd, Peeters, & Orban, 2008; Kourtzi & Kanwisher, 2000; Sereno, Trinath, Augath, & Logothetis, 2002), including areas sensitive to the perception of human faces (Kanwisher, McDermott, & Chun, 1997), little consensus has emerged in characterizing the location of the neural mechanisms that extract information about 3D shape from those initial 2D images that are projected onto the retina.

Much of the research characterizing the perception of 3D shape from monocular cues has focused on and lighting and shading (Arcizet, Jouffrais, & Girard, 2009; Breton & Zucker, 1996; Georgieva et al., 2008; Kleffner & Ramachandran, 1992; Mingolla & Todd, 1986; Norman, Todd, & Orban, 2004), and texture (Blake, Bulthoff, & Sheinberg, 1993; Cutting & Millard, 1984; Gibson, 1950; Knill, 2001; Li & Zaidi, 2000, 2004; Rosenholtz & Malik, 1997; Todd & Akerstrom, 1987; Zaidi & Li, 2001).

Previous studies in our lab have shown that the ability to perceive 3D shape from texture cues in projected images of textured 3D surfaces relies on the visibility of orientation flows -- patterns that run parallel to the surface curvature of a 3D shape. The purpose of the current research was to further characterize the neural mechanisms that underlie the extraction of these orientation flows and thus the perception of 3D shape from texture through a series of psychophysical experiments using selective adaptation. However, before we present our current research, it is important to place it in the context of the historical work that has been done in the field to date.
Classic Studies in Visual Aftereffects and Orientation Selectivity

Since the first perceptual experiments by Gustav Fechner, the psychophysical method has been the gold standard for studying visual perception. Psychophysics, which focuses on the relationship between the stimulus and the response of a subject, provides a non-invasive, economical, and efficient way in which to assess brain-behavior relationships. While frequently used in isolation, psychophysics has also been commonly used in conjunction with physiological techniques, and more recently, combined with neuroimaging in order to help isolate areas of interest in the visual system.

Early psychophysical research began to use adaptation as a method for characterizing the neural mechanisms that underlie visual perception, and today, visual adaptation continues to be used in psychophysical and neuroimaging experiments. In this way, these two different approaches, one classic and one cutting edge, can provide complementary findings, further bolstering the strength of findings in the field of visual perception.

The premise of visual adaptation is simple: if one looks at an image for an extended period of time, the image can induce perceptual “aftereffects,” in that a subsequently viewed image will be perceptually different from its physical composition. Visual adaptation can be described as a perceptual distortion of a particular attribute in a given image that has been biased by the visual field being exposed to an opposite distortion of that attribute. Aftereffects can be experienced as changes in detection thresholds, in apparent contrast, in perceived spatial frequency, slant or tilt, convexity or concavity, and in other factors contributing to appearance. What aftereffects represent is a change, however brief, in neural coding, and they are thus indicative of the natural plasticity of the brain (Dragoi, Sharma, & Sur, 2000; Ghisovan, Nemri,
Furthermore, the spatial and temporal parameters of the adaptation paradigm can be selectively manipulated to examine specific characteristics of the underlying mechanisms, such as pattern selectivity, temporal requirements, retinal specificity, and relative locus in the visual pathway.

Visual adaptation to motion has been alluded to as far back as 300BC. In *Parva Naturala*, Aristotle discussed it as natural phenomena related to sensory perception (Anstis & Cavanagh, 1983). However, in modernity, Robert Addams first noted the phenomenon in the first half of the 19th century. During a visit to Scotland’s Falls of Foyers, he found that after staring at the water cascading over the ledge for a period of time, when he shifted his gaze to the surrounding cliff walls they appeared to be rising (Addams, 1834). He attributed the motion aftereffect to the movement of his eye muscles. When he stared at the waterfall, his eyes were swept downward with the movement, so much so that when he looked away at the stationary rocks, his eyes continued to move involuntarily, giving the perception that the cliffs were moving in the opposite, upward, direction, appearing to rise. While today we know this theory of involuntary eye movement to be untrue, Addams’ explanation, which was supported by, among others, the scientists Jan Evangelista Purkinje and Hermann von Helmholz (Hunter, 1914), represents an early modern attempt to characterize the aftereffect phenomenon.

Aftereffects are not limited to motion, however. The great German writer Goethe, best known for penning Faust, noticed that staring for a period of time at a blue color field elicited the perception of the color orange afterwards. He described these negative afterimages that occur in color perception in his 1810 scientific volume *Zur Farbenluhre* (Cook & Kunkel, 1916).

These kinds of perceptual experiences led James J. Gibson in 1933 to use selective adaptation to study visual perception. Gibson became intrigued by the aftereffect phenomenon
when a subject in an earlier experiment who had worn prism glasses (that have special lenses that bend light and displace the visual scene) during waking for a substantial period of time (45 hours over several days) reported that, after removing the glasses, vertical lines in the environment had a distinct curvature. When the observer had first put on the prism glasses, she reported a curvature to the right that diminished substantially by the fourth day she wore the glasses. After the glasses were removed, the observer reported that the environment around her now curved in the opposite direction as it had at the beginning of the experiment. Gibson embarked upon a series of experiments that tested adaptation across the modalities of vision and kinesthesia (Gibson, 1933). In these studies, he systematically manipulated observers’ visual and tactile perceptions and, from the findings, he was able to make several assertions. His first conclusion was that adaptation and what he termed “negative after-effects” (meaning the measureable adaptive change represented as a perceptual shift toward the opposite direction of the adapting image) are of the same magnitude -- in other words there is an association between the strength of the adaptation and the aftereffect it elicits. He also showed that negative aftereffects were limited to the area of the visual field that was adapted, that they could be generated by manipulating the contrast of the adapting images, and they are binocularly transferrable, although the magnitude of the aftereffect is less in the non-adapted eye. Gibson concluded that the phenomenon of adaptation was not a product of the initial input of the stimulus that fell onto the retina, but rather, that the mechanisms underlying adaptation existed somewhere else in the visual system.

A few years later, Gibson characterized the perceptual aftereffects of adaptation to tilted lines -- the tilt aftereffect (Gibson & Radner, 1937). He and his co-author found that a shift of 10° from vertical or horizontal produced the most robust negative aftereffects, and that negative aftereffects could be elicited following adapting durations as brief as five seconds in length and
did not appreciably change in magnitude after an adapting period of 90 seconds. Lastly, Gibson and Radner were able to identify the degree of tilt where negative aftereffects were abolished: 40° from the vertical and horizontal planes. At degrees beyond 45, an aftereffect of smaller magnitude in the same direction as the adapting image -- was noted. Gibson labeled the first type of after-effect “direct” and the second “indirect.”

Later, Köhler and Wallach (1944) would conclude that adaptation aftereffects are the result of the “satiation” of cortical tissue. One of the major findings their comprehensive set of experiments revealed was that parallelograms such as rectangles and squares could be perceived as trapezoids with the non-parallel sides converging in the opposite direction of an adapting angle. The authors also found that the relationship between two identical geometric shapes could be distorted in such a way that one would be perceived as larger than the other simply by virtue of both shapes’ relationships to a larger, adapting angle. The researchers reasoned that the satiation was actually an artifact of electric current activating the tissue; this activation, for a short time span, would make that particular area of tissue a poor conductor. The current flow cut off from that tissue would then divert to regions that had been little affected or unaffected at all.

From their conclusions, one of the major theories of what occurs physiologically during adaptation evolved: that an adapting stimulus fatigues cortical neurons that are sensitive to the pattern presented, and, subsequently, when a test stimulus is then shown, the cortical neurons that are sensitive to its pattern are activated. However, the cells that were originally stimulated by the adapting stimulus are less likely to respond because they have been fatigued, and the neural activation is now shifted toward the opposite direction of the pattern in the original adapting image (Paradiso, Shimojo, & Nakayama, 1989).
In the 1950s, some scientists began to study the underlying physiology of the visual system. Kuffler (1953) identified the ganglionic property of concentric on center/off periphery receptive fields in cat retina and determined that the different parts of a receptive field worked in opposition to each other. Because of this, light restricted to a small spot that shone on the center would provoke a greater response than ambient light that flooded the entire receptive field (Barlow, Fitzhugh, & Kuffler, 1957).

Hubel and Wiesel (1959, 1962, 1965) mapped the receptive fields of hundreds of neurons located in the striate cortex of cat by drifting light spots of different shapes and sizes across a large screen that covered most of the animal’s visual field and recording the points at which the light evoked responses. Using this method, they discovered that most of the receptive fields were comprised of excitatory and inhibitory regions. A typical excitatory region produced an increase in the frequency of firing when illumination fell on it, and a typical inhibitory region’s firing was suppressed when illumination fell on it and fired when the light was removed. Consistent with Kuffler’s findings, these regions acted in opposition to each other and their response was weaker when both regions were illuminated than when one or the other region was illuminated on its own. However, unlike ganglion cells in the retina, the orientation and shape of the stimulus light was critical to eliciting a response from cortical neurons. Overall, the receptive fields that Hubel and Wiesel mapped tended to be elongated in shape with central regions flanked by opposing fields (see Figure 1). Hubel and Wiesel classified two types of cells: simple cells and complex cells, both of which are sensitive to orientation, despite differing in receptive field size, and position and movement preferences.

Campbell and Kulikowski (1966) used psychophysical experiments to test if humans had perceptual neural mechanisms analogous to the ones that Hubel and Wiesel (1959, 1962,
1965) had found in cat. Using an orientation masking paradigm in which observers adjusted target stimuli to contrast thresholds (the point at which a grating is detected) in the presence of a superimposed oriented mask, while controlling for luminance and spatial frequency (the number of cycles a pattern repeats per degree of visual angle), Campbell and Kulikowski found a pattern of orientation selectivity in their results -- a window of approximately 30° -- that was surprisingly similar to the one Hubel and Wiesel described in their ground-breaking studies.

Following closely on the heels of those findings, Blakemore and Campbell (1969) sought to find if there were neural mechanisms in the human occipital lobe that were sensitive to the orientation and size of retinal images. In a series of experiments, the authors held the value of mean luminance constant while varying the contrast and spatial frequency of simple sinusoidal gratings. Key findings included the following: 1) Optimal adaptation aftereffects could be achieved from an initial exposure of 60 seconds to the adapting image, “topped off” with 10 second exposures in between test images; 2) neural mechanisms exist in humans that are “tuned” to specific spatial frequencies; 3) the neural mechanisms sensitive to higher spatial frequencies seem to be more narrowly tuned than those sensitive to lower spatial frequencies; and, 4) adapting one eye could provoke an attenuated aftereffect in the non-adapted eye, indicating that some spatial frequency tuning may occur after binocular combination.

Blakemore and colleagues (1970) asserted that tilt aftereffects were a product of the phenomenon of lateral inhibition due to their finding that aftereffects decreased as the inducing angle grew larger and larger. In lateral inhibition, it is established that neighboring neurons with similar orientation preferences laterally inhibit one another, which the authors believed accounted for the repulsion (negative aftereffect) in the tilt aftereffect.
These studies suggested that there exist neural mechanisms that are highly selective to line orientation (Campbell & Kulikowski, 1966; Gibson & Radner, 1937; Hubel & Wiesel, 1959, 1962, 1965), and the measurable aftereffects may be the product of fatiguing specific neural populations (Köhler & Wallach, 1944; Paradiso et al., 1989) and/or may be influenced by lateral inhibition (Blakemore, Carpenter, et al., 1970). These and similar studies spawned a generation of research that sought to characterize the nature of the neural mechanisms sensitive to the perception of 2D and 3D shape, which proceeded in two general directions: the extraction of shape from contour and line orientation and the extraction of shape from shading and texture.

**Tilt and Line Orientation**

Although much of the literature on orientation perception up to this point focused on stimuli in which boundaries were defined by luminance differences, presumably because that is what V1 neurons respond to best, others investigating the percept of orientation used stimuli in which orientation was defined by non-luminance boundaries.

Vogels and Orban (1987) found that edges created by illusory contours were equally as visible at all orientations as edges defined by luminance differences (see Figure 2 for examples). In addition, Cavanagh and Mather (1989) distinguished two properties that characterized neural mechanisms selective to line orientation. “First order” neural mechanisms respond to changes in luminance (e.g. Figure 2, top panel), a property that is responded to at the earliest levels of the visual system (Hubel & Wiesel, 1968), and “second order” neural mechanisms respond to changes in spatial frequency and textural properties, while mean luminance is maintained (e.g. Figure 2, middle and bottom panels). Illusory contours fall into the latter category.
Findings from psychophysical studies investigating orientation selectivity of first and second order stimuli have had mixed conclusions with regard to the nature of the underlying mechanisms. Tilt aftereffects have been elicited from illusory contours when adapting stimuli are real contours -- ones in which edges are defined by changes in luminance; however illusory contour adapting stimuli did not elicit aftereffects in real contour stimuli (Paradiso et al., 1989). In another study, orientation contours (another type of second order property) elicited stronger aftereffects than those defined by illusory contours, and both types of second order stimuli adapted a real contour equally as strong as a real contour adapting stimulus (Hawley & Keeble, 2006).

Asymmetries have been found in interocular transfers of the tilt aftereffect: Significantly stronger aftereffects are elicited in interocular transfer when the adapting stimulus is a real contour and the test stimulus is an illusory contour than vice versa (Paradiso et al., 1989). Paradiso and colleagues attributed the asymmetries of their results to two possibilities, which are not necessarily mutually exclusive: 1) that a corresponding asymmetry of receptive field types exists in the visual cortex; and, 2) the cells activated by illusory contours may represent a subset of cells in V2 that can be activated by real contours as well. This assertion is supported by physiological evidence in macaque monkey that neural mechanisms sensitive to illusory contour can be found in V2, which is more sensitive to binocular combination than V1 (von der Heydt, Peterhans, & Baumgartner, 1984). However, others postulated both illusory contours and real contours are processed by the same neural mechanisms, and that the repulsion and attraction phenomena observed in the direct and indirect aftereffects were actually due to orthogonal illusory tilts (van der Zwan & Wenderoth, 1995).

Contrast modulated textures are also considered second order stimuli, because their mean luminance remains constant. Luminance modulated plaid textures have been shown to induce tilt
aftereffects in contrast modulated gratings and vice versa, suggesting that the underlying mechanisms that code for luminance and contrast are similar. One conclusion that can be drawn is that first order and second order cues are processed in parallel, not necessarily by the same mechanisms (Smith, Clifford, & Wenderoth, 2001). However, there are alternate theories. One is that at some level of the visual system there are neural mechanisms that are sensitive to global shape, regardless of whether it is defined by first order or second order properties (Smith, Wenderoth, & van der Zwan, 2001), and the other posits that while there may be neural mechanisms that respond selectively to first order and second order cues, they may share mechanisms sensitive to adaptation (Cruickshank & Schofield, 2005).

Neuroimaging and physiological studies have not added much more clarity to the characterization of the neural mechanisms sensitive to second order cues. In an fMRI study, Larsson and colleagues found that luminance-modulated adapt/test stimuli activated areas in V1 and extrastriate cortex (V2, V3, V3A/B) to a similar degree, however, in two second order conditions (contrast modulated and orientation modulated), the response magnitude in extrastriate cortex (V3, V3A/B) was significantly larger than that of V1. The results for cross-property adaptation (luminance modulated adapt/orientation modulated tests) showed no consistent effect (Larsson, Landy, & Heeger, 2006). This suggested that the neural mechanisms they observed were sensitive specifically to second order cues rather than cue invariant across first and second order cues. However, illusory contours have been shown to activate V1, V2, V3, V4 and other visual areas (Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007). From these results the authors asserted that both primary visual cortex and higher visual areas contain neural mechanisms selective for orientation defined by illusory contours.
Song and Baker (2007) found correlations in area A18 of cat cortex that supported the assertion that first order and second order properties arise from similar neural mechanisms or pathways. In vitro single-cell recordings provided evidence that both simple and complex neurons responded to illusory contour and contrast-modulated stimuli at preferred orientations; however, no neurons responded to only one of the two conditions presented. Nor was there any significant difference between response to contrast modulated and illusory contour stimuli in either simple or complex cells. This suggested a mechanism selective for orientation that was cue-invariant to second order cues.

