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The Impact of Affect on Neural Mechanisms Underlying Orientation Perception

Michelle L. Fowler
Graduate Center, City University of New York

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The Impact of Affect on Neural Mechanisms Underlying Orientation Perception

by

Michelle L. Fowler

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.

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

____________________________________________________________________
Andrea Li

Date
Chair of Examining Committee

____________________________________________________________________
Maureen O’Connor

Date
Executive Officer

Joshua Brumberg

Justin Storbeck

Joan Borod

Jennifer Stewart
Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK
Abstract

The Impact of Affect on Neural Mechanisms Underlying Orientation Perception

by

Michelle L. Fowler

Advisor: Andrea Li, PhD

The underlying mechanisms used to process 2D visual information to form a unified 3D percept of the world remain largely unknown. Previous work in our lab has shown that accurate 3D perception of textured surfaces depends on the presence of specific patterns of orientation flows in the retinal image. Recent research has shown that affective state may influence the visual perception of oriented patterns. Relative to neutral face stimuli, fearful face stimuli have been shown to increase sensitivity to orientation of low spatial frequency patterns and decrease sensitivity to orientation of high spatial frequency patterns. How affective state influences the perception of orientation as used in more complex patterns and in patterns that convey 3D shape, which is processed higher in the visual pathway, is currently not known. Using the Radboud face database, we examined the effects of affective fear versus neutral face primes on orientation sensitivity using grating and plaid stimuli of low (2cpd) and high (4cpd) spatial frequency, and on 3D curvature sensitivity using images of 3D surfaces textured with 2cpd and 4cpd gratings. In Experiment One, we examined the role of fear on 2D orientation sensitivity of tilted gratings and plaid stimuli at both low and high spatial frequencies. Results replicated previous research showing increased orientation sensitivity to low frequency patterns and decreased orientation sensitivity to high frequency patterns; however, our results limit this finding as orientation-specific to vertically oriented stimuli only. Therefore, differences in tilt thresholds for spatial
frequency were shown to be dependent on orientation information contained within the pattern. In Experiment Two, we investigated the role of fear on 3D shape perception for surfaces slanted and corrugated in depth patterned with low and high frequency gratings. Results indicate that differences in the affective influence of orientation sensitivity for each spatial frequency were specific to processing area along the visual pathway. For 2D images conveying 3D shape, fear diminished, rather than increased, sensitivity for the low spatial frequency condition. However, for slanted surfaces, results indicated affective influence per spatial frequency for direction of slant. For corrugated surfaces, affective influence was found to be orientation specific for vertically corrugated stimuli patterned with horizontal gratings but was not found to have differential effects on spatial frequency. Therefore, affect may differentially influence visual processing of spatial frequency on orientation at multiple areas along the pathway. In Experiment Three, we assessed the contributions of the presence of a face prime, paradigm, and ordering effects on our results from Experiment One. Results confirm the robust nature of the affective influence of fear on the relationship between spatial frequency and orientation, as differences were not shown to be a result of no face primes, paradigm differences, or ordering effects. Taken together, our results indicate that the top-down modulation of affect differentially influences the saliency of spatial frequency information for orientation processing differently along multiple areas of the visual pathway.
Acknowledgements

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Additionally, I would like to thank Elliot Lockerman, who has been my undergraduate research assistant throughout this project. It was such a pleasure to work with him every day, as Elliot is so talented at everything he touches and was essential to its success. To my wonderful lab mates, Carole Filangieri and Danny Tam, thank you for your friendship and support through the years. I cannot imagine doing this with anyone else. To my good friends, Danielle Malkusz, Jennifer Morrison, Kristena Newman, and Agnieszka Mlodnicka, thank you for your insightful feedback, moral support, and occasional shenanigans throughout this process.

Finally, I whole-heartedly wish to thank my family for being with me every step of the way. I could not have achieved this without your love and encouragement. I am lucky to have such wonderful parents. I am even luckier that this includes an amazing sister. As I begin whatever new adventures lie ahead, I know that I have a strong foundation from which to build and/or even leap. So, thank you Debra, Terry, and Melanie for all you have done. Even more, thank you for being all that you are!
Dedication

This dissertation is dedicated to the memories of my grandparents, all of whom I lost while on this adventure, but whose strengths I needed to carry me through the journey. From my MeMaw, I got my sense of humor. From my Grandma, I learned positivity and patience. From my Grampa, I inherited his stubbornness to never quit.
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CHAPTER ONE