More recently, Knebel and Murray (2012) investigated neuronal responses to illusory contours in the temporal domain using visual evoked potentials (VEP), in order to test whether illusory contours are processed in a feed-forward manner or are first processed in higher levels of the visual pathway. The data they collected, based on spatio-temporal responses, supported the theory that illusory contours are processed in higher cortical regions, particularly the lateral occipital cortex (Mendola, Dale, Fischl, Liu, & Tootell, 1999).

The findings from psychophysical studies that examine the nature of the tilt aftereffect all seem to implicate activation of neural mechanisms very early in the visual pathway (e.g., V1, V2) that are dependent upon the properties of luminance, contrast, and illusory contour. However, neurophysiological and neuroimaging studies have found activation in extrastriate cortex as well as primary visual cortex (Knebel & Murray, 2012; Larsson et al., 2006; Montaser-Kouhsari et al., 2007). Furthermore, the findings from these studies suggest that the nature of the mechanisms sensitive to second order cues is such that they may represent a population of neurons that responds to both first and second order cues (Paradiso et al., 1989), can exhibit cue invariance (Smith, Clifford, et al., 2001; Song & Baker, 2007), and may be evidence of neural
mechanisms sensitive to global shape (Paradiso et al., 1989). However, these studies have focused on simple planar patterns (e.g., tilted lines) and neural mechanisms that respond to low level features such as orientation.

At the other end of the spectrum there has been much research that has characterized the nature of our ability to detect faces, which implicates mechanisms that are much less sensitive to position and size (Rhodes, Jeffrey, Watson, Jaquet, & Winkler, 2004), and has shown evidence that these mechanisms reside in higher levels of visual processing (e.g. inferotemporal cortex, fusiform face area) (Kanwisher et al., 1997). However, little research seems to explain the nature of basic shape perception, the mechanisms of which are believed to occur at some level in between mechanisms responsible for orientation and face perception, and thus, is often referred to as a “mid-level” visual process. Because of this, more recently, some researchers have been interested in characterizing the neural mechanisms sensitive to simple 2D and 3D shape. Visual adaptation has proven to be a commonly used technique in this domain as well.

**Spatial Frequency**

Spatial frequency, which is quantified as the number of cycles a pattern repeats per degree (cpd) of the visual angle, is another visual cue that is available for accurately processing our environment. It is one of the components of texture, in both the visual and tactile senses. All images can be mathematically broken down into repeating pattern components called sinusoidal gratings of different frequencies and orientations (see Figure 3 for examples) in a process called Fourier analysis (R. L. De Valois, Albrecht, & Thorell, 1982). In images and scenes, low spatial frequencies (e.g. Figure 3, left) convey coarse, global information while high spatial frequencies (e.g. Figure 3, right) convey fine detail and local information (Boeschoten, Kemner, Kenemans,
Sinusoidal gratings have been particularly useful in investigating how the visual system processes spatial frequency, as these gratings only contain one frequency (Blakemore & Campbell, 1969).

In human vision, there are spatial frequency “channels” -- neural mechanisms that are “tuned” to relatively narrow band-widths of grating frequencies (Campbell & Robson, 1968; Sachs, Nachmias, & Robson, 1971), and there is evidence in cat that the entire range of observable spatial frequencies are represented throughout primary visual cortex (Everson et al., 1998; Issa, Trepel, & Stryker, 2000).

These neural mechanisms are adaptable, such that after adapting to a high frequency grating, the bars of a medium frequency grating test image will appear lower in spatial frequency than it actually is, and after adapting to a low frequency grating, that same medium frequency grating will appear higher in spatial frequency than it actually is (Blakemore, Nachmias, & Sutton, 1970). Adaptation has also been used to determine the range of frequencies to which a particular channel responds, by measuring contrast sensitivity after adaptation. In this paradigm, using sinusoidal gratings, aftereffects have been elicited in human observers up to approximately one octave away (i.e. two times greater or half as much) from the adapting grating (Blakemore & Campbell, 1969; Campbell & Robson, 1968; K. K. De Valois, 1977), and they taper off to baseline when the test frequencies are three times or one third the magnitude of adapting frequencies (Blakemore & Campbell, 1969; Tolhurst, 1972). Neurophysiological studies have isolated cells in primary visual cortex of macaque and cat that support these findings (Campbell, Cooper, & Enroth-Cugell, 1969; R. L. De Valois et al., 1982; Movshon & Lennie, 1979). However, location also plays a role in determining the bandwidth of a spatial frequency channel. In one study, neurons in V1 and V2 of macaque with parafoveal (peripheral) representation have slightly wider
bandwidths than those with foveal (central) representation, and neurons in V1 with foveal representation have the narrowest tuned bandwidths (Foster, Gaska, Nagler, & Pollen, 1985).

Lower spatial frequency channels that are adaptable to luminance-modulated sinusoidal gratings have somewhat wider bandwidths than higher spatial frequency channels (Blakemore, Nachmias, et al., 1970; Foster et al., 1985; Wilson, McFarlane, & Phillips, 1983), and the mechanisms that adapt to very low luminance-modulated spatial frequencies appear to be sensitive to orientation and position-specific (Stromeyer III, Klein, Dawson, & Spillman, 1982), whereas mechanisms that are sensitive to second order features exhibit invariance to spatial frequency (Landy & Oruç, 2002). However, mechanisms in cat V18 cortex that are adaptable to illusory contours, exhibit selectivity to spatial frequencies that are less than .18 cpd, and mechanisms in cat V17 appear invariant to spatial frequencies that are greater than 1.6 cpd (Zhan & Baker, 2008).

Some have accounted for the variety of neuronal responses to changes in spatial frequency as indicative of the existence of two types of spatial frequency channels: simple and complex. Simple channels are narrowly tuned and operate in a linear fashion (Campbell & Robson, 1968). Complex channels, which are more broadly tuned, consist of linear and nonlinear filtering stages (Graham, Sutter, & Venkatesan, 1993). The linear function of a complex filter is tuned to both orientation and spatial frequency, which serves to sharpen and enhance edges (R. L. De Valois et al., 1982; Landy & Oruç, 2002). Another possible function of the linear filter could be to prevent first order characteristics from reaching the nonlinear filter -- sensitive to second order features -- and which could otherwise diminish its ability to detect second order characteristics (Schofield & Georgeson, 2002). One characteristic of a nonlinear filter is invariance to spatial frequency (Landy & Oruç, 2002; Schofield & Georgeson, 2002), although
there is disagreement to what that implies (i.e., a single filter for second order features [Schofield & Georgeson, 2002] or multiple mechanisms that are analogous to the ones sensitive to luminance modulations [Landy & Oruç, 2002]).

**Two-Dimensional Shape from Contour**

While there appears to be consensus that neural mechanisms sensitive to orientation are sensitive to position, size and contrast, sensitivity to spatial frequency may be dependent upon the nature of the adapting stimuli. And the same holds true for mechanisms sensitive to shape that is determined by contour. Some have found these mechanisms are sensitive to local orientation (Dickinson, Almeida, Bell, & Badcock, 2010; Gheorghiu & Kingdom, 2007), while others have found evidence for position and size invariance (Anderson, Habak, Wilkinson, & Wilson, 2007; Gheorghiu & Kingdom, 2006; Gheorghiu, Kingdom, & Witney, 2010; Suzuki & Cavanagh, 1998).

Suzuki and Cavanagh (1998) found that an adapting stimulus distorted the shape of a subsequently presented test stimulus in the opposite direction of the adapting stimulus. For example, adapting to a triangle pointing to the right causes a subsequently shown square to be perceived as a trapezoid tapered to the left. This type of distortion suggests nonlocal mechanisms, because there is little retinal overlap between the contours of the adapting and test stimuli. These findings implicate neural mechanisms similar in expression to those located in higher visual areas (i.e., inferior temporal cortex or superior temporal sulcus) where a population of neural mechanisms has been found that is sensitive to shape, independent of retinotopic properties such as spatial frequency, distance and scale (Tanaka, 1996).
Anderson and colleagues (2007) found negative shape aftereffects in radial frequency patterns that transferred across adapting patterns with regard to the properties of contrast and size, suggesting a global shape mechanism. Furthermore, aftereffects occurred in conditions where the adapting image was 10% of the contrast of test images and when the size of the adapting stimulus and test stimuli differed by factors of 2 and 4, suggesting evidence of visual processing beyond primary visual cortex. However, the authors also found evidence of response by mechanisms sensitive to local changes of orientation when observers adapted to a radial frequency that varied in pattern from the test stimuli but shared the same radius. In this case, observers exhibited response uncertainty, in that they seemed to have difficulty judging the phase of test stimuli after adaptation. In another study, no aftereffects were obtained in conditions that used luminance gratings or line gratings as adapting stimuli when the frequency and amplitude of test gratings were varied (Gheorghiu et al., 2010). However, because modest aftereffects were recorded in cross conditions, this suggests there are mechanisms sensitive to local curvature, i.e., shape detectors (Gheorghiu & Kingdom, 2007).

An alternate theory to the idea of shape detectors is that local oriented line detectors enhance shape contrast between similar shapes (Dickinson et al., 2010). In this way, the tilt aftereffect could substantially contribute to the perceptual changes that occur in adaptation to shape by serving to enhance the ability of an observer to notice differences in shape by making the patterns of subsequently presented shapes appear more distinct. The authors posit that it was a tilt aftereffect field -- a regional population of mechanisms sensitive to local effects -- that accounted for global aftereffects not only in radial frequency circles and Cartesian grids, but also in the processing of a familiar face.
In terms of the perception of 2D shape, some researchers have characterized neural mechanisms that may be sensitive to local changes in orientation (Dickinson et al., 2010; Gheorghiu & Kingdom, 2007). Others have suggested that these neural mechanisms are position invariant (Suzuki & Cavanagh, 1998) and show evidence of size and contrast invariance (Anderson et al., 2007). Taken as a whole, the characteristics of these neural mechanisms seem to have more similarity to mechanisms located at higher levels of the visual pathway than those located in V1, and some have suggested that these mechanisms are located in V4 (Gheorghiu & Kingdom, 2006), due to properties (i.e. sensitivity to contrast polarity) that are consistent with neural mechanisms sensitive to face adaptation (Yamashita, Hardy, De Valois, & Webster, 2005). Others have noted characteristics in these mechanisms that are similar to those found in the inferotemporal cortex or superior temporal sulcus (Suzuki & Cavanagh, 1998).

**Three-Dimensional Shape**

Up until this point, the research presented has focused on 2D shape processing; it sheds little light on how cues to 3D shape are extracted from retinal images. What can be concluded so far is that low-level visual mechanisms selective for orientation are sensitive to properties such as luminance, contrast, spatial frequency, and retinal position, while mechanisms sensitive to second order texture cues and 2D shape seem to exhibit less sensitivity to contrast, spatial frequency, retinal position, and size.

What remains to be discovered is where in the visual system are we able to extract 3D shape from 2D retinal images, and, as such, what are the characteristics of the neural mechanisms that enable us to perceive basic 3D shape? Research on the perception of 3D shape from monocular cues has largely focused on shape defined by shading and shape defined by
texture (see Figure 4 for examples). It should be noted that research examining 3D shape perception from monocular cues utilizes 2D images from which 3D cues have been projected. The images that are created as stimuli, which project images on the retina that are identical to those that would be projected if the observer were viewing a real 3D object, are facsimiles that represent 3D shape and are presented on a computer monitor. For example, Figure 5 illustrates how a surface corrugated in depth with an amplitude of 14 cm, viewed at 1 m, is projected into the image, creating a retinal image of the actual 3D surface viewed at that distance. The projecting rays connecting the surface to the eye dictate what part of the surface is projected into which location in the image. It is the 2D changes in these images that are examined as cues to 3D shape perception.

There are several advantages to using 2D representations of 3D shape, rather than actual 3D shapes. First, it is easier to manipulate curvatures and deformations of the 2D representations. Also, 2D representations can be presented on a computer monitor screen, which enables experimenters the ability to control (or remove) outside light sources, and the ability to briefly and to rapidly expose observers to stimuli with minimal distraction.

**Shape from Shading**

Renaissance artists such as Dürer, El Greco, and Caravaggio understood the contributions of shading in the accurate perception of 3D shape and incorporated the technique of *chiaroscuro* (the contrast of light and shadows to imitate volume) to create the realistic masterpieces that are a hallmark of the art of that era and set its style apart from the flat, 2D style of gothic painting. The deep shadows in Renaissance paintings illustrate gradient changes in luminance, which in turn, realistically define folds of fabric and human figures, among other subjects.
Two assumptions in the accurate perception of shape from shading are that illumination occurs from a single light source and a bias that the light source generally shines from above (Kleffner & Ramachandran, 1992; Symons, Cuddy, & Humphrey, 2000). Furthermore, it appears that observers rely on retinal cues (i.e., location and size of retinal images) to determine shape, suggesting that shape from shading is processed fairly early in the visual system (Kleffner & Ramachandran, 1992; Wenderoth & Hickey, 1993). However, it has also been shown that the perception of shape is influenced by an external light source, regardless of its position (Johnston & Passmore, 1994; Proulx, 2014).

Others have shown that shading flow fields, found in the region between illumination and shadow, hold critical information for the perception of 3D shape. While the illumination and surface reflectance of an object are contingent upon the position of the object with regard to the source of illumination, shading flow fields depend upon the geometric properties of an object and are independent of illumination and reflectance. The may therefore be a more likely target for the accurate perception of 3D shape (Breton & Zucker, 1996).

More recently, Arcizet and colleagues (2009) have found that individual neural mechanisms in macaque V4 show broad selectivity in 3D corrugated shapes defined by shading and contained populations of neurons that respond to complex shape from shading.

**Shape from Specular Highlights**

Specular highlights are properties of glossy surfaces. They are created by one or multiple light sources and have been found to provide information in the processing of 3D shape (Norman et al., 2004; Todd, Norman & Mingolla, 2004). While surface texture is compressed by slant, specular highlights are compressed by curvature (Fleming, Torralba & Adelson, 2004). Unlike
surface texture, which is a fixed property, specular highlights slide across glossy surfaces and change shape, depending upon light source, viewing angle, and motion (Fleming, et al., 2004). Because of this, specular highlights are anisotropic -- visible only from limited viewpoints (Todd, et al., 2004).

Fleming and colleagues (2004) posited that specular reflections -- the warped and distorted views of the surrounding environment that are reflected on a shiny (or specular) surface could be considered textural “orientation fields.” Although these orientation fields can become highly distorted, depending upon the curvature of a surface, their findings suggested that observers were able to extract accurate 3D shape information from the orientation fields, without being provided any context with regard to the environmental surround (reflected on the surface).

Liu & Todd (2004) found that, absent of specular highlights (and cast shadows), observers did not perform significantly above chance on a task judging convexity or concavity of a textured surface, but the addition of those features significantly improved observers’ accuracy. More recently, other researchers have found that specular highlights are more helpful in judging convexities over concavities (Kerrigan & Adams, 2013; Adams & Elder, 2014).

Very little research has been done, to date, with regard to where in the visual system our ability to extract 3D information from specular highlights resides. In a recent neuroimaging study Wada and colleagues (2014) implicated right hV4, right VO-2 and right V3A/ B. However, casting the information in the context of orientation (a property preferred by V1 neurons) may lead to testable neural models of 3D shape from shading in the future. This trend has already been seen in research investigating 3D shape from texture.
Shape from Texture

Texture also provides information that aids in the accurate perception of 3D shape. Texture patterns on the surface of an object can be stretched or compressed, illustrating convexities and concavities. Textures can also indicate depth by the variation of the size of the individual components that make up a texture. Three cues of 3D texture gradients have been identified: compression -- the change of aspect ratio of individual elements in a texture; density -- the change in distance between elements in a texture; and size -- the magnitude of the elements in a texture (Cutting & Millard, 1984; Gibson, 1950; Todd & Akerstrom, 1987). Of these cues, compression seems to be the primary indicator of the curvature of a surface texture while surface density and size seem to be the best cues for conveying slant and tilt (Cutting & Millard, 1984).

Two assumptions that are thought to enable the perception of 3D shape from texture are isotropy and homogeneity. Isotropy refers to the property of omnidirectional uniformity in the texture of a pattern, i.e. an isotropic pattern has no orientation bias (see Figure 6, top panel). Homogeneity refers to a pattern that is uniform in both composition and character across locations of the pattern. Homogeneous patterns can have orientation bias (See for example Figure 6, bottom panel) or they can be isotropic. Some researchers believed that the detection of deviation from isotropy is what was crucial to perceiving 3D shape (Blake et al., 1993), while others believed that the detection of texture/gradient distortion was integral to perceiving 3D shape (Todd & Akerstrom, 1987).

Rosenholtz and Malik (1997) contended that if a surface texture was assumed to be homogeneous, then observers would still be able to correctly perceive its shape even if the surface were anisotropic -- irregularly textured. The authors believed that it was a change in gradient texture between one part of an image and another that was crucial to the detection of surface
orientation. In a series of monocular experiments, the authors had observers estimate slants (the slope of the surface) and tilts (the direction of the slant) of surfaces patterned with isotropic textures; anisotropic textures compressed in the direction of tilt, anisotropic textures stretched in the direction of tilt, and anisotropic textures compressed at an angle of 45° of tilt, so that the texture was non-tilt-aligned. Their results indicated that both cues -- change from isotropy and change in gradient texture -- were integral to perceiving 3D shape correctly.

In contrast to texture gradient theories, which require assumptions about isotropy and homogeneity and do not posit any neural explanations for these assumptions, Li and Zaidi (2000) proposed that it was visible orientation changes across the curvature of a surface that is crucial to the accurate perception of 3D shape. In a series of neurally motivated experiments that took advantage of the understanding that the visual system is equipped with mechanisms very early on that respond to orientation and are frequency selective, the authors used vertically oriented depth corrugations patterned with simple gratings and plaids as well as complex plaids and filtered noise patterns (Figure 7). The results of their experiments showed that it was the pattern of visible orientation “flows” that were parallel to the surface curvature and aligned with lines of maximum surface curvature that enabled observers to accurately perceive the 3D shape (Figure 7, left and middle panels). When these flows are absent or obscured, observers are unable to accurately judge the 3D shape of a stimulus (Figure 7, right panel). Furthermore, these results hold true regardless of whether the surface texture is isotropic or homogeneous, and thus the assumptions about the properties of isotropy and homogeneity are not required in this approach. From their findings, the authors postulated that the mechanisms in the human visual system sensitive to changes in orientation across the image of a textured surface extract the orientation flows. However, their findings suggest that spatial frequency is not as reliable a cue as
orientation; when defined purely by spatial frequency modulations, slant and curvatures appear to be more susceptible to perceptual misinterpretation than slants and curvatures defined by orientation flows. Li and Zaidi’s findings supported computational findings that the “texture flow” of a developable surface followed the parallel geodesics that characterized the surface (Knill, 2001), and are supported by others’ findings that the convergence and compression of patterns that include parallel lines that occur on slanted and tilted surfaces convey important information about 3D shape (Fleming, Holtmann-Rice, & Bülthoff, 2011).

To examine the generalizability of orientation flows as cues to 3D shape, Li and Zaidi (2004) conducted experiments utilizing multiple types of surface texture mappings. In a series of experiments using developable, carved volumetric, and deformable stretched surfaces the authors found that the same patterns of critical orientation flows that run parallel to the curvature of a surface that convey 3D shape arise in all three texture mappings, and that the detection of 3D shape was contingent upon the visibility of these orientation flows. In the absence of these critical flows, concavities were often misperceived as convexities. The authors found that although the same patterns of orientation flows arose for folded, carved, and stretched surfaces, frequency changes were dependent upon on the type of surface. Because of this, orientation flows appear to be more generic and reliable as a cue to 3D shape.

The one class of stimuli that did not conform to Li and Zaidi’s conclusion were those in which orientation flows were defined by illusory contours, the 3D shapes of which were also correctly perceived by observers. These orientation flows are created by a visual illusion, and are not actually physically present in the texture pattern. In an investigation to better understand this discrepancy and to further characterize the neural mechanisms sensitive to 3D shape, Li and colleagues (2008) adapted observers to stimuli in which 3D concavities and convexities were
created from real and illusory contours of checkerboard patterns called Zabutons (Kitaoka, Pinna & Brelstaff, 2004) (see Figure 8 for examples). The adapting and test stimuli that observers were shown were either in-phase, opposite-, or quadrature-phase (a condition in which the checks were shifted horizontally and vertically by $\frac{1}{2}$ a cycle, or $\frac{1}{4}$ of the check). Because the contours of the checkerboard pattern of the illusory contour condition remained vertical/horizontal yet still generated significant aftereffects consistent with non-vertical/horizontal contours in luminance-contoured stimuli, V1 and V2 were ruled out as primary areas containing neural mechanisms sensitive to 3D shape when adapting to orientation flows. In a separate experiment, the authors tested luminance-modulated horizontal-vertical corrugated plaids to see whether aftereffects were selective for spatial frequency and found some evidence for cross adaptation for patterns of frequencies differing by a factor of three when the adapting stimuli were convex, indicating that some adaptation was occurring in cells beyond V1 and V2. However, although significant, cross adaptation aftereffects were generally weaker than and not as consistent as they were in the same frequency conditions.

Physiological and neuroimaging studies have isolated areas implicated in 3D shape from texture. Stimuli defined by contour, texture, shading, and motion presented to anesthetized monkeys were found to activate areas in V1, V2 and V3, MT, areas of the temporal cortex (FST, STS, AMTS), the parietal occipital juncture, and two frontal lobe areas (Sereno et al., 2002). The diversity of the areas activated may be a reflection of the multiple uses in which 3D shape representation is necessary and facilitative (i.e., perception, recognition, navigation, etc.). In human fMRI studies, Georgieva and colleagues (2008) identified cortical regions sensitive to the perception of 3D shape from texture: the caudal inferior temporal gyri, the lateral occipital sulcus, and areas of the intraparietal sulci. Furthermore, the areas activated by the shape from
texture stimuli shared many regions as areas that are also activated by shape from motion (Murray, Olshausen, & Woods, 2003; Orban, Sunaert, Todd, Van Heck, & Marchal, 1999).

Together, these studies have found evidence for neural mechanisms that enable the perception of 3D shape from texture. In particular, the visibility of orientation flows is integral for the accurate perception of 3D shape (Li & Zaidi, 2000). Some characteristics of these neural mechanisms that have been isolated by adaptation are that they are adaptable to first and second order cues and they appear to be more broadly tuned for spatial frequencies than mechanisms found earlier in the visual pathway, both findings that place them outside primary visual cortex (Li et al., 2008).

However, neurophysiological studies have found evidence for the processing of 3D shape from texture as early as V1 and as remote as the frontal lobes. What these seemingly contradictory findings may point to is the diversity of the roles that 3D shape plays in the interaction with the environment around us (Mishkin, Ungerleider, & Macko, 1983).

**Conclusions**

Basic shape perception is one of the fundamental functions of the visual system. However, there remains little conclusive evidence with regard to the nature of the neural mechanisms underlying the perception of basic 3D shape. While many studies have concentrated on neural mechanisms located in the early visual system that are sensitive to line orientation and the properties of luminance, contrast, and textural patterns, after 100 years of research, we are still searching for answers to one of the foundational experiences of our perceptual world: at what point in the visual system is 3D shape extracted from the 2D image that is projected onto the retina to create an accurate representation of the environment.
CHAPTER TWO

Purpose of the Research

Through the psychophysical, physiological, and neuroimaging investigations of the tilt aftereffect, spatial frequency tuning, and 2D contours, scientists have become reasonably confident that the extraction of 2D shape occurs early in the visual pathway. Evidence from 2D shape studies has also given possible clues to the nature of the perception of 3D shape. These neural mechanisms seem to be sensitive to properties of luminance, contrast, and illusory contours, but also appear to exhibit cue invariance (Li et al., 2008; Smith, Clifford, et al., 2001; Song & Baker, 2007), and further, they appear to be sensitive to local changes in line orientation (Dickinson et al., 2010; Gheorghiu & Kingdom, 2007). However, in some cases, these neural mechanisms have also exhibited qualities of position invariance (Suzuki & Cavanagh, 1998), and size and contrast invariance (Anderson et al., 2007).

Research Questions

With regard to 3D shape mechanisms, questions still remain. How similar are these mechanisms to the mechanisms that respond to 2D shape? Do they share similar characteristics of cue and position invariance? How selective are these neural mechanisms to features, such as texture pattern, spatial frequency, and position? How adaptable are these mechanisms to orientation flows that are defined by first and second order cues (i.e., changes in luminance, in contrast, and illusory contours)? Are these mechanisms adaptable to changes in spatial frequency greater than one octave? Is the adaptation of these neural mechanisms dependent upon retinal location? And finally, what can we infer from the properties of these neural mechanisms with
regard to where in the visual system they are located? Our research presented here addresses these questions using the paradigm of selective adaptation.

Specifically, the aims of this research were:

1) To characterize the pattern specificity of the neural mechanisms underlying the perception of 3D shape by using adapting and test stimuli in which the orientation flows are defined by luminance modulation, contrast modulation, and illusory contours.

2) To characterize whether neural mechanisms underlying the perception of 3D shape are invariant to differences in spatial frequency by adapting to stimuli that differ by a factor of three from test stimuli.

3) To characterize the position-selectivity of the neural mechanisms underlying the perception of 3D shape by retinally misaligning the adapting and test stimuli.

**Approach**

The goal of this research was to further characterize the nature of neural mechanisms in the visual system sensitive to the detection of 3D shape from texture. To address this goal, we used the psychophysical paradigm of visual adaptation.

**Visual Adaptation**

The fatigue model of visual adaptation operates under the premise that in the visual system there are neural mechanisms tuned to all different values of a particular property (e.g. amplitudes of concavity and convexity, or orientation, or spatial frequency). Adaptation to one value of a property (e.g., concavity) causes an imbalance in the visual system because the
mechanisms that prefer concave shape become briefly fatigued, whereas other mechanisms that do not prefer concavity are unaffected and thereby left relatively more sensitive to other stimuli (e.g., convexity [see Figure 9]).

**General Methods**

For each study, we first measured 3D shape perception in the absence of an adapting stimulus to obtain a baseline for shape perception and then compared baseline group means with group means from the data collected from each observer after adapting to concave and convex stimuli.

**Apparatus and presentation**

All stimuli were presented on a calibrated 22” Mitsubishi Diamond Pro 2070 flat screen CRT monitor with a 1024 x 768 pixel screen running at a refresh rate of 100 frames per second. The monitor is driven by a Cambridge Research Systems ViSaGe 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, preferred eye for all conditions. 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 were encouraged and allowed to take breaks as they felt necessary.
Baseline sessions were conducted first in random order within and across observers, followed by adaptation conditions that were randomized within and across observers.

**Stimuli**

Stimuli consisted of textured surfaces corrugated sinusoidally in depth, perspective images of which spanned 6.5° of visual angle. The stimuli used in the three experiments were comprised of one or more of the following three different surface textures: a luminance-modulated horizontal-vertical plaid (these stimuli were generated in full contrast grating and low contrast grating sets); a vertical full contrast grating contrast-modulated by a horizontal grating envelope of the same frequency; and an abutting grating illusory contour. The illusory contour stimuli were created by overlaying one pixel white lines on the white or black regions of the contrast modulated stimulus in alternating high contrast bands. To minimize effects of light adaptation, the contrast between the dark background and the white lines were such that the mean luminance of the illusory contour stimulus was equivalent to the mean luminance of the luminance and contrast modulated stimuli. Nine distinct corrugations were generated for each set (i.e., one texture pattern), 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) (see Figure 10 for an example of one set of stimuli). The two most curved stimuli of each set (+14 and -14 cm) were used as the adapting stimuli. All nine corrugations were used as test stimuli.

All textures were mapped onto sinusoidally corrugated surfaces using a carved volumetric solid texture mapping (Li & Zaidi, 2004). Orientation flows occur in projected images generated from this surface mapping while frequency modulations are minimized. We
specifically chose a texture mapping with minimal frequency modulations because we wanted to focus on the effects of orientation modulations in the absence of frequency modulations and we have shown previously that frequency modulations can be unreliable cues to depth, (Li & Zaidi, 2000, 2003, 2004). In this mapping, first the texture pattern is repeated along the depth axis to form a volumetric solid, and then the solid is carved sinusoidally in depth as a function of horizontal position. These textured carved corrugations are then projected in perspective into the image plane (see Figure 5).

Each stimulus image contained 1.5 cycles of the corrugation with either a central concavity or convexity. The mean luminance of all stimuli was held constant at 54 cd/m². A central fixation cross spanning 17x17 arc min was present on the monitor screen at all times.

**Procedures**

We assessed 3D shape perception by measuring the perceived flat point, which was defined as the curvature amplitude at which the surface appears neither concave nor convex. This was determined using a two-alternative forced-choice (2AFC) task within a constant stimulus paradigm. In this paradigm, 9 different curvature amplitudes were presented nine times each in random order for a total of 81 trials. For each stimulus presentation (which we defined as a trial) observers judged whether it appeared concave or convex.

All conditions began with a grey screen that was presented for 60 seconds in order to adapt observers to the mean luminance of all subsequently presented stimuli. In adaptation conditions (see Figure 11), this was followed by a two-minute adaptation to a concave or convex adapting stimulus. Then, a 200 ms inter-stimulus interval of the grey background was displayed, followed by one of the nine test stimuli from a single set presented at 200 ms (for the luminance
modulated, contrast modulated, and low contrast luminance modulated test stimuli) or 600 ms (for the illusory contour test stimuli). It was determined in preliminary trials that the extra time would be necessary for observers to perceive the shapes of the illusory contour stimuli. 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 then returned to the grey background until the observer responded whether the stimulus appeared concave or convex by pressing the appropriate button on the infrared response box. The number of times that convex was indicated by an observer for each of the nine presented curvature amplitudes was tallied by the experimental program. Once the response was recorded, in all subsequent trials of the adaptation condition, the adapting stimulus was presented for five seconds before each test stimulus to maintain the level of adaptation. Within each adaptation condition, a single adapting stimulus (e.g. concave contrast modulated stimulus) and a single set of test stimuli (e.g. luminance modulated stimuli) was used. Each adaptation condition lasted approximately 15 minutes.

In addition to the adapting conditions, for each set of test stimuli, baseline conditions were completed. The only difference between baseline and adaptation conditions was the presence of an adapting stimulus. The data from each completed condition comprised one data set, which consisted of the percentage of times the stimulus was reported as convex for each of nine different test curvature amplitude values.