Introduction

**Background and Significance**

Knowledge of the veridicality of the external world is dependent upon the interpretation by the brain of electrical signals originating from our sensory systems. The visual system is the most dominant system by which we experience and thereby perceive our world. This sentiment dates as far back as Ancient Greece. In *Metaphysics*, Aristotle’s opening remarks propose that it is within human nature to desire knowledge about the world and the sensory system most responsible (and therefore most preferred) for achieving such knowledge is the visual system (Barnes, trans. 1984, as cited in Hergenhahn, 2005). However, in *Physics*, Aristotle asserts that the external world [nature] is limited by our senses, as the nature – including shape and form – of objects within the world cannot be distinguished from what exists actually and the properties that could exist possibly. In other words, knowledge of the world to the observer is self-evident only to the observer and may not be perceived as the same self-evident truth to another observer (Hardie & Gaye, trans. 1984, as cited in Baird & Kaufmann, 2000). Moreover, objects in the external environment may or may not be accurately interpreted by the brain because the actual nature of the object may not be truly encoded. This viewpoint is echoed in modern philosophers, such as Hume and Kant, 1,000 years later. Specifically, knowledge of the external world cannot be attained, since the properties of objects in the real world are not directly experienced. Despite these possible limitations, sensory experiences and perceptions are stable and reliable reflections of the external world. Specifically, sensory perception, which is the result of both bottom-up and top-down processing, seems to largely reflect entities in the external world, as sensory experience has developed to encode evolutionarily advantageous information within the external
environment in order to facilitate efficient interaction by humanity. Additionally, the ability of the brain to interpret these encoded signals into percepts appears consistent from one human being to another human being. The field of psychophysics is concerned with explaining the relationship between the external stimulus and the perceptual response to that stimulus, in which the perceptual response is presumed to be the result of the brain’s top-down processing of bottom-up sensory information. How top-down and bottom-up neural mechanisms interact and combine to result in the visual percept remains a central query in visual research. Of recent interest is the role of affective state on neural processing of the physical 3D world. Recent studies suggest that visual perception can in fact be altered by emotional states, specifically fear, as information is conveyed to higher visual areas of processing. The purpose of this paper is to investigate the role of affective influences on neural mechanisms underlying visual perception. Specifically, how affect might influence 3-Dimensional (3D) shape perception from 2-Dimensional (2D) patterns will be examined. The specific goal of the proposed work is to elucidate how affective factors might impact the perception of spatial frequency and orientation information within a visual scene that may be used for 3D shape perception.

The organization of neural mechanisms underlying visual perception

The physiology of visual pathways from retina to striate cortex (V1)

The visual system is a dynamically complex system that must rapidly convert 2D light information from the environment into an electrical signal for the brain to rebuild as the perception of a 3D world. When light energy reflects off object surfaces and enters the eye, this projection is 2D input onto the retina (Schriever, 1925). For every location within the visual field, there are neurons within the retina whose receptive fields code for either the presence or
absence of reflected light at that location. In cat retina, Kuffler (1953) found that the properties of ganglion neurons in the retina have concentric receptive fields with antagonistic center-surround organization. For neurons that have excitatory centers with inhibitory surrounds, diffuse light across the receptive field will excite the center but inhibit the surround producing a weak signal from the neuron. In contrast, a small patch of light in the center of the receptive field will yield a greater neural response from the neuron. In neurons that contain inhibitory center and excitatory surrounds, the absence of light diffused equally across the receptive field will produce weaker neuronal response than a small dark patch in the center (Barlow, Fitzhugh, & Kuffler, 1957).

Inputs from the retina, lateral geniculate nucleus of the thalamus (LGN), striate cortex (V1), and subsequent extra-striate areas of the visual cortex are processed along three parallel tracts: the magnocellular pathway (starting with ganglion cells called M-cells), the parvocellular pathway (starting with P-cells), and the koniocellular pathway (starting with K-cells) (Livingstone & Hubel, 1984a, 1984b, 1987, 1988; Callaway, 1998). Each pathway processes different aspects of light information from the retinal ganglion cells. In general, these pathways not only serve to process information regarding the type of visual input but also may have functional significance in establishing the underlying architecture that sustains the cortical circuitry of the visual system. In primates, axons of ganglion cells contained within the retina of each eye exit the eye and bundle together to form the optic nerve, from which 50% of these fibers decussate at the optic chiasm located between the retina and the LGN. Ipsilateral afferents enter into layers 2, 3, & 5 of the LGN; while, contralateral projections enter into layers 1, 4, and 6 (see Figure 1). In general, layers 1 and 2 of the LGN continue along the dorsal/magnocellular pathway, while the ventral/parvocellular pathway incorporates layers 4-6. M-cells, which project
to the dorsal pathway are characterized by larger cell bodies and receptive fields, which are more sensitive to low spatial frequency information, movement, and contrast. P-cells, which project to the ventral pathway are smaller, have smaller receptive fields, and transmit information regarding color, detail and finer spatial discrimination. Finally, K-cells have the smallest diameter axonal projections, and innervate the interconnected areas between the magnocellular and parvocellular layers of the LGN. The function of the K-pathway is still largely debated in visual research. In general, it is thought to play a role in integrating proprioception information from visual inputs with somatosensory visual inputs as a function of the location and movement of the eye. Given the inputs of the K-pathway to cytochrome oxidase (CO) blobs in V1, the K-pathway might play a direct role in object recognition and color vision. Finally, the K-pathway may govern vision during saccadic expression (Casagrande, 1994).