**Observers**

For each experiment, five observers were recruited: two researchers (C. Filangieri and A. Li) and three naïve observers. All had normal or corrected-to-normal visual acuity. Observers
gave informed written consent to participate in the research, and the Institutional Review Board of the City University of New York approved all research.

Data Analysis

In each experiment, for each of the 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 generate a Weibull psychometric function (a response function that is illustrated as an S curve, and in this case, describes the relationship between each of the nine test stimuli and each observer’s perception of each stimulus) to fit each data set, and which was used to extract the observer’s perceived flat point -- the point at which the observer judged a stimulus to be physically flat (i.e., which was reported as convex 50% of the time). As an example, Figure 12 depicts data for one observer for the baseline and two adaptation conditions for a single set of test stimuli. Each curve represents data from a single condition.

The perceived flat point was estimated from the fit for each data set as the amplitude of corrugation that yielded convex responses on 50% of the trials. If there were 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 (i.e. all three curves would overlap). A negative shape aftereffect from adaptation to a convex surface (Figure 12, 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 and the greater the shift of the curve away from the baseline curve. A negative shape aftereffect elicited by adaptation to a concave
surface (Figure 12, 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. In all subsequent data plots, the magnitude and direction of shape aftereffects will be quantified by perceived flat points summarized in bar graphs like the one shown at the bottom of Figure 12.
CHAPTER THREE: Preliminary Experiment

Testing for Selectivity of Orientation Flow Patterns of 3D Shape Mechanisms

Recently, many have found psychophysical evidence for neural mechanisms that respond to both first and second order orientation cues (Cruickshank & Schofield, 2005; Hawley & Keeble, 2006; Paradiso et al., 1989; Smith, Clifford, et al., 2001; van der Zwan & Wenderoth, 1995). These results may be indicative of neural mechanisms sensitive to pattern-invariant 2D shape. Neurophysiological studies examining second order orientation cues have generally found that activation is greater in extrastriate cortex (Knebel & Murray, 2012; Montaser-Kouhsari et al., 2007; Song & Baker, 2007; von der Heydt et al., 1984). However, these studies employed 2D stimuli in which patterns were defined by luminance modulation, contrast modulation, orientation modulation, or illusory contours.

Li and Zaidi (2001, 2004) have provided evidence for neural mechanisms that extract information monocularly from visible orientation flows from surface curvature to reveal 3D shape. Furthermore, Li and colleagues (2008) have found that the mechanisms they have isolated appear to be pattern invariant, specifically for stimuli in which flows are defined by luminance (first order) and by illusory tilts (second order) created by a specific visual illusion. The goal of this experiment was to further investigate the nature of the pattern specificity of these neural mechanisms. Specifically, we were interested in determining whether 3D shape aftereffects can be obtained when orientation flows are defined by additional non-Fourier, second order contours (created by contrast modulations [see Figure 17, center panels] or offset lines [see Figure 17, right panels]), 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).

Li and Zaidi (2000) found that the visible contours along maximum lines of curvature that flow across a 3D surface in perspective projection are responsible for the accurate perception of 3D shape. In previous studies, Li and colleagues have shown that the neural mechanisms that are able to extract 3D information from these orientation flows are adaptable (Li & Zaidi, 2004), and 3D shape is conveyed perceptually even when the flows are illusory (Li et al., 2008). In this preliminary study, we were interested in determining to what extent those mechanisms are dependent upon the orientation flows running parallel to the surface curvatures, i.e., along lines of maximum curvature. In order to do this, we created a set of adapting stimuli in which there were two patterns of orientation, one flow that ran parallel to the surface curvature, and one flow that ran across the surface curvature at an oblique angle of 45°.

**Experimental Procedures**

**Apparatus and presentation**

All hardware, software, viewing conditions, response apparatus and data collection are the same as described in the General Methods section on page 28.

**Stimuli**

Two sets of adapting stimuli (which were each comprised of one concave and one convex stimulus at a single spatial frequency) were created using a luminance-modulated plaid tilted at an angle of 45° (see Figure 13 left and center panels), as well as a set of nine test stimuli that were comprised of luminance-modulated horizontal-vertical plaids at a spatial frequency of 2.6
cpd (Figure 13 right panel). All were generated and projected onto corrugated surfaces in the manner described in the General Methods section on page 28. One set of adapting stimuli was generated with a spatial frequency of 2.6 cpd. For this oblique plaid, we observed that the black and white checks of the plaid tend to be perceptually grouped to form second order contours (which in fact lie along the orientation flows of the texture). Since these flows, when visible, have been shown to convey accurate 3D shape (see Figure 14), in one set of adapting stimuli, we matched the spatial frequency of the luminance gratings of the test and the spatial frequency of the second order contours of the adapt. The spatial frequency of this set of adapting stimuli was calculated at 1.8 cpd, in order to match the frequency found along the contours of the horizontal-vertical stimuli. The formula for this calculation is as follows:

\[ SFO = \frac{SFHV}{\sqrt{2}} \]

Where SFO is the spatial frequency of the oblique plaid and SFHV is the spatial frequency of horizontal-vertical plaid (see Figure 15 for a comparison of the spatial frequencies).

**Procedure**

Observers were verbally instructed as to the nature of the experiment. Prior to hearing about the task, observers were asked to describe a concave and convex stimulus in their own words to ensure that they could correctly perceive the 3D shape they would be asked to judge.

Each observer ran a total of five conditions as described in the General Methods section: one baseline condition with no adapting stimulus and four adaptation conditions in which the oblique plaid stimuli (1.8 cpd and 2.6 cpd concave and convex) served as adaptors. The luminance-modulated horizontal-vertical plaids were test stimuli in all conditions.
Results

Data were fit using a Weibull function and perceived flat points were extracted as explained in General Methods. Perceived flat points averaged across the five observers are shown in Figure 16. Each panel plots the averaged perceived flat points, which were extracted by a Weibull psychometric function fitted to the data for the horizontal-vertical plaids in five conditions: Baseline, 1.8 cpd Oblique Plaid Convex Adapt, 2.6 cpd Oblique Plaid Convex Adapt, 1.8 cpd Oblique Plaid Concave Adapt, and 2.6 cpd Oblique Plaid Concave Adapt. Error bars represent 95% confidence intervals. The perceived flat point in the baseline condition did not vary significantly from physically flat (flat point = 0), indicating that observers were able to accurately perceive the 3D shape of the test stimuli: physically concave stimuli were perceived as concave, convex as convex, and flat as flat (see Figure 12, circle symbols for a visual representation). In the 1.8 cpd Oblique Plaid Convex adapting condition, modest positive shape aftereffects were obtained; in this condition, adapting to a convex stimulus caused a physically flat stimulus to appear convex. In all the other adapting conditions, the perceived flat points did not vary significantly from physically flat. This indicates that, in general, the neural mechanisms were not adapted, and in the condition that did elicit aftereffects, it appears that the adapting stimulus did not elicit an accurate percept of 3D shape. Thus, these adaptable mechanisms require orientation flows that run parallel to the maximum curvature of a surface.
CHAPTER FOUR: Experiment One

Testing for Pattern Invariance of 3D Shape Mechanisms

We have shown previously that adaptation seems to depend on the visible orientation flows that follow the maximum curvature of a 3D surface. However, the orientation flows along the maximum curvature in the oblique plaids are not defined by changes in luminance, they are second order contours -- created by the abutting black and white squares of the checkerboard pattern (see Figure 14), and it may be that these second order flows are not sufficiently visible to convey 3D shape. On the other hand, it may be the case that 3D shape neurons only respond to first order orientation flows. We addressed this preliminary finding in the following set of experiments in which we investigated more generally whether second order flows are able to activate 3D shape neurons, and to what degree adaptation is dependent upon texture pattern. To do this, we used stimuli in which the second order flows were visible enough along the lines of maximum curvature to accurately convey 3D shape. Thus, they would be able to be used as adapting and test stimuli, and from this we would be able to determine in what conditions aftereffects may occur.

Experimental Procedures

Apparatus and presentation

All hardware, software, viewing conditions, response apparata and data collection are the same as described in the General Methods section on page 28.
Stimuli

Four sets of test stimuli were created as described in the General Methods section on page 28 using three different surface textures: a full contrast 2.6 cpd luminance-modulated horizontal-vertical plaid (LM); a low contrast 2.6 cpd luminance-modulated horizontal-vertical plaid; a 2.6 cpd vertical full contrast grating contrast-modulated by a horizontal grating envelope of the same frequency (CM); and an abutting grating illusory contour stimulus (IC) (see Figure 17 for examples of the stimuli).

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 present in the CM adapting stimulus, such that, for example, the mean luminance of the black-white check contours of the CM stimuli could be different from that of the interleaved grey contours of the CM stimuli. These artifacts can occur due to imperfections in the display monitor, and since the CM and LM stimuli were the same spatial frequency, any artifacts present in the CM stimuli, could hypothetically be adapting simple cells. 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. For comparison, we included the low contrast (10%) LM stimuli to see if luminance artifacts could explain these results. The 10% contrast was chosen as a control comparison with the CM stimulus because we believe any luminance artifact in the CM stimulus should be substantially less than 10%. Indeed, the luminance artifacts found in Zhou and Baker (1994) for comparable displays were estimated to be no greater than 0.6%. Given the contrast levels used in the CM stimuli, any luminance artifacts resulting from the monitor would be substantially less than 10% contrast.
Stimuli were presented in circular apertures 6.5° in diameter to minimize the possibility that 3D shapes could be perceived based on systematic orientation differences between the texture patterns and the straight sides of a square aperture.

For each condition, 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, to rule out the influence of local adaptation.

**Procedure**

Observers were verbally instructed as to the nature of the experiment with the help of a document that included descriptions of the purpose of the study, the task they were asked to perform, examples of the different stimuli, and a flow chart of how each trial in both the baseline and adaptation conditions was to be presented (see Appendix A). Prior to hearing about the task, observers were asked to describe the different stimuli in their own words to ensure that they could correctly perceive the 3D shape they would be asked to judge.

Each observer ran a total of 32 conditions as described in the General Methods section: four baseline conditions (one baseline for each type of stimulus), eight adaptation conditions each for each set of test stimuli (one concave and one convex adapting condition for each type of stimulus), and four adaptation conditions for the low-contrast control stimuli (see Table 1 for conditions). The task in all the conditions was to judge whether the center of the test stimulus presented appeared convex or concave. Baseline conditions for each set of test stimuli were run prior to the adaptation conditions in order to determine shape percepts in the absence of adaptation.
Results

A least-squares procedure was implemented to generate a Weibull function fit to each data set and perceived flat points were extracted as explained in General Methods. Perceived flat points averaged across the five observers are shown in Figure 18. (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 (see Figure 12, square symbols for an example) and adaptation to concave stimuli produced a shift of the averaged perceived flat point towards negative (concave) values (see Figure 12, triangle symbols for an example).

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 (Figure 18A, black bars). Results for CM tests (Figure 18B) 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 (Figures 18A and 18B), when used as tests, they were strongly affected by adapting stimuli of all types (Figure 18C). 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 (Figures 18B and 18C).

If the CM stimuli were encoded purely because 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 (Figure 18A), both CM and low contrast LM adapting stimuli elicited aftereffects of about the same magnitude. Similarly, for CM tests (Figure 18B), 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 adapt; however, no shape aftereffects were obtained in this condition.

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 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 (Figures 18A and 18B) 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 (3D). As in the original experiment, stimuli spanned 6.5 deg, and were separated by a gap of 1 deg. 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, so that for each pairing, each texture pattern was presented on the left and on the right of the stimulus. Five observers (two of three original naïve observers along with another naïve observer and the two authors) ran one condition in which the 12 stimuli were each presented six times in random order. At the start of the condition, each observer adapted for 60 s 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.

Figure 19 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. 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.

Summary

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.
CHAPTER FIVE: Experiment Two

Testing for Invariance to Spatial Frequency of 3D Shape Mechanisms

It is generally accepted that neural mechanisms found in V1 are sensitive to spatial frequencies within an octave of the cell’s preferred frequency (Blakemore & Campbell, 1969; Campbell & Robson, 1968; K. K. De Valois, 1977), and these mechanisms do not respond to stimuli with spatial frequencies that are three times higher or one third lower than their preferred frequencies (Blakemore & Campbell, 1969; Tolhurst, 1972), indicating that they have relatively narrow bandwidth tunings. However, the relationship between neural mechanisms that are sensitive to second order cues is more complex. Some have found evidence for invariance to changes in spatial frequency (Landy & Oruç, 2002), while others have found that whether or not a second order mechanism exhibits invariance or selectivity is contingent upon the cycles per degree, with mechanisms responding to lower spatial frequencies appearing to be more narrowly tuned, and those that respond to higher spatial frequencies showing invariance, or broader tuning (Zhan & Baker, 2008). Others have characterized these disparities as evidence for more narrowly tuned, simple channels comprised of linear filters (Campbell & Robson, 1968) and more broadly tuned, complex channels, which include both linear and nonlinear filters (Graham et al., 1993). However, it appears that the role spatial frequency plays in the perception of 3D shape from texture has not been extensively studied. Li and colleagues (2008) reported preliminary evidence that neural mechanisms sensitive to 3D shape defined by luminance-modulated horizontal-vertical plaids show invariance to frequency in some conditions but not others, and to date, no one else has investigated to what extent
the neural mechanisms sensitive to 3D shape that exhibit pattern invariance are sensitive to changes in spatial frequencies.

In this study, as in Li and colleagues (2008), we were interested in investigating the extent to which the neural mechanisms selective for 3D shape, as conveyed by luminance defined orientation flows, are invariant to spatial frequencies that differ by a magnitude of three. As a more stringent test of the effectiveness of orientation flows in conveying 3D shape, we used circular apertures on our stimuli. In Li and colleagues’ study, the stimuli apertures were square, and thus it was possible that observers were able to compare orientation flows with the straight edges of the stimuli. Using circular apertures causes 3D shape to be conveyed by perceived orientation changes along the orientation flows, and prevents comparing those changes to straight edges. Additionally, we were interested in determining whether 3D shape aftereffects can be obtained in stimuli with orientation flows defined by second order contours when adapting to a luminance-modulated stimulus of a spatial frequency that is three times greater than the test stimuli. The transfer of aftereffects between adapting and test stimuli that differ in first- vs. second order contours and a large spatial frequency magnitude would further strengthen the evidence for pattern-invariant 3D shape-selective mechanisms.

**Experimental procedures**

**Apparatus and presentation**

All hardware, software, viewing conditions, response apparata and data collection are the same as described in the General Methods section on page 28.
Stimuli

Four sets of test stimuli were used, three sets that were generated as stimuli for Experiment One (a full contrast 2.6 cpd luminance-modulated horizontal-vertical plaid [LM]; a 2.6 cpd vertical full contrast grating contrast-modulated by a horizontal grating envelope of the same frequency [CM]; and an abutting grating illusory contour stimulus [IC]) (see Figure 17). A new set of full contrast LM horizontal-vertical plaids was generated in the same manner as described in the General Methods section on page 28 with a spatial frequency of 8.2 cpd (See Figure 20, left panel). As in Experiment One, all stimuli were presented in circular apertures 6.5º to minimize the possibility that 3D shapes could be perceived based on systematic orientation differences between the texture patterns and the straight sides of a square aperture.

For each of the eight adapting conditions, the corrugation amplitude (and sign) of the adapting stimulus was different from eight of the nine test stimuli, and for six of the adapting conditions the spatial frequency of the adapting stimulus differed from the text stimuli by a multiple of greater than three. This ensured that the orientation flows of the adapting and test stimuli would almost always be retinally misaligned and ruled out the influence of local adaptation.

Procedure

Observers were verbally instructed as to the nature of 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 conditions were to be presented (see Appendix B). Prior to hearing about the task,
observers were asked to describe the different stimuli in their own words to ensure that they could correctly perceive the 3D shape they would be asked to judge.

Each observer ran a total of nine conditions as described in the General Methods section on page 28: one baseline condition for the 8.2 cpd luminance-modulated stimuli, and eight adaptation conditions: two (one concave and one convex 8.2 cpd luminance-modulated adapting stimulus) for each set of 2.6 cpd contrast-modulated, 2.6 cpd luminance-modulated, 8.2 cpd luminance-modulated, and illusory contour test stimuli (see Table 2 for conditions).

**Results**

As in the previous two experiments, for each of the nine data sets per observer, the percentage of trials reported as convex was plotted vs. the curvature amplitude of the test stimulus, quantified in centimeters, and a least-squares procedure was implemented to fit a Weibull function to each data set.

If the neural mechanisms underlying 3D shape perception are invariant to changes in spatial frequency, then we would expect to see negative shape aftereffects in every adaptation condition: adaptation to centrally convex stimuli would result in a shift of the averaged perceived flat point towards positive (convex) values and adaptation to centrally concave stimuli would produce a shift of the averaged perceived flat point towards negative (concave) values.

Data averaged across the five observers in each condition are presented in Figure 21. Each panel plots the averaged perceived flat points for each test stimulus class (2.6 cpd luminance modulated plaid [LSF LM], 2.6 cpd contrast modulated plaid [CM], illusory contour [IC], and 8.2 cpd full contrast luminance modulated plaid [HSF LM]) as affected by each of the adapting stimuli (convex or concave HSF LM stimulus). Error bars represent 95% confidence
intervals, and 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 of the test stimuli (three baseline data sets were used from Experiment One: LM, CM, and IC). Although there was a slight bias toward convexity in the LM baseline condition, the perceived flat points in the baseline conditions did not vary significantly from physically flat (perceived flat point = 0 cm). This indicates that observers were able to accurately perceive the 3D shapes.

In each adaptation condition (LM, CM, IC, and HSF LM) negative shape aftereffects were obtained, meaning that adaptation to a centrally convex stimulus resulted in a shift of the averaged perceived flat point towards a convex amplitude (which is represented as a positive value), and adaptation to a concave stimulus resulted in a shift of the averaged perceived flat point towards a concave amplitude (represented as a negative value) (see Figure 21).

If the adapted mechanisms were sensitive to a difference in spatial frequency by a factor of three, then we would expect to only observe aftereffects in the conditions in which the spatial frequency of the test stimuli was equal to that of the adapting stimuli. However, this was not the case. Even so, the magnitude of the aftereffects in the conditions in which there was a difference in spatial frequencies was not as strong as the magnitude of the aftereffects in the condition in which the spatial frequency of the test stimuli matched that of the adapting stimuli.

Summary

These results suggest that the neural mechanisms we’ve isolated exhibit both pattern invariance and have broad spatial frequency tuning (by at least a factor of three). Shape aftereffects were elicited in 2.6 cpd LM, CM and IC test stimuli when adapted to an 8.2 cpd LM stimulus.
CHAPTER SIX: Experiment Three

Testing for Position-Selectivity of 3D Shape Mechanisms

In their 2007 study, Anderson and colleagues found evidence for mechanisms that code for 2D shape and are invariant to position, contrast, and size. Using radial frequency patterns, the authors were able to elicit shape aftereffects when the adapting pattern and test stimuli were different frequencies but shared the same radius, differed in contrast by 80%, and differed in size by a factor of four. Other researchers have found evidence for position invariance in higher levels of visual processing, particularly in neural mechanisms that are sensitive to faces (Rhodes, et al., 2004). In their study, the researchers varied the size magnitude between the adapting and test stimuli by a factor of two and obtained negative shape aftereffects. Furthermore, Suzuki (2005) showed evidence that adapting to misaligned contours generated aftereffects in predicted directions. However, little, if any, research exists examining the position selectivity of the neural mechanisms underlying our perception of simple 3D shapes.

In this study, we were interested in investigating the extent to which the neural mechanisms selective for 3D shape are invariant to the retinal position of the stimulus. To address this question, we spatially misaligned the adapt and test stimuli so that retinal locations stimulated by the adapting curvatures were different from the retinal locations stimulated by the test curvatures. Specifically, we were interested in testing if aftereffects can be obtained from orientation flows that convey depth in vertical corrugations, stimuli in which the depth varies as a function of horizontal position (see Figure 22A), when the adapting images are misaligned from test images either laterally (to the left or to the right) or vertically (to the top or to the
bottom) by 2°. This misalignment is roughly equivalent to ½ cycle of corrugation (see Figure 22A, panels 1, 2 and 3). In the laterally misaligned adapting conditions, the area of the retina being adapted is exposed to one of the curvatures flanking the central curvature, which is the opposite sign of the central curvature of the adapting stimulus (see Figure 22A, panel 3). In the vertically misaligned conditions, the curvatures presented to the retinal adapting and test locations are the same sign as the central curvatures used in the aligned conditions.

If these mechanisms are position invariant, then we would expect to obtain shape aftereffects in the opposite direction of the shape of the adapting stimulus (negative shape aftereffects), regardless of the position of the adapting stimulus (see Figure 23 top panel). However, if these mechanisms are position selective, for the vertical corrugations, we would expect to obtain negative shape aftereffects in the vertically misaligned conditions, and in the laterally misaligned conditions, we would see positive shape aftereffects (shape aftereffects in the same direction as the shape of the adapting stimulus) (see Figure 23 middle panel).

We also tested analogous conditions using horizontal corrugations, stimuli in which the depth of the surface varies as a function of vertical position (see Figure 22B). Likewise, in the horizontally corrugated stimuli, if these neural mechanisms are position-selective, we would expect to see positive shape aftereffects for vertically offset stimuli, and negative shape aftereffects for horizontally offset stimuli (see Figure 23, bottom panel).

**Experimental procedures**

**Apparatus and presentation**

All hardware, software, viewing conditions, response apparata and data collection are the same as described in the General Methods section on page 28. However, in this experiment, in
addition to conditions in which the adapting and test stimuli were presented centered, the adapting stimuli were also presented misaligned 2° vertically or laterally.

**Stimuli**

Two sets of test stimuli were created using a full contrast 2.6 cpd luminance modulated horizontal-vertical plaid as described in the General Methods section on page 28. In this experiment, for one set of stimuli, the depth of the corrugations will be varied as a function of horizontal position, creating a vertical corrugation, and for the other, the depth of the corrugations will be varied as a function of the vertical position, creating a horizontal corrugation. For vertical corrugations, the orientation flows of the horizontal component of the texture convey differences between concavities and convexities (Li et al., 2008; Li & Zaidi, 2000, 2004). Similarly, for horizontal corrugations, we expected that the orientation flows of the vertical component of the texture would serve the same role. Unlike our first experiment, these stimuli were square. They were not presented with circular apertures out of concern that in the misaligned conditions there would be too little stimulus falling into the foveal region to generate robust aftereffects.

Each observer ran a total of 22 conditions as described in the General Methods section, two baseline conditions, and 20 adaptation conditions (see Table 3 for conditions). For 16 of the 20 adaptation conditions, the adapting stimulus and test stimuli were misaligned by 2° of the visual angle (See Figure 22A and 22B, panels 1, 2, and 3). In each of the conditions in which the adapting stimulus was not misaligned, the corrugation amplitude 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, in order to rule out local adaptation.
Procedure

Observers were verbally instructed about the experiment with the help of a document that included descriptions of the purpose of the study and the task they were being asked to perform (see Appendix B). Prior to instruction, observers were asked to describe examples of concave and convex stimuli in their own words to ensure that they were perceived as 3D in the correct direction.

In both the vertical corrugation and the horizontal corrugation conditions, each observer ran a total of 11 conditions as described in the General Methods section on page 28. For each of the two sets of stimuli, there was one baseline condition and 10 adaptation conditions: two in which the adapting stimuli were presented in the same location as the test stimuli, four in which the adapting stimuli and test stimuli were vertically misaligned by 2º, and four in which the adapting stimuli and test stimuli were laterally misaligned by 2º. In the misaligned conditions, lateral misalignment of the vertical corrugations and vertical misalignment of the horizontal corrugations were considered Opposite Axis conditions, because the axis of depth of the corrugation is perpendicular to the misalignment in those conditions. Vertical misalignment of the vertical corrugations and lateral misalignment of the horizontal corrugations were considered Same Axis conditions, because the axis of depth matched (was parallel to) the misalignment in those conditions.

Results

In both types of stimuli (vertical corrugations and horizontal corrugations), for each of the 11 data sets per observer, the percentage of trials reported as convex was plotted vs. the curvature amplitude of the test stimulus, which was quantified in centimeters. As in the previous experiments, a least-squares procedure was implemented to fit a Weibull function to each data set.
If the neural mechanisms underlying 3D shape perception are position-invariant, then we would expect to see negative shape aftereffects in every adaptation condition: adaptation to centrally convex stimuli would result in a shift of the averaged perceived flat point towards positive (convex) values, and adaptation to centrally concave stimuli would produce a shift of the averaged perceived flat point towards negative (concave) values (Figure 23, top panel). However, if the adapted mechanisms are position-selective, then we would expect to see a different pattern of results. Figure 22 helps to illustrate these predictions. Since the stimuli contain 1.5 cycles of a sinusoidal corrugation (each peak and trough is $\frac{1}{2}$ cycle), the central curvature is flanked symmetrically on both sides by curvatures of the opposite sign (i.e., a stimulus with a centrally convex curvature is flanked on either side by concave curvatures). The amount of misalignment of the test and adapting stimuli was chosen specifically so that the central visual field would be locally adapted by one of these flanking curvatures of the opposite sign. This occurred specifically when the axis of depth change along the corrugation and the axis of misalignment matched, that is: 1) for vertical corrugations in which depth varied as a function of horizontal position, when the test and adapting stimuli were misaligned along the horizontal axis (Figure 22A, panel 3), and 2) for horizontal corrugations in which depth varied as a function of vertical position, when the test and adapting stimuli were misaligned the vertical axis (Figure 22B, panel 2). If the mechanisms are position-selective, we would expect positive shape aftereffects due to adaptation to these flanking curvatures in these conditions rather than negative shape aftereffects to the central curvature of the adapting stimulus. For example, if the adapting stimulus were centrally convex, misalignment would cause foveal adaptation to one of the concave flanks, which would in turn cause a flat test stimulus to appear convex. As a control, we also examined conditions in which the axis of depth change and the axis of misalignment were perpendicular (vertical misalignment in corrugations
whose depth varies as a function of horizontal position, and lateral misalignment in corrugations whose depth varies as a function of vertical position). In these conditions, the misalignment does not result in foveal adaptation to a flanking curvature, but rather to a displaced central curvature (Figures 22A, panel 2 and 22B, panel 3). Thus, the sign of the adapting curvature is the same as the aligned condition. For example, when a vertical adapting convex corrugation is shifted vertically, the central visual field is still adapted to a convex curvature but in general less of the visual field is adapted. Thus, in these conditions, we would predict negative shape aftereffects, possibly of lesser magnitude than those found in conditions in which the test and adapting stimuli are aligned (Figures 22A, panel 1 and 22B, panel 1), because in the misaligned conditions the central retinal region is exposed to approximately 33% less adapting stimulus than in the aligned conditions. Thus, in summary, for position-selective mechanisms, we predict positive shape aftereffects in opposite axis conditions -- when the adapting stimulus and test stimuli are misaligned laterally in the vertical corrugation conditions (Figure 23, middle panel, red bars), and when the adapting image and test stimuli are misaligned vertically in the horizontal corrugation conditions (Figure 23, bottom panel, blue bars). Additionally, we predict negative shape aftereffects in same axis conditions -- when vertical corrugations are misaligned vertically (Figure 23, middle panel, blue bars) and horizontal corrugations are misaligned laterally (Figure 23, bottom panel, red bars).

Data averaged across the five observers in each condition are shown in Figure 24. Each panel plots the averaged perceived flat points for each test stimulus condition (Aligned, Vertically Misaligned, and Laterally Misaligned) as affected by each of the adapting stimuli (Convex or Concave). 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. In both baseline conditions, the
perceived flat point did not vary significantly from physically flat (perceived flat point = 0 cm). This indicates that observers accurately perceived the 3D shapes.

For both the vertical and horizontal corrugations, negative shape aftereffects were not surprisingly obtained in both the aligned adaptation conditions, meaning that adaptation to a centrally convex stimulus resulted in a shift of the averaged perceived flat point towards a convex amplitude (positive value), and adaptation to a concave stimulus resulted in a shift of the averaged perceived flat point towards a concave amplitude (negative value) (see Figure 2, purple bars). In the same axis conditions, negative shape aftereffects were obtained in the vertical corrugations when adapting to both convex and concave stimuli and in the horizontal corrugations when adapting to a concave stimulus only see Figure 2, top panel, blue bars and bottom panel, red bars). In the opposite axis conditions, positive shape aftereffects were obtained in both the horizontal and vertical corrugations when adapting to both convex and concave stimuli, meaning that adaptation to a centrally convex stimulus resulted in a shift of the averaged perceived flat point towards a concave amplitude (negative value), and adaptation to a concave stimulus resulted in a shift of the averaged perceived flat point towards a convex amplitude (positive value) (see Figure 2 top panel, red bars and bottom panel, blue bars). These results are consistent with neural mechanisms that are position selective.

The aftereffects we obtained in the misaligned conditions were consistently smaller than the aftereffects that were obtained in the aligned condition. This is not unexpected, as approximately 33% less of the central visual field was being adapted to the corrugations in the misaligned conditions. We were interested in quantifying that difference by comparing the aftereffects obtained in each of the misaligned conditions to the appropriate aligned condition, by computing a ratio from the perceived flat points. What this means is that the perceived flat point
for each condition in which we obtained negative shape aftereffects was compared to the analogous aligned condition (i.e., we compared the vertically misaligned vertical corrugation convex adaptation condition to the aligned vertical corrugation convex adaptation condition). However, for each condition in which we obtained positive shape aftereffects, those aftereffects were compared to the aftereffects obtained in the opposite adapted condition (i.e., we compared the laterally misaligned horizontal corrugation convex adaptation condition to the aligned horizontal corrugation concave adaptation condition). This is because the area adapted in the conditions in which we obtained positive aftereffects was in the opposite sign of the central corrugation of the adapting stimulus. The results of our calculations, presented in Table 4, quantify the differences in magnitude. While the magnitude of aftereffects in the misaligned conditions was consistently smaller than in the aligned conditions, there is considerable variability in the magnitudes of difference. For example, the aftereffect in the vertically misaligned convex adapting condition of the vertical corrugations was only 15% of the magnitude of the aftereffect in the aligned condition, which is about half of what would be predicted, based on the 33% reduction of retinal area exposed to the adaptation stimulus. However, upon inspection of the area of the adapting stimulus being presented foveally (i.e., the top 1/3 or bottom 1/3 of the stimulus), the orientation flows are identical to the opposite side of the adapting image of the opposite curvature. For example, as shown in Figure 25, the orientation flows in bottom third of the convex stimulus are identical to the orientation flows in top third of the concave stimulus. This ambiguity with regard to the sign of the stimulus that is being adapted, in addition to less overall stimulus falling over central vision, is likely to have affected observers’ percepts.