As visual information is transmitted via the optic nerve from the retina of the eye to visual areas of the brain, the axons of these neurons converge onto subsequent neurons along the visual pathway. Specifically, the axons of ganglion cells exit the eye and converge onto neurons in the LGN of the thalamus, V1, and extra-striate cortex of the brain. The discharge of a neuron depends on summated charges of these converging neurons. Therefore, the receptive fields of neurons higher along on the visual pathway are aggregates of the receptive fields from neighboring neurons lower in the visual pathway. As neurons converge, the antagonistic nature of ON versus OFF properties in neurons is generally maintained from retina (Kuffler, 1953) through the LGN and V1 (Hubel & Wiesel, 1959). After mapping the neurons in V1, Hubel and Wiesel (1965) found that the receptive fields of these neurons were elongated and varied in size and shape. As previously shown by Kuffler (1953), mapped receptive fields were shown by Hubel and Wiesel to have opposing regions that flanked a central region (see Figure 2) in which
neural response was weaker when light was diffused across the entire receptive field than light being diffused across the central region versus the surrounding regions. Specifically, the receptive fields for neurons in V1 tend to respond to bars of light more than spots of light. This finding showed that V1 neurons are selective for shape, size, position, and orientation for light information within corresponding areas of the visual field (Hubel & Wiesel, 1962, 1965). Where simple and complex cells have preferences for bars of light/dark, end-stopped cells specifically respond to different lengths, angles, and corners. By placing electrodes perpendicular to the surface of the cortex, Hubel and Wiesel found that these cells were organized in hypercolumns, which are 1mm tracts of cells that respond to a single location in visual space. As electrodes were placed at oblique angles to the surface of the cortex, hypercolumns were found to contain a full set of orientation columns for adjacent locations relative to the retina (1965). Hypercolumns, which contain areas rich in cytochrome oxidase (blobs) and poor (interblobs) in cytochrome oxidase (Wong-Riley, 1979), may play a role in contour integration of boundaries given their sensitivity to orientation (Grossberg & Mingolla, 1985). Located in layers 2 and 3 of V1, interconnectivity between CO blobs and interblobs may provide a mechanism underlying the processing of contour features. CO blobs are insensitive to orientation but sensitive to color and contrast (Livingstone & Hubel, 1984a). Interblobs, which are interleaved among CO blobs, are thought to be selective for orientation information (Livingstone & Hubel, 1984b). While interlinked CO blobs are thought to convey monocular information, interblobs are linked with other interblobs to convey binocular information. Axons of pyramidal spiny stellate neurons in visual areas 2 and 3 establish episodic clusters connecting areas within a visual column.
Projections from V1 enter extra-striate cortical areas by two pathways: magnocellular and parvocellular. As previously discussed, the magnocellular pathway relays information about movement and low spatial frequency from layers 1 and 2 of the LGN. From V1, the M-pathway extends dorsally to V2, V3, and medial temporal/medial superior temporal (MT/MST) towards the parietal lobe. Parvocellular projections regarding information about form, high spatial frequency, and color extend ventrally to V2, V4, and the inferior temporal gyrus (IT) towards the temporal pathway. In 1982, Ungerleider and Miskin showed a distinction of functionality between these two pathways using a double dissociation experiment. Monkeys were trained to perform both an object discrimination task and landmark discrimination task. Subsequently, surgical ablations were performed either to the temporal pathway or the parietal pathway in rhesus monkeys (*Macaca mulatta*). Findings of this experiment showed that the monkeys with the surgical removal to the temporal lobe were unable to perform the object discrimination task but were able to perform the landmark task. In contrast, removal of the parietal lobe yielded an inability by monkeys to perform the landmark discrimination task but remain able to discriminate between objects. This study not only showed that each pathway is specialized for processing type but also the two pathways work independently. The parietal, or “where,” pathway processes information regarding movement. The temporal, or “what,” pathway processes information regarding form and color (Ungerleider & Mishkin, 1982; Mishkin, Ungerleider, & Macko, 1983). In 1992, this finding was supported and extended in human vision by Goodale and Milner, in which a patient with visual form agnosia caused by damage to her temporal pathway was unable to identify pictures but was able to draw them from memory. In a subsequent experiment involving orientation matching, the patient was unable to make
perceptual judgments regarding static orientation or dimensions (e.g., size or shape) of visual objects in an orientation-matching task but was able to correctly interact with the object. This showed correct action-based perceptual judgments. In normal populations, fMRI has shown a double-dissociation in activation patterns for object identity and object-directed actions for the ventral/temporal and dorsal/parietal pathways (respectively), as well (Valyear, Culham, Sharif, Westwood, & Goodale, 2006). As a result of these findings, the dorsal/parietal pathway has been extended from the “where” pathway to be commonly referred to as the “where/how” pathway.