In the laterally misaligned concave vertical corrugation adapting condition, which was also compared to the aligned convex vertical corrugation adapting condition, the magnitude of
the aftereffects (64%) was nearly twice what would be predicted. This may simply be due to a natural bias toward convexity. These explanations, however, cannot explain all the variation that was found.

Summary

These results suggest that the neural mechanisms we isolated in this experiment are position selective. In vertical corrugations, when adapting to concave stimuli, negative shape aftereffects were found in the vertically misaligned condition and positive shape aftereffects were found in the laterally misaligned condition. In the horizontal corrugations, negative shape aftereffects were found in the laterally misaligned condition when adapting to a concave stimulus. This suggests that the neural mechanisms that code for 3D shape appear to be sensitive to shifts in position that span a single convexity or concavity, in the case of this experiment, $2^\circ$ of the visual angle. Furthermore, the position selectivity appears to be more consistent within vertical corrugations, which may be indicative that there are more neurons in the visual system that are tuned to vertical orientations. The position selectivity also seems more specific for concave adapting stimuli, consistent with a perceptual bias toward convexity that has been found by other researchers (Mamassian & Landy, 1998; Liu & Todd, 2004; Sherman, Papathomas, Jain & Keane, 2011; Bertamini, Helmy & Hulleman, 2013; Adams & Elder, 2014). This has led many to conclude that there may be a natural bias for processing convexity, and one reason for this bias could be that we are more likely to encounter convex shapes in our environment. Finally, the aftereffects obtained in the aligned conditions may be stronger than those obtained in the misaligned conditions because there is less curvature that is being adapted to in the misaligned conditions, simply as a result of the misalignment.
CHAPTER SEVEN

Discussion

Experiment One

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).

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 (Figure 18B & 18C).

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 (Grosol et al., 1993, Sheth et al., 1996; Hirsch et
al., 1995), and in and beyond V2 (Mareschal & Baker, 1998b; Leventhal et al., 1998; Song &
Baker, 2007; Zhan & Baker, 2006). We cannot rule out the possibility that adaptation of arrays of
these pattern-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 (Sary, 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-Kouhsari 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 pattern 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 across pattern types 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 extrastriate 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 concave 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 adapts 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 (Paradiso et al., 1989; van der Zwan & Wenderoth, 1995; Smith et al., 2001; Cruickshank & Schofield, 2005). In addition, although CM and IC orientation flows conveyed correct 3D shape, our observers anecdotally 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 (Figure 19). 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 (Figure 18A), while still accounting for the robust aftereffects obtained with IC adapting and test stimuli (Figure 18C). 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 pattern-invariant neurons in extrastriate 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 (Suzuki, 2001; Clifford & Weston, 2005; Anderson, Habak, Wilkinson & Wilson, 2007). 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 extrastriate 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 pattern-invariant 2D form. However, it does appear that pattern invariance plays an important role in the processing of both 2D and 3D shapes.
Experiment Two

In this experiment we were interested in determining if the 3D shape mechanisms we isolated in experiment one, that are pattern invariant, are able to be adapted by stimuli with spatial frequencies that are greater than a multiple of three. If these 3D shape mechanisms are adaptable, it would provide further support that they are located beyond V1, where cells do not respond to changes in spatial frequency that differ by a factor of three (Blakemore & Campbell, 1969; Tolhurst, 1972; Campbell, Cooper, & Enroth-Cugell, 1969; R. L. De Valois et al., 1982; Movshon & Lennie, 1979).

Our findings suggest that pattern invariant 3D shape mechanisms are adapted by LM horizontal-vertical textures that differ in spatial frequency by a factor of three, indicating that the locus of these mechanisms is beyond V1. With regard to second order mechanisms, some have found evidence for broadly tuned channels (Landy & Oruç, 2002), while others have found that the mechanisms are tuned to frequencies that do not differ by more than a multiple of two in bandwidth (Foster, Gaska, Nagler, & Pollen, 1985; McGraw, Levi, & Whitaker, 1999), and there is evidence that the locus of neural response to second order stimuli can shift between V1 and V2 depending upon the spatial frequency of the stimulus (Zhan & Baker, 2008). One limitation to these studies, however, is that they all rely on 2D stimuli; our stimuli contain 3D shape modulations. Even though there is evidence for second order mechanisms in V1, they still cannot explain our findings. This is because second order mechanisms in V1 are more likely to be activated by very low spatial frequencies (Hallum, Landy, & Heeger, 2011; Zhan & Baker, 2008); far lower than our 8.2 cpd adapting stimuli, which induced aftereffects on lower spatial frequency second order test stimuli.
Experiment Three

In the first two experiments, we’ve shown that neural mechanisms able to extract orientation flows and thus lead to accurately perceived 3D shape exhibit pattern invariance and can tolerate differences in spatial frequency of at least a factor of three. In this study, we were interested in testing the position selectivity or position invariance of neural mechanisms that are adaptable to LM plaid.

Our results suggest that the mechanisms we’ve isolated are position selective. Shape perception tested foveally was only affected by adapting curvatures that were presented foveally and not by adapting curvatures that were presented peripherally. For example, when the central curvature of the corrugated stimulus fell over the adapting location, negative shape aftereffects were obtained. This happened with the vertical corrugations in the vertically misaligned conditions (Figure 24, top panel), and only in the concave condition of the horizontal corrugation in the laterally misaligned condition (Figure 24, bottom panel). However, when the flanking curvature of the corrugated stimulus fell over the adapting location, the aftereffects obtained were positive -- in the same direction as the central curvature. This was the case in the in the vertically misaligned horizontal corrugation conditions (Figure 24, bottom panel) and in the laterally misaligned vertical corrugation conditions (Figure 24, top panel).

Notably, the aftereffects obtained in the misaligned conditions were consistently smaller than in the aligned conditions (see Table 4). The most parsimonious explanation for this is that a smaller population of neurons was initially adapted in the misaligned conditions, due to less of the adapting stimulus falling over the adapting region, however, this does not explain the variability of the magnitudes found in the aftereffects of the misaligned conditions. One explanation for this is the ambiguous nature of some of the adapting stimuli (see Figure 25).
Another explanation for the variability may be a natural bias for convexity. Overall, larger aftereffects were elicited from neural mechanisms that were adapted to concave stimuli than those that were adapted to convex stimuli. In discrimination tasks, it has been shown that observers exhibit a bias toward convexity (Liu & Todd, 2004; Mamassian & Landy, 1998; Pasupathy & Connor, 2002), and this bias persists when judging shape deformities in motion contours (Barenholtz, 2010). Furthermore, the bias toward convexity has been detected by neuroimaging (Haushofer, Baker, Livingstone, & Kanwisher, 2008). Our results also suggest a bias toward convexity and may possibly be indicative of the existence of a greater number of adaptable neurons that are sensitive to 3D convexities. If this is the case, when fatiguing mechanisms that are sensitive to concave shape, the aftereffect would be stronger toward convexity, as the imbalance created in the visual system would be greater (i.e., in general there would be a smaller population responding to the concavities), and the shift in psychometric function away from zero would be larger. Likewise, if there is a larger population of neurons sensitive to convexities, it is possible that not all of the population preferring convex shape would be fatigued when exposed to convex stimuli. Thus the imbalance in the visual system when adapting to convex stimuli would not be as great, and subsequently, the shift in psychometric function away from zero would be smaller.

We also found that adaptation aftereffects were generally larger in the horizontal corrugation conditions. It is well established that visual acuity is improved around the cardinal orientations (i.e., vertical and horizontal) (Appelle, 1972; Durgin & Li, 2011; Girshick, Landy, & Simoncelli, 2011). Others have shown there is an overrepresentation of neural mechanisms that prefer horizontal orientations in early visual cortex as well as in the middle temporal visual region (Li, Peterson, & Freeman, 2003; Sun et al., 2012). The horizontally corrugated stimuli we
created are comprised of orientation flows that run parallel to the *vertical* axis, whereas the vertically corrugated stimuli we created contain orientation flows that run parallel to the *horizontal* axis. In consideration of this, it is reasonable to suggest that the smaller aftereffects in the vertical corrugations may be a direct result of a greater number of mechanisms preferring horizontal orientations: For the vertical corrugations, horizontally tuned mechanisms are fatigued, but if there are more of them than vertically tuned mechanisms, after adaptation, the imbalance in the visual system may be overall less (and the aftereffects may thus be more modest) than the imbalance that occurs after adapting to the vertical orientation flows found in the horizontal corrugations.

Some have found evidence for cells selective for 2D curvature in V2 (Hegdé & Van Essen, 2000) and in V4 (Habak, Wilkinson, Zakher, & Wilson, 2004) and selective to photographic representations of objects (Rust & DiCarlo, 2010) that also exhibit limited position invariance (i.e., tolerated changes in position that spanned up to approximately 1.5º of the viewing angle). While the neural mechanisms we’ve isolated show position selectivity, our misalignment spanned 2º of the viewing angle; subsequently, we are not able to rule out V4 as a possible locus for these mechanisms.
CHAPTER EIGHT

Conclusions

We have found evidence for 3D shape mechanisms that are able to extract 3D information when orientation flows that follow the lines of maximum curvature are visible. These mechanisms appear to be pattern-invariant, in that they are activated by changes in luminance, by changes in contrast, and by textures such as illusory contours. We have also found that pattern invariant 3D shape mechanisms can be adapted by stimuli that differ in spatial frequency from test stimuli by a factor of three. However, 3D shape mechanisms that are adapted by luminance cues appear to be sensitive to shifts in stimulus position of 2°, corresponding to a half cycle of sinusoidal corrugation.

Overall, these findings place 3D shape mechanisms in extrastriate cortex. However, their exact location remains unknown. Even so, there are clues to where these mechanisms may possibly be located. We know that most mechanisms in V1 respond to changes in luminance, are selective for spatial frequencies, do not respond to changes in spatial frequency beyond a multiple of three (Blakemore & Campbell, 1969; Campbell, Cooper, & Enroth-Cugell, 1969; Campbell & Robson, 1968; De Valois, 1977; Foster, Gaska, Nagler, & Pollen, 1985), and there is evidence that some cells in V1 respond to second order cues. Furthermore, we know that most neurons that respond to second order cues are located in extrastriate cortex; however, some have suggested that cells in V2 can respond to luminance as well as non-Fourier cues (Paradiso, Shimojo, & Nakayama, 1989).

The position selectivity of the neural mechanisms suggests that they are retinotopically organized, perhaps placing them at or earlier than V4, which has been shown to have mechanisms that tolerate changes in position up to 1.5° of stimulus position (Rust & DiCarlo,
and also mechanisms that are selective for 2D curvature (Pasupathy & Connor, 2002) and 3D shape (Sharpee, Kouh, & Reynolds, 2013).

The diversity of locations in which these neural mechanisms appear to reside may be a reflection of the diversity of the stimuli used across the experiments whose findings have been mentioned in this thesis (i.e., curved contours, shading, specular highlights, radial frequency patterns, Cartesian and non-Cartesian [irregular] grids, sinusoidal gratings and plaids, etc.) and which also varied in retinal size.

However, another possibility remains. It could be that the visual system does not operate as a clear, hierarchical system. Recently, some have found evidence for recurrent processing in V1 and V2 after activation of the LOC (Koivisto, Revonsuo, Vanni, & Salminen-Vaparanta, 2011). There is even evidence that feedback from extrastriate cortex to V1 occurs before the time-course of object recognition, which is approximately 150 ms (Wyatte et al., 2014). The nature of recurrent processing remains largely unknown (Crouzet & Cauchoix, 2011), although some have suggested that it plays an important role in object recognition when a stimulus is degraded in some respect (e.g., occluded) or ambiguous in nature (Wyatte, Jilk & O’Reilly, 2014). Others have hypothesized that neural inhibition of competitive stimuli, in conjunction with top-down feedback, facilitates the processing of the most relevant information (Wyatte, Herd, Mingus, & O’Reilly, 2012).

In this type of system, attention appears to play a significant role in both shaping neuronal responses and processing along the visual pathway. Even the simplest perceptual tasks require attention and, therefore, top-down processing. In order to judge a feature, we not only must perceive it, but we must attend to it. It has been a long-held belief that neural mechanisms located early in the visual pathway were engaged in automatic perceptual processes. These
processes by nature are relatively stable and were therefore thought to be impervious to the influence of attention, which is traditionally associated with high-level cortical processes. However, recently attention studies have shown evidence for attention enhancing as well as inhibiting low-level perception (Neill, Valdes, & Terry, 1995; Murray, Kersten, Olshaussen, Schrater, & Woods, 2002). In the case of our work, it may be that attending to stimuli presented foveally attenuated the influence of peripheral information. This would be particularly evident in the results of our third study, where opposite axis misalignments elicited positive shape aftereffects -- in the same direction of the sign of the central curvature of the stimulus, which was presented peripherally. It may be that attending to the central curvature presented peripherally would elicit negative shape aftereffects even when the curvature presented foveally is the opposite sign of the central curvature.

There is evidence that the tilt aftereffect is influenced by selective visual attention (Spivey & Spirn, 2000). Suzuki (2001) found that the properties of mechanisms sensitive 2D contours exhibit: 1) broad orientation tuning; 2) indifference with respect to how the contour is defined; 3) strong attentional modulation; and 4) relative scale tolerance. All of these features are consistent with adaptation of mechanisms that reside in higher-level regions of visual processing (e.g., V4 and IT). With the exceptions of attention and scale tolerance, which we did not examine, we have found similar properties with regard to orientation tuning and pattern invariance in mechanisms that extract accurate information about 3D shape from texture.

A Neural Model for 3D Shape Mechanisms

It is likely that such a mechanism is widely tuned to many different orientations and configured in such a way that its preferred orientations align with the orientation flows associated
with a particular 3D shape (e.g. concavity or convexity). That this mechanism is pattern invariant with regard to first- and second order cues indicates that it receives inputs from orientation-tuned cells in V1 sensitive to changes in luminance and cells in V2 that are broadly tuned for spatial frequency and can respond to both real and illusory contours. The position selectivity of this mechanism places it relatively early in the visual system, and perhaps it is indicative of a population of neurons in V4, which is known to be retinotopically organized and contain mechanisms that can tolerate shifts in retinal position of up to 1.5º of the visual angle (Rust & Decarlo, 2010).

**Limitations**

Our stimuli are computer-generated plaids and illusory contours that are generally oriented along the cardinal axes; the mechanisms that are adaptable to these textures most likely only represent a small sample of the mechanisms that process the myriad components that comprise the rich, varied environments in which we live. However, our findings contribute to the growing knowledge base of 3D shape processing.

Our findings are limited to adaptable 3D mechanisms that are sensitive to the monocular cues of texture patterns; our research does not shed any light on 3D shape mechanisms that respond to specular highlights or shading or any combination of monocular cues. Because our stimuli are all greyscale (i.e., produced from variations of black and white), we can draw no conclusions about how color vision may affect the perception of 3D shape. Our stimuli were all the same physical size. As such, we are not able to predict how changes in scale would affect these 3D shape mechanisms. We are also unable to quantify the role attention plays in 3D shape perception.
All the observers in our study had normal or corrected to normal vision, which assumes an effortless ability to extract 3D shape from 2D retinal images. We cannot make any conclusions with regard to how any type of visual impairment may affect that ability.

The nature of psychophysical research is to study brain-behavior relationships. Therefore, we can only infer any conclusions with regard to the locus of the neural mechanisms we’ve isolated based on similar findings, analogous animal models or from the inferences of neuroimaging studies.
Future Directions

Future research could incorporate color in defining 3D texture patterns. Are there neural mechanisms that are sensitive to color with similar properties as those that we have identified in our studies? Similarly, future experiments could combine shading and specular highlights with texture to see if those properties enhance or inhibit 3D shape perception.

To date, no research has considered how attention may modulate the perception of 3D shape. Future research could focus on the role attention plays in the accurate perception of 3D shape from texture. Along those lines, quantifying reaction times in future experiments may offer insight into the effect of attention on basic shape perception. Using occluded stimuli, or degrading adapting stimuli in a controlled and consistent manner may help in furthering our understanding of the nature of feedback mechanisms in the visual system.

To date, we have only recruited individuals without significant visual impairment. It would be interesting to investigate if there are any differences in the way in which individuals with vision impairments perceive 3D shape. Of particular interest would be amblyopes -- individuals who can only extract 3D shape from monocular cues.

Finally, combining our psychophysical approach with neuroimaging studies would help to identify the locus of neural mechanisms sensitive to 3D shape that is defined by texture patterns.
Table 1. Conditions in Experiment One. Observers ran four baseline conditions and 28 adaptation conditions. The spatial frequency of all stimuli is 2.6 cpd.

<table>
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<tr>
<th>TEST STIMULUS</th>
<th>Luminance Modulated</th>
<th>Contrast Modulated</th>
<th>Low Contrast</th>
<th>Illusory Contour</th>
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<td>X</td>
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<tr>
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Table 2. Conditions in Experiment Two. Observers ran one baseline condition and 8 adaptation conditions. (Data from Experiment One was used for three baseline conditions.)

<table>
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<td>Data from Experiment One</td>
<td>Data from Experiment One</td>
<td>Data from Experiment One</td>
</tr>
<tr>
<td>ADAPT STIMULUS</td>
<td>8.2 cpd Luminance Modulated CVX</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>ADAPT STIMULUS</td>
<td>8.2 cpd Luminance Modulated CCV</td>
<td>X</td>
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<td>X</td>
</tr>
</tbody>
</table>
Table 3. Conditions in Experiment Three. For each set of corrugations (vertical and horizontal), there was a total of 11 conditions: one baseline, five adapting to a convex stimulus, and five adapting to a concave stimulus (an aligned condition, and conditions in which the adapting stimulus, orientation flows of which are in pink below, was laterally misaligned to the left, laterally misaligned to the right, vertically misaligned above, and vertically misaligned below with respect to the test stimulus, orientation flows of which are in blue below). The two sets of data obtained for each adaptation stimulus (ccv/cvx) were averaged together for lateral conditions and for vertical conditions. The spatial frequency of all stimuli is 2.6 cpd.

<table>
<thead>
<tr>
<th>VERTICAL CORRUGATION CONDITIONS</th>
<th>Baseline</th>
<th>Aligned</th>
<th>Laterally Misaligned</th>
<th>Laterally Misaligned</th>
<th>Vertically Misaligned</th>
<th>Vertically Misaligned</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
<td><img src="image3.png" alt="Image" /></td>
<td><img src="image4.png" alt="Image" /></td>
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<tr>
<td>CVX</td>
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<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>HORIZONTAL CORRUGATION CONDITIONS</th>
<th>Baseline</th>
<th>Aligned</th>
<th>Laterally Misaligned</th>
<th>Laterally Misaligned</th>
<th>Vertically Misaligned</th>
<th>Vertically Misaligned</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td><img src="image9.png" alt="Image" /></td>
<td><img src="image10.png" alt="Image" /></td>
<td><img src="image11.png" alt="Image" /></td>
<td><img src="image12.png" alt="Image" /></td>
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<tr>
<td>CVX</td>
<td><img src="image15.png" alt="Image" /></td>
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<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>CVX</td>
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<td>X</td>
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<td>X</td>
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</table>
Table 4. Magnitude of aftereffects obtained in misaligned conditions when compared to aftereffects obtained in aligned conditions.

<table>
<thead>
<tr>
<th>ADAPTATION CONDITION</th>
<th>ALIGNED</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CVX Horizontal</td>
</tr>
<tr>
<td>Vertically Misaligned</td>
<td>CVX Vertical</td>
</tr>
<tr>
<td></td>
<td>CCV Vertical</td>
</tr>
<tr>
<td></td>
<td>CVX Horizontal</td>
</tr>
<tr>
<td></td>
<td>CCV Horizontal</td>
</tr>
<tr>
<td>Laterally Misaligned</td>
<td>CVX Vertical</td>
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<tr>
<td></td>
<td>CCV Vertical</td>
</tr>
<tr>
<td></td>
<td>CVX Horizontal</td>
</tr>
<tr>
<td></td>
<td>CCV Horizontal</td>
</tr>
</tbody>
</table>

* Indicates conditions in which positive shape aftereffects were obtained.
Figure 1. Schematic of a receptive field, after Hubel and Wiesel. In this schematic, flanking fields oppose the central region.
Figure 2. Examples of first order and second order contours. Top: luminance modulated first order grating. Middle: contrast modulated, second order plaid. Bottom: Illusory, second order contour. Each pattern has the receptive field of a hypothetical simple cell superimposed. Unlike luminance-modulated contours, both contrast-modulated and illusory contours should not elicit responses from a simple cell because in those contours there is no change in mean luminance across the cell’s receptive field.
Figure 3. Examples of sinusoidal gratings at increasing spatial frequencies (from left to right) and different orientations (from left to right: vertical, oblique, and horizontal).
Figure 4. Examples of 3D spheres illustrating shape from shading (left) and shape from specular highlights (center), and shape from texture (right).
Figure 5. This is a schematic showing how a 3D surface is projected into a 2D image (dotted lines from the image plane to the projected corrugations show which locations on the surface of the corrugations are projected into the image plane).
Figure 6. Top: Example of an isotropic texture. The pattern has no orientation bias. Bottom: Example of a homogenous texture, a pattern that is spatially uniform (isotropic or not) from location to location across the pattern.
Figure 7. Orientation flows formed by a horizontal texture component in a simple (left panels) and complex plaid surface texture (center panels) enable accurate perception of 3D shape of a vertically corrugated surface. Subtracting the horizontal component from the complex plaid (right panels) induces an incorrect shape percept (Li & Zaidi, 2001).
Figure 8. Left: Three-dimensional convex and concave curvatures created by warping checkerboards. Contours defining checkerboard deviate from horizontal and vertical. Right: Zabutons consist of regular checkerboards (contours defining checkerboard are physically horizontal and vertical) that contain black and white stars at intersections, inducing illusory tilts of the contours, thereby creating illusory 3D curvatures (Li, et al, 2008).
Figure 9. Schematic illustrating fatigue model of visual adaptation. Extended exposure to a concave stimulus (left) will fatigue neural mechanisms that prefer concave shape (red Xs), leaving the visual system imbalanced and relatively more sensitive to convex shapes.
Figure 10. One complete set of luminance modulated horizontal-vertical plaid test stimuli. The corrugations vary in amplitude in 3.5 cm increments from -14 to +14 (the negative number is an expression of concavity and the positive number is an expression of convexity). The -14 cm and +14 cm stimuli were also used as adapting stimuli.
Figure 11. Sequence of events during an adaptation condition. Baseline conditions were identical in sequence except that the adaptation stimuli were not presented.
Figure 12. Top: Sample data from a single baseline condition (solid line) and two adaptation conditions (dashed lines) for a single class of test stimuli, illustrating negative shape aftereffects in the adaptation conditions. Percent of trials reported as convex was plotted vs. curvature amplitude of the test stimulus. Perceived flat points were extracted from the Weibull fits as the curvature amplitude that yielded convex responses on 50% of the trials. Adaptation to a convex stimulus (squares) causes the psychometric function to shift towards convex (positive) values, and adaptation to a concave stimulus (triangles) causes shifts towards concave (negative) values. Bottom: Perceived flat points presented in a bar graph.
Figure 13. From left to right: 2.6 cpd luminance modulated oblique plaid, 1.8 cpd luminance modulated oblique plaid, and 2.6 cpd luminance modulated horizontal-vertical plaid, all at +14 cm amplitude (convex).
Figure 14. The semi-transparent red lines highlight the second order orientation flows contained in the oblique plaid stimulus. These illusory lines are created from the abutting alternating squares of the black and white checkerboard pattern.
Figure 15. Detail of vertical-horizontal and oblique plaid. Left and Center panels: The red bars are the same physical size and illustrate that the grating components of the horizontal-vertical plaid (left) and oblique plaid (center) textures were identical in spatial frequency at 2.6 cpd. Right panel: The spatial frequency of the oblique plaid texture has been decreased to 1.8 cpd in order to match the size of the black and white diamond shapes of the vertical-horizontal plaid (left).
Figure 16. Results of Preliminary Study. 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. Positive shape aftereffects were obtained in the 1.8 cpd convex adaptation condition.
Figure 17. Left to right: Examples of luminance modulated, contrast modulated, and illusory contour stimuli. Top row: concave corrugated stimuli. Bottom row: convex corrugated stimuli.
Figure 18. Results of Experiment One. 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.

**Luminance Modulated (LM) Test Stimuli**

<table>
<thead>
<tr>
<th>Adaptation Condition</th>
<th>Baseline</th>
<th>Luminance Modulated (LM)</th>
<th>Contrast Modulated (CM)</th>
<th>Illusory Contour (IC)</th>
<th>Low Contrast LM</th>
</tr>
</thead>
<tbody>
<tr>
<td>B/L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CONVEX</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>CONCAVE</td>
<td></td>
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</table>

**Contrast Modulated (CM) Test Stimuli**

<table>
<thead>
<tr>
<th>Adaptation Condition</th>
<th>Baseline</th>
<th>Luminance Modulated (LM)</th>
<th>Contrast Modulated (CM)</th>
<th>Illusory Contour (IC)</th>
<th>Low Contrast LM</th>
</tr>
</thead>
<tbody>
<tr>
<td>B/L</td>
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</tr>
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<td>CONCAVE</td>
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</table>

**Illusory Contour (IC) Test Stimuli**

<table>
<thead>
<tr>
<th>Adaptation Condition</th>
<th>Baseline</th>
<th>Luminance Modulated (LM)</th>
<th>Contrast Modulated (CM)</th>
<th>Illusory Contour (IC)</th>
<th>Low Contrast LM</th>
</tr>
</thead>
<tbody>
<tr>
<td>B/L</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>CONVEX</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CONCAVE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 19. Percentage of times stimuli of one texture type appeared more curved than stimuli of another texture type. Data are averaged across 5 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.
Figure 20. Left: An 8.2 cpd luminance modulated adapting stimulus. Right: A 2.6 cpd luminance modulated sample test stimulus, both at +14 cm amplitude (convex).
Figure 21. Results of Experiment Two. 8.2 cpd luminance modulated horizontal-vertical plaid adapting stimuli. Negative aftereffects were obtained in all test stimuli conditions: 2.6 cpd luminance modulated, 2.6 cpd contrast modulated, illusory contour, and 8.2 cpd luminance modulated control.
Figure 22(A). Vertical corrugation. (B). Horizontal corrugation. Schematics to the right of the convex stimuli represent the aligned, vertically misaligned, and laterally misaligned adapting conditions. The pink lines represent the direction of the orientation flows of a centrally convex adapting stimulus. The blue lines represent a physically flat test stimulus. Misalignment conditions were analogous for the opposite sign (i.e., concave) curvatures.
Figure 23. Experiment Three Predictions. Top graph: If the mechanisms are position invariant, we expect negative shape aftereffects in all conditions. Middle graph, vertical corrugations: If the mechanisms are position selective, we expect positive shape aftereffects in the laterally misaligned conditions and negative aftereffects in the vertically misaligned conditions. Bottom graph, horizontal corrugations: If the mechanisms are position selective, we expect positive shape aftereffects in the vertically misaligned conditions and negative aftereffects in the laterally misaligned conditions.
Figure 24. Results of Experiment Three. Top panel: For the vertical corrugation test stimuli, negative aftereffects were obtained in the aligned conditions and in the vertically misaligned conditions. Positive aftereffects were obtained in the laterally misaligned conditions. Bottom panel: For the horizontal corrugation test stimuli, negative aftereffects were obtained in the aligned conditions and in the horizontally misaligned concave adapt condition only. Positive shape aftereffects were obtained in the vertically misaligned conditions.
Figure 25. Comparison of the curvature of a centrally convex and centrally concave stimulus. The bottom portion of the convex corrugation (left) is the same curvature as the top portion of the concave corrugation (right). The same holds true for the top portion of the convex and bottom portion of the concave corrugation.
Appendix A

Instructions given to observers in Experiment One: Naïve participants were read instructions and one of the authors supervised the sessions; those participants who were members of the lab and were familiar with the experimental set-up were able to run sessions at their own pace and keep track of their own progress.

Purpose of the study

The purpose of this study is to determine if there is a change in one's percept of the 3-D curvature of a textured surface depending upon an adaptation image. In order to do this, you will be asked to make judgments on black, white and grey images that will be shown to you on a computer monitor. There are four different sets of images that you will be asked to judge, the images in each set will vary in how concave or convex they look, so some will be harder than others for you to make a choice. In any case, go with your instinct, even if you aren’t sure. There are no right or wrong answers.

Structure of the study

The entire study should be completed in approximately 8 hours. At the beginning of each session you will be asked to fixate on a small black cross at the center of a grey screen for 60 seconds, after which the session begins.

In the four baseline sessions, your task is simply to determine whether the test image is concave or convex by making your choice on the response box. If the image appears to be concave (the center is further away than the edges), press the top red button – the one closest to the experimental monitor. If the image appears to be convex (the center is popping out at you, press the bottom red button – the one closest to you.

Bear in mind that the images will be flashed on the monitor, so it is important that your eye remains fixated on the cross in the center of the screen. After the test image, a noise pattern will flash very briefly before the next test image is shown (see flow chart following image examples). If at any time you feel you need a break, just hold off on responding; it is your response that prompts the next test image. Tones will alert you that the test image is going to be flashed, and that the program has received your response.

Your task in the adaptation sessions, of which there are 28, is essentially the same, except that now before each test image, there will be an adaptation image. At the beginning of each session, you will stare at an image from one of the sets for two minutes then a test image for you to judge will flash on the screen, followed by the noise pattern. Before the next test image is served up, the image that you stared at the beginning of the trial will be shown on the screen for five seconds before the test image is flashed (see flow chart following image examples). It is only the test image that is flashed on the screen that you should judge! The task is the same, if the image appears to be concave (the center is further away than the edges), press the top red button – the one closest to the experimental monitor. If the image appears to be convex (the center is popping out at you, press the bottom red button – the one closest to you. Once again, try to keep your eye fixated on the center cross and, if you need a break, delay your response. Tones will alert you that the test image is going to be flashed, and that the program has received your response.

You can keep track of your progress using the grid at the end of this document. The baseline sessions are represented at the top of the table in the boxes labeled 1-4. The adaptation sessions are represented in...
boxes of the lower part of the grid. The first number in each box refers to the adaptation image, the second to the set of test images you will be judging.

Images

The following pages contain samples from the sets of images on which you will be tested. In each set, you should be able to determine that one image is convex (the center appears to pop out towards you) and one is concave (the center seems to be further away from you than the edges).

**High contrast grating: Adaptation conditions 1 & 2; Test condition 1**

![High contrast grating](image1)

**Mixed contrast grating: Adaptation conditions 3 & 4; Test condition 2**

![Mixed contrast grating](image2)
Low contrast grating: Adaptation conditions 5 & 6; Test condition 3

Illusory contour: Adaptation conditions 7 & 8; Test condition 4
Flow charts

This is an illustrated chart showing an example of one trial of a **baseline session**. After an initial 60-second adaptation to a grey screen, you will be shown 81 trials in the following sequence:

1. **Example test image** (brief!)