Within these two pathways, research has shown that areas within extra-striate cortices are specialized. Although there seems to be some intermingling of magnocellular and parvocellular inputs into the blob-interblob system, the divisions between these two pathways seem relatively intact as they progress beyond the primary visual cortex (Livingstone & Hubel, 1987, 1988). In early stages of V1, the visual system is preferential for orientation for edge-based information. Higher processing beyond V1 may then link these features into contours for shape discrimination (Landy & Bergen, 1991) and spatial precision (Lee, Mumford, Romero, & Lamme, 1998), perhaps in order to facilitate integration of surface features (Nakayama, 2005). The interactions of higher level processing of V1 for spatial discrimination may be modulated by its interactions with V2. Both the magnocellular and the parvocellular pathways have projections to V2, which is implicated in the processing of high complexity spatial discrimination (Merigan, Nealy, & Maunsell, 1993) as well as combining depth cues of stereoscopy for texture segmentation or figure-ground organization (Qiu & von der Heydt, 2005). In 1995, Lamme showed an increased response of neurons in V1 in awake macaque monkeys when tasked with the detection of visual elements pertaining to ‘figure’ relative to similar visual elements pertaining to ‘background’, a
phenomenon called contextual modulation. Moreover, in a backward masking paradigm, masking by extra-striate areas selectively suppressed contextual modulation of neurons in V1, which typically signal the segregation of figure and ground. However, earlier activity in V1 conveying orientation information contributing to texture segmentation of the scene is not affected (Lamme, Zipser, & Spekreijse, 2002). In the parietal pathway, projections from V2 input into V3 and MT (V5) and are implicated in global motion and movement, respectively. MST lies beyond MT and is associated with optic flow. In the temporal pathway, projections from V2 neurons connect to V4 then IT. Additionally, V4 has direct inputs from V1 and may be modulated by attention (Moran & Desimone, 1985). Visual information processed in V4 includes orientation, spatial frequency, and color (Desimone & Schein, 1987; Heywood, Gadotti, & Cowey, 1992). Furthermore, V4 may play a role in the perception of shape (Pasupathy & Connor, 2002), particularly in deciphering curvature of complex shape contours (Habak, Wilkinson, Zakher, & Wilson, 2004; Dumoulin & Hess, 2006). IT has been implicated in object recognition. Within this structure, regions have been identified for processing of discrete types of activations. The Fusiform Face Area (FFA) has been implicated for face recognition (Rolls & Tovee, 1995; Kanwisher, McDermott, & Chun, 1997; Tsao, Freiwald, Tootell, & Livingstone, 2006), the Extra-striate Body Area (EBA) for the recognition of body parts (Downing, Jiang, Shuman, & Kanwisher, 2001), the Parahippocampal Place Area (PPA) for scenes (Epstein & Kanwisher, 1998; Epstein, 2005), and the Lateral Occipital Complex (LOC) for shapes over textures (Grill-Spector et al, 1999; Grill-Spector, 2003). Additionally, IT has been linked to perception of 3D concave and convex surfaces in monkeys (Verhoef, Vogels, & Janssen, 2012). Finally, IT shares connections with areas of the medial temporal lobe (MTL), which is a
structure essential for memory. The MTL includes the parahippocampus, the entorhinal cortex, and the hippocampus (Scoville & Milner, 1957).