2. **Noise pattern** (brief!)

3. **Grey screen** (waits for response)
This is an illustrated chart showing an example of one trial of an adaptation session. As in the baseline sessions, there are 81 trials to each adaptation session, but the first trial in each adaptation session is different from the rest of the trials in that session. After an initial 60-second adaptation to a grey screen, for the first trial in the session, you will view an adaptation image for two minutes before the test image flashes on the screen. For each of the rest of the trials in the session, you will view the adaptation image for 5 seconds before the test image flashes on the screen.

**TRIAL 1**

**Example adaptation image**
(2 minutes on screen)

1.

**Example test image** (brief!)

2.

**Noise pattern** (brief!)

3.

**Grey screen** (waits for response)

4.
TRIALS 2 - 81
“Top-off” adaptation image
(5 seconds on screen)

1. Test image
   (brief!)

2. Noise pattern
   (brief!)

3. Grey screen
   (waits for response)
Running the Study

The path to the MatLab program file is:
VSGV8 → Adaptation → adaptationprogram.m

When you start the program, you will be asked a series of questions in the command window.

Q1: Baseline? (0=no, 1=yes)
To answer this question, type the number 0 if you are running a baseline session or the number 1 if it is an adaptation session.

Q2: Name of output file?
To answer this question, type your initials.

Q3A: Adaptation stimulus?
If you typed ‘1’ as an answer to Q1, this question prompts you to choose an image that will be used for adapting. Your choices are the numbers 1-8. If you look at the grid on the last page of this document, you will see those numbers correspond to the first number in the boxes that make up all the adaptation sessions.

Q3B: Test stimulus?
This question prompts you to type in a number from 1-4 that corresponds with the four sets of test images. You will need to answer this for both the baseline and the adaptation sessions (in the adaptation sessions, it is the second number in the boxes on the grid. It is also the only number in the boxes for the baseline sessions.

At this point, you are ready to begin! Complete the baseline sessions in random order first, and then move on to the adaptations sessions, again in random order.

Note: this study is monocular, you must wear an eye patch. Please patch the same eye for every session.
Participant’s initials:  __________

Consent form signed:  ____

Use this grid to keep track of the sessions you have completed. **Remember, complete baseline sessions first (in random order) then move on to the adaptation sessions (random order).**

**Key**

**Baseline Sessions**
The numbers in the boxes of the Baseline Sessions row are the number you type in to call the set of test images named in the row below.

1 = High contrast
2 = Mixed contrast
3 = Low contrast
4 = Illusory contour

The first number in the boxes of the Adaptation Sessions calls the adaptation image; the second number calls the set of test images.

**Adaptation Sessions**

*First number* (adaptation image)  
*Second number* (test image)

- 1 or 2 = High contrast
- 3 or 4 = Mixed contrast
- 5 or 6 = Low contrast
- 7 or 8 = Illusory contour

Response: Concave = top red button | Convex = bottom red button

<table>
<thead>
<tr>
<th>TEST STIMULUS</th>
<th>[\text{Baseline Sessions:} ]</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
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<td></td>
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<td>1,1</td>
<td>1,2</td>
<td>1,4</td>
</tr>
<tr>
<td>Mixed Contrast</td>
<td></td>
<td>2</td>
<td>2,1</td>
<td>2,2</td>
<td>2,4</td>
</tr>
<tr>
<td>Low Contrast</td>
<td></td>
<td>3</td>
<td>3,1</td>
<td>3,2</td>
<td>3,4</td>
</tr>
<tr>
<td>Illusory Contour</td>
<td></td>
<td>4</td>
<td>4,1</td>
<td>4,2</td>
<td>4,4</td>
</tr>
</tbody>
</table>

**Debriefed:**  ____
Appendix B

Instructions given to observers in Experiment Two: Naïve participants were read instructions and one of the authors supervised the sessions; those participants who were members of the lab and were familiar with the experimental set-up were able to run sessions at their own pace and keep track of their own progress.

Participant’s initials: _________
Consent form signed: ____

Purpose of the study

The purpose of this study is to determine if there is a change in one's percept of the 3-D curvature of a textured surface depending upon an adaptation image. In order to do this, you will be asked to make judgments on black, white and grey images that will be shown to you on a computer monitor. There are four different sets of images that you will be asked to judge, the images in each set will vary in how concave or convex they look, so some will be harder than others for you to make a choice. In any case, go with your instinct, even if you aren’t sure. There are no right or wrong answers.

Running the Study (use experimental set up in Rm 230). Total time required: approximately 3.5 hours.

The path to the MatLab program files is: VSGV8 → Adaptation_Study3

When you start the each of the programs, you will be asked a series of queries in the command window.

Q1: Please type in your initials Type your initials in ALL CAPS.

Q2: Is this a baseline session? (0=no, 1=yes) To answer this question, type the number 1 if you are running a baseline session or the number 0 if it is an adaptation session.

Q3: Adaptation stimulus? (1=convex, 2=concave) If you typed '0' as an answer to Q1, this question prompts you to choose an image that will be used for adapting. Your choices are the numbers 1 and 2 -- convex or concave. If you look at the grid below, you will see those numbers correspond to the first number in the boxes that make up the adaptation sessions.

At this point, you are ready to begin! When the test stimulus flashes on the screen, press the top red button on the response box if you judge the center of the stimulus as concave (further away from you), press the bottom red button on the response box if you judge the center of the stimulus as convex (closer to you). Complete the baseline sessions first, and then move on to the adaptations sessions, in random order.

Note: This study is monocular; you must wear an eye patch. Please patch the same eye for each session.

Use grid below to keep track of the sessions you have completed. Complete baseline session first then move on to the adaptation sessions (random order).

Response: Concave = top red button | Convex = bottom red button

<table>
<thead>
<tr>
<th>Filename</th>
<th>Baseline</th>
<th>Convex</th>
<th>Concave</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0, 1</td>
<td>0, 2</td>
</tr>
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<td>0, 2</td>
</tr>
<tr>
<td>HSF_CMtest.m</td>
<td></td>
<td>0, 1</td>
<td>0, 2</td>
</tr>
<tr>
<td>HSF_IC.test.m</td>
<td></td>
<td>0, 1</td>
<td>0, 2</td>
</tr>
</tbody>
</table>

Debriefed: ____
Adaptation & Test Stimuli

Test Stimuli
Flow charts

This is an illustrated chart showing an example of one trial of the baseline session. After an initial 60-second adaptation to a grey screen, you will be shown 81 trials in the following sequence:

1. **Example test image**
   (brief!)

2. **Noise pattern**
   (brief!)

3. **Grey screen**
   (waits for response)
This is an illustrated chart showing an example of the initial trial of an adaptation session as well as the top-off adapting trial. As in the baseline session, there are 81 trials to each adaptation session, but the first trial in each adaptation session is different from the rest of the trials in that session. After an initial 60-second adaptation to a grey screen, for the first trial in the session, you will view an adaptation image for two minutes before the test image flashes on the screen. For each of the rest of the trials in the session, you will view the adaptation image for 5 seconds before the test image flashes on the screen.

**TRIAL 1**

**Example adaptation image**

(2 minutes on screen)

1. Example test image (brief!)

2. Noise pattern (brief!)

3. Grey screen (waits for response)
TRIALS 2 - 81

“Top-off” adaptation image
(5 seconds on screen)

1. Test image
(brief!)

2. Noise pattern
(brief!)

3. Grey screen
(wait for response)
Appendix C

Instructions given to observers in Experiment Three: Naïve participants were read instructions and one of the authors supervised the sessions; those participants who were members of the lab and were familiar with the experimental set-up were able to run sessions at their own pace and keep track of their own progress.

Participant’s initials: __________

About the Study
This is a visual adaptation study. You are being asked to judge the convexity or concavity of corrugated surfaces. For all sessions except the baseline, the adaptation stimulus is offset laterally to the left in the same position for the entire session, or vertically to the top for the entire session, all test stimuli that you are to judge are centered on screen; the fixation cross is in the same position on the screen throughout the experiment. Please focus on the fixation cross throughout the entire experiment.

Running the Study (use experimental set up in Rm 230)

The path to the MatLab program file is: VSGV8 → SigmaXi → jitter_pilot_SX.m

When you start the program, you will be asked a series of questions in the command window.

Q1: Baseline? (0=no, 1=yes)
To answer this question, type the number 1 if you are running a baseline session or the number 0 if it is an adaptation session.

Q2: Your initials? Type your initials.

Q3: Adaptation stimulus? (1=convex, 2=concave)
If you typed ‘1’ as an answer to Q1, this question prompts you to choose an image that will be used for adapting. Your choices are the numbers 1 and 2 -- convex or concave. If you look at the grid below, you will see those numbers correspond to the first number in the boxes that make up the adaptation sessions.

Q4: Offset? (1=horizontal, 2=vertical)
This chooses the offset for the adaptation stimulus. Your choices are the numbers 1 and 2 -- horizontal offset or vertical offset. If you look at the grid below that number represents the second number in the boxes that make up the adaptation sessions.

At this point, you are ready to begin! When the test stimulus flashes on the screen, press the top red button on the response box if you judge the center of the stimulus as concave (further away from you), press the bottom red button on the response box if you judge the center of the stimulus as convex (closer to you). Complete the baseline sessions first, and then move on to the adaptations sessions, in random order.

Note: This study is monocular; you must wear an eye patch. Please patch the same eye for each session.

Use grid below to keep track of the sessions you have completed. Complete baseline session first then move on to the adaptations sessions (random order).

Response: Concave = top red button | Convex = bottom red button

Baseline session: ____

<table>
<thead>
<tr>
<th>Offset</th>
<th>Horizontal (1)</th>
<th>Vertical (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Convex Adapt (1)</td>
<td>1, 1</td>
<td>1, 2</td>
</tr>
<tr>
<td>Concave Adapt (2)</td>
<td>2, 1</td>
<td>2, 2</td>
</tr>
</tbody>
</table>

Consent form signed: ____  Debriefed: ____
Participant’s initials: _________

About the Study
This is a visual adaptation study. You are being asked to judge the convexity or concavity of corrugated surfaces. For all sessions except the baseline, the adaptation stimulus is offset laterally to the right in the same position for the entire session, or vertically to the bottom for the entire session, all test stimuli that you are to judge are centered on screen; the fixation cross is in the same position on the screen throughout the experiment. Please focus on the fixation cross throughout the entire experiment.

Running the Study (use experimental set up in Rm 230)
The path to the MatLab program file is: VSGV8 → SigmaXi → jitter_pilot_SX_b.m

When you start the program, you will be asked a series of questions in the command window.

Q1: Baseline? (0=no, 1=yes)
To answer this question, type the number 1 if you are running a baseline session or the number 0 if it is an adaptation session.

Q2: Your initials? Type your initials.

Q3: Adaptation stimulus? (1=convex, 2=concave)
If you typed ‘1’ as an answer to Q1, this question prompts you to choose an image that will be used for adapting. Your choices are the numbers 1 and 2 -- convex or concave. If you look at the grid below, you will see those numbers correspond to the first number in the boxes that make up the adaptation sessions.

Q4: Offset? (1=horizontal, 2=vertical)
This chooses the offset for the adaptation stimulus. Your choices are the numbers 1 and 2 -- horizontal offset or vertical offset. If you look at the grid below that number represents the second number in the boxes that make up the adaptation sessions.

At this point, you are ready to begin! When the test stimulus flashes on the screen, press the top red button on the response box if you judge the center of the stimulus as concave (further away from you), press the bottom red button on the response box if you judge the center of the stimulus as convex (closer to you). Complete the baseline sessions first, and then move on to the adaptations sessions, in random order.

Note: This study is monocular; you must wear an eye patch. Please patch the same eye for each session.

Use grid below to keep track of the sessions you have completed. Complete baseline session first then move on to the adaptation sessions (random order).

Response: Concave = top red button | Convex = bottom red button

Baseline session:

<table>
<thead>
<tr>
<th>Offset</th>
<th>Horizontal (1)</th>
<th>Vertical (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Convex Adapt</td>
<td>1, 1</td>
<td>1, 2</td>
</tr>
<tr>
<td>Concave Adapt</td>
<td>2, 1</td>
<td>2, 2</td>
</tr>
</tbody>
</table>

Consent form signed: _______ Debriefed: ____
About the Study
This is a visual adaptation study. You are being asked to judge the convexity or concavity of corrugated surfaces. For all sessions except the baseline session you run first and the two sessions of the no_offset program, the adaptation stimulus is offset laterally to the left in the same position for the entire session, or vertically to the top for the entire session, all test stimuli that you are to judge are centered on screen; the fixation cross is in the same position on the screen throughout the experiment. Please focus on the fixation cross throughout the entire experiment.

Running the Study (use experimental set up in Rm 230). Total time required: approximately 3 hours.

The path to the MatLab program file is: VSGV8 → Adaptation2011

There are three programs to run: 
- offset_horizcorrugationA.m
- offset_horizcorrugationB.m
- no_offset.m

When you start the offset programs, you will be asked a series of questions in the command window.

Q1: Baseline? (0=no, 1=yes)
To answer this question, type the number 1 if you are running a baseline session or the number 0 if it is an adaptation session.

Q2: Your initials? Type your initials.

Q3: Adaptation stimulus? (1=convex, 2=concave)
If you typed ‘0’ as an answer to Q1, this question prompts you to choose an image that will be used for adapting. Your choices are the numbers 1 and 2 -- convex or concave. If you look at the grid below, you will see those numbers correspond to the first number in the boxes that make up the adaptation sessions.

Q4: Offset? (1=horizontal, 2=vertical)
This chooses the offset for the adaptation stimulus. Your choices are the numbers 1 and 2 -- horizontal offset or vertical offset. If you look at the grid below that number represents the second number in the boxes that make up the adaptation sessions.

The no_offset program prompts you as follows:

Q1: Please type your initials Type your initials

Q2: Adaptation stimulus? (1=convex, 2=concave)

At this point, you are ready to begin! When the test stimulus flashes on the screen, press the top red button on the response box if you judge the center of the stimulus as concave (further away from you), press the bottom red button on the response box if you judge the center of the stimulus as convex (closer to you). Complete the baseline sessions first, and then move on to the adaptations sessions, in random order.

Note: This study is monocular; you must wear an eye patch. Please patch the same eye for each session.

Use grid below to keep track of the sessions you have completed. Complete baseline session first then move on to the adaptation sessions (random order).

Response: Concave = top red button | Convex = bottom red button

Baseline session: _____ (only run ONE baseline session for the entire experimental study)

<table>
<thead>
<tr>
<th>Program</th>
<th>Offset</th>
<th>horizcorrugationA</th>
<th>horizcorrugationB</th>
<th>no_offset</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Horizontal (1)</td>
<td>Vertical (2)</td>
<td>Horizontal (1)</td>
</tr>
<tr>
<td>Convex Adapt</td>
<td>I</td>
<td>1,1</td>
<td>1,2</td>
<td></td>
</tr>
<tr>
<td>(1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Concave Adapt</td>
<td>2,1</td>
<td>2,1</td>
<td>2,2</td>
<td>2,2</td>
</tr>
<tr>
<td>(2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Consent form signed: ____ Debriefed: ____
References


Hallum, L. E., Landy, M. S., & Heeger, D. J. (2011). Human primary visual cortex (V1) is selective for second order spatial frequency. *Journal of Neurophysiology, 105*, 2121-2131. doi: 10.1152/jn.01007.2010


Rosenholtz, R., & Malik, J. (1997). Surface orientation from texture: Isotropy or homogeneity (or both)? *Vision Research, 37*(16), 2283-2293.