The organization from features to form in striate cortex

Feature extraction relies heavily on information from the striate cortex (V1)

In the early to mid-19th century, a large body of work by Gestalt psychologists used visual illusions to demonstrate the automaticity by which the brain integrates visual elements into the perception of shape using perceptual grouping heuristics. Although not fully explained neurophysiologically or even operationally at the time, the mechanisms that govern perceptual organization by the brain seem to produce a high degree of computational processing in effort to build objects within an image. How the visual system extracts and organizes these electrical signals conveying available light information into perceptual wholes remains undetermined. In response to light stimuli, the elongated receptive fields of V1 neurons are selective for shape, size, and orientation information contained within a location of a visual scene (Hubel & Wiesel, 1959, 1962, 1965). Coupled with the antagonistic property of ON-OFF receptive fields, the retention of retinotopic organization as these neurons converge along the visual pathway allows for the neuronal processing of specific patterns of light as a function of spatial location in the visual field. Every location in the visual field has neurons that code for every possible orientation and frequency within that particular location. Objects within our visual field are thereby encoded by combining orientation and frequency signals across many different neurons. Specifically, neuronal selectivity to specific elements of visual stimuli, such as orientation and spatial frequency, is thought to produce a particular response pattern. It is thought that any image can be mathematically deconstructed into sinusoidal gratings of different spatial
frequencies and orientations (De Valois, Albrecht, & Thorell, 1982), in which neuronal 
expression varies in response to differences in orientation and frequency information.

Orientation processing is the result of low-level processing of V1. In 1966, Campbell 
and Kulikowski provided psychophysical support for the neurophysiological findings regarding 
line orientation selectivity. Psychophysical measurements were performed to evaluate whether 
the neural mechanisms underlying human perception paralleled findings from the series of 
physiological experiments performed by Hubel and Wiesel, which presented evidence that 
neurons in V1 responded preferentially to specific orientations. In the Hubel and Wiesel 
experiments (1962, 1965), neuronal response diminished considerably for deviations from 
preferred orientations around 10-15 degrees and did not respond to orientations that deviated 
from preferred orientation greater than 30 degrees. In Campbell and Kulikowski’s experiment, 
participants were tasked with adjusting the contrast of a vertically oriented test grating to the 
point of just noticeable detection when superimposed with a mask grating at suprathreshold 
contrast levels (1966). Mask gratings were presented at horizontal, oblique (20, 30, and 40 
degrees), and vertical orientations. Findings of this experiment were analogous to Hubel and 
Wiesel, as the masking effect by superimposed gratings decreased as the angle between the mask 
grating and the test grating increased. Analogous to the findings presented by Hubel and Wiesel 
(1965), these findings suggest that neural mechanisms are highly selective to line orientation. In 
general, neural mechanisms must extract stimulus features, such as the orientation of an edge, 
and integrate these features from visual information contained within lower processes (Hubel & 
Nauhaus, Benucci, Carandini, and Ringach (2008) found that V1 neurons lying in homogeneous 
areas of orientation preference have a higher degree of tuning response than neurons in
heterogenous areas of orientation preference; in that, a region of cells will preferentially respond to only one type of stimulus. The authors suggest that there is a relationship between tuning bandwidth and cortical mapping, as neural computation varies across the cortical surface. From this patterning, the visual system may group these elements, which allows for the eventual detection of features as unified percepts within the visual scene. Specifically, low-level processing by neurons in V1 seems to code orientation information; whereas, the integration of orientation into object boundaries, or contour integration, is considered to be the result of processing beyond V1 (Marr, 1982).

Blakemore and Campbell (1969) found that neural mechanisms are also differentially “tuned” to specific spatial frequencies. Spatial frequency generally refers to spatial scale or grain and is typically quantified by the amount of pattern repetition in cycles per degree (cpd). By varying contrast and spatial frequency of sinusoidal gratings, the authors observed that neural mechanisms sensitive to lower spatial frequencies are more broadly tuned than neural mechanisms that respond to higher spatial frequencies, which are more narrowly tuned. Typically, it is thought that low spatial frequencies convey coarse, global information within a visual image or scene while high spatial frequencies convey information regarding refined, local information (Lamb & Yund, 1993; Boeschoten, Kemner, Kenemans, & van Engeland, 2005).

Taken together, this link between physiology and perception suggests that neurons in V1 are differentially selective to features within an object, such as line orientation, direction of movement, and size. Object boundaries and textures are encoded by neurons in V1 selective to the combination of these elements into edges and corners (Hebb, 1949; Hubel & Wiesel, 1959, 1962, 1965; Campbell & Kulikowski, 1966), which form intracortical neuronal circuits that may be cohesively linked both temporally and spatially (von der Malsburg, 1981; Eckhorn et al.,
1988; Singer & Gray, 1995; Eckhorn, 1999; Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Quiroga, Kreiman, Koch, & Fried, 2008). Additionally, low-level neural mechanisms selective for orientation are sensitive to spatial frequency as well as other monocular cues, such as shading, contrast, luminance, and retinal size. However, interaction with our environment depends on the visual system’s ability to correctly perceive 3D shape. The nature of the neural mechanisms responsible for the extraction of 3D shape from 2D retinal images has been investigated over a wide range of studies. To date, research regarding the underlying neural mechanisms responsible for 2D and 3D perception has bifurcated primarily along two paths: 1) the extraction of shape from shading and texture and 2) the extraction of shape from line orientation and contours. Furthermore, the possible role of cognitive factors, such as affect, on orientation and spatial frequency information in 3D shape perception remains uncharacterized.

*The role of orientation in 2D shape perception*

The perception of the form of an object hinges on the perception of orientation signals (Gibson, 1950). Hubel and Wiesel found that cells within V1 varied in preference for complexity within the visual scene. Neurons are not only specific for orientation but also respond preferentially for length, corners, and angles (1959, 1962, 1965). In order to identify components within the visual scene, the properties of an object must be contained within a border in order for the form of the object to be distinguished from the rest of the visual scene, and thus contours and borders must be extracted early in the process (see Figure 3). In V1, the summed reflectance of light from the object’s surface area is demarcated by these oriented borders. Thus, the surface of an object reflects light relatively uniformly across the surface area. Neurons that correspond to an object’s uniform surface produce weaker signals. Change in
available light from cessation of an object’s surface area, which creates the object’s edge, produces stronger signaling patterns in V1 (Barlow, Fitzhugh, & Kuffler, 1957; Hubel & Wiesel, 1965). Provided that objects within a visual environment have properties containing patterns of oriented components, basic shapes – or forms – of objects within the visual environment can be encoded. The visual system’s ability to distinguish objects in the visual field stems from the recognition of these object contours and boundaries, which are conveyed by neuronal activation of differences in contrast, shape, and surface texture (Gibson, 1950; Hubel & Wiesel, 1962, 1965). By distinguishing features of objects within the visual environment, regions within the visual scene may be perceptually grouped as objects from their neuronal activation patterns.

However, Marr (1982) poses a problem for contour grouping within V1. Specifically, there is an overabundance of “edge” contenders available for detection within a visual scene (e.g. those created by shadows which do not define objects); this creates greater noise from redundant signals from overlapping RFs (von der Malsburg, 1981). In order to achieve the perception of a 3D world, the visual system must first segment these signals not only by object but also by features within an object. To accomplish this, the visual system must identify the boundaries of object(s) relative to a background within a 3D space by unifying line segments according to their particular orientations. However, the process by which contours are bound together to form a unified percept is inherently problematic, as it bears a risk for incorrect feature binding among objects that share similar receptive fields (Humphreys, 2001). Additionally, objects within a naturalized visual environment do not necessarily follow symmetrically or linearly linked groupings, as object contours have greater variability in terms of direction and orientation (Hess & Field, 1999).
The role of orientation and spatial frequency in tilt/slant underlying 3D shape perception

Surface textures, and how they change across the image of a 3D surface, play an important role in conveying 3D shape. Deviations of surfaces within the fronto-parallel plane, or x-y plane, refer to tilt; slant refers to deviations out of the x-y plane, such that the surface contains variations in depth within the z axis. Two paths in which changes in surface textures have been studied are texture gradients and orientation information. Figure 4 shows changes in spatial frequency and orientation information that may occur within the x-y plane to components contained within a visual image. In existing models of 3D shape perception from surface texture (Gibson, 1950), there are assumptions of uniformity across the surface, in which 3D shape is extracted from the disparities of homogeneous (Todd & Akerstrom, 1987) or isotropic (Blake, Bulthoff, & Sheinberg, 1993) surface patterns. Isotropy refers to the uniformity in any particular direction; while, the assumption of homogeneity denotes uniformity for location, such as composition of elements between locations. With these assumptions in place, variation in uniformity across a textured surface can then be interpreted as modulations of 3D shape. Specifically, 3D shape may be derived from cues taken from these variations within images of the textured surface, including compression, density, and size. According to Cutting and Millard (1984), compression, which refers to the disparity between feature ratios within a textured surface, serves an essential role in conveying curvature of a surface; whereas, size and density best indicate slant and tilt. Rosenholtz and Malik (1997) revealed that discrepancies in both isotropic and homogeneous elements were necessary for correct 3D shape perception, as a simple linear algorithm could be applied to deconstructed linear parts of both planar and curved surfaces to produce good estimates of both surface orientation and shape.
A major shortcoming of texture gradient approaches is a lack of plausible biological models of gradient extraction. In contrast to texture gradient approaches, other approaches emphasize variation in the orientation of components across the projected image. Specifically, it has been shown that 3D perception from images of textured surfaces relies on the perception of orientation, a low-level feature, and that in this kind of approach the conditions of homogeneity and isotropy need not be assumed (Li & Zaidi, 2000, 2004). Additionally, biological plausibility of this model stems from the reliance of orientation and spatial frequency information, which are features visual neurons are well-equipped to detect.

Accurate 3D shape perception is dependent on the visibility of orientation flows (Knill, 1992; Li & Zaidi, 2000, 2001a, 2001b, 2001c, 2004; Zaidi & Li, 2006) (see Figure 5). Orientation flows within surface patterns run parallel to the surface curvature, such that the oriented component critical to 3D shape depends on the shape of the surface. For example, in the vertically corrugated surfaces in Figure 5, it is horizontal texture components that create the necessary wave-like flow patterns that enable the correct perception of the shape of the surface. For horizontally corrugated surfaces, vertical texture components would create the necessary flows. The visibility of orientation flows is affected by surface curvature, spatial frequency (Li & Zaidi, 2009), number of oriented components, and the proximity of oriented components to the flow (Fowler & Li, 2013). Spatial frequency cues can convey incorrect information about depth in the absence of orientation information, and thus 3D shape may be misperceived (Li & Zaidi, 2000, 2003, 2004). The dominance of orientation over spatial frequency in the perception of 3D shape was further shown for both shallow and steep surface shapes for slanted and curved surfaces (Tam, Shin, & Li, 2013). Taken together, this evidence supports the existence of 3D selective neurons along the visual pathway (von der Malsburg, 1981) located in extra striate
areas, which are sensitive to orientation flows conveying information about convexity and concavity (Li, Tzen, Yadgarova, & Zaidi, 2008; Filangieri & Li, 2009; Verhoef, Vogels, & Janssen, 2012).

Three-dimensionality is automatically derived from 2D inputs (Koffka, 1935). Thouless (1931) suggests that 3D shape takes slant (of orientation information) into account, in which the perception of depth depends on the angle between the figural plane and frontoparallel. Although spatial frequency has been found to be unreliable for accurate depth and 3D shape perception (Li & Zaidi, 2000, 2003, 2004), it is still critical in the perception of form and should be simultaneously considered alongside orientation (Daugman, 1980) in investigating perception. Webster and De Valois (1985) found that responses by striate neurons were confined by frequency for only one preferred orientation. In other words, sensitivity to spatial frequency was dependent on orientation.

Global information of an image is conveyed via low spatial frequency changes and local information provides information in regards to details (Ginsburg, 1984). In turn, these changes in spatial frequency may contribute to perceptual organization of texture segmentation in determining figure-ground configurations of boundary contours (Wong & Weisstein, 1985; Klymenko & Weisstein, 1986; Merigan, Nealy, & Maunsell, 1993; Qiu & von der Heydt, 2005), feature contours, and depth cues (Frisby & Mayhew, 1979; Pentland, 1986; Brown & Weisstein, 1988; Grossberg, 1994). For example, higher spatial frequency sine wave gratings were more often perceived as figure than lower spatial frequency grating (Wong & Weisstein, 1985; Klymenko & Weisstein, 1986; Brown & Weisstein, 1988). However, when higher spatial frequencies were placed adjacent to regions of differing in spatial frequency (Schor & Howarth,
Three-dimensional shape information can arise from both monocular (Wheatstone, 1838; Schriever, 1925) and binocular (Julesz, 1971) cues, in which the retina may play a role in spatiotemporal prefiltering of visual images. The perception of 3D shape can be directly related to sensory experience apparatus, in that perceptual rules of organization are not needed to extract 3D shape from 2D inputs (Gibson, 1950). Given the noise of overlapping receptive fields, Marr (1982) suggests that computations were required by the visual system to achieve perception. In this theory, shape is considered a spatial property, in which retinal images of 2D contour depict 3D shape. Gollisch and Meister (2010) suggested that retinal neurons may provide selective computations regarding stimulus features, such as light adaptation and image sharpening (Ratliff & Hartline, 1959; Fuortes & Hodgkin, 1964). Specifically, early visual neurons can obtain information about visual images from the averages of pooled firing responses and removes the need to assume overly complicated neural networks to accomplish visual tasks (Gollisch & Meister, 2010). The extraction of 3D shape may be the result of feature detection by extra striate areas sensitive to orientation flows (Knill, 1992; Li & Zaidi, 2000, 2001a, 2001b, 2004; Zaidi & Li, 2006). The changes in a pattern or surface along the vertical or horizontal axis in the fronto-parallel x-y plane refer to tilt; whereas, changes to surface orientation out of the fronto-parallel plane refers to slant. Therefore, the projected visual image will contain many components at different orientations and spatial frequencies resulting from the tilt and slant of the projected surface.

Whereas the detection of orientation flows credits the presence of feature detectors in extra striate areas for the extraction of 3D shape, there is an alternative viewpoint suggesting that
3D shape is added by innate constraints on retinal inputs (Perkins, 1972, 1976; Poggio, Torre, & Koch, 1985; Pizlo & Stevenson, 1999; Pizlo & Chan, 2005; Chan, Stevenson, Li, & Pizlo, 2006). Stavrianos (1945) found that orientation information is not needed to match shape accurately, as 3D orientations were judged from the perception of object shape. Specifically, Stavrianos found that a decrease in slant is not matched by a consequent decline in shape perception. Therefore, shape is not the result of slant but more likely that slant is the result of shape (Attneave, 1954, 1959; Attneave & Frost, 1969). Li and Pizlo (2006) extended this finding to suggest that shape is not derived from depth or surface perception. This finding led researchers to view shape perception to be the result of a priori constraints that govern visual perception. Specifically, the visual system is a natural geometer, in which the world is reconstructed according to the rules of perspective projection relative to the geometry of the eyeball (Perkins, 1972, 1976) as well as the knowledge that the visual environment is 3D for which figure-ground organization must be applied (Pizlo & Chan, 2005; Chan, Stevenson, Li, & Pizlo, 2006; Pizlo, 2010). Constraints are therefore a product of evolutionary development of the visual system to not view the world as an assortment of parts to be assembled but rather to predict visual information from all possible interpretations of neural signals as a gestalt (Poggio, Torre, & Koch, 1985). Thus, 3D shape is not the result of the interaction of depth cues. Rather, volume can be thought of as an innate constraint that must be added to the 2D retinal image to produce 2D retinal shape in order to reconstruct 3D shape (Pizlo, 2010).

However, competing evidence has shown that what might be considered “innate” may actually be the result of perceptual learning during visual development (Hochberg & Brooks, 1962). For example, the preferential selectivity of monocular neurons toward a particular orientation may occur during visual development (Blakemore & Sluyters, 1974), as kittens
reared in environments comprised of only vertical lines seemed to be blind towards horizontal stimuli. Furthering the debate, the existence of learning mechanisms was shown in long-term optimization of feature binding for shape recognition within cluttered scenes (Kourtzi & Welchman, 2015). Using brain-imaging techniques, the authors found that the visual system may use experience to tune the dynamic underlying neural mechanisms of intermediate processes towards particular features by which feature templates may be utilized for perceptual decisions. For example, global shape of objects may emerge from mechanisms involved with intermediate levels of processing (Bell, Gheorghiu, Hess, & Kingdom, 2011; Loffler, 2015), such as those selective for orientation flows (Li, Tzen, Yadgarova, & Zaidi, 2008; Filangieri & Li, 2009).

Research into late onset of vision has shown a remarkable ability of visual learning (Ostrovsky, Andalman, & Sinha, 2006). Though visual acuity may be compromised following congenital blindness, mid and higher level vision exhibit notable plasticity and function. Additionally, visual capabilities, such as visual parsing of images, are the result of the learning how images relate to one another in the visual scene (Ostrovsky, Meyers, Ganesh, Mathur, & Sinha, 2009). For example, motion-dependent experience was implicated as playing an important role in perceptual learning, which implicates top-down mechanisms of learning in low-level tasks (Jones, Sinha, Vetter, & Poggio, 1997).

The organization of visual information is influenced by extra-striate areas

The synchronization of linear neural networks

In the classic feed-forward model, perception results from the strict linear summation of convergence by receptive fields onto subsequent cells with larger receptive fields in a serial fashion (Hubel & Wiesel, 1959, 1962, 1965; Gross, Rocha-Miranda, & Bender, 1972). In order
to delineate the belongingness of visual elements into objects, perceptual organization may result from the brain’s use of algorithms applied to neural networks contained within areas of the visual system. One source of information for such purported algorithms may be synchronous timing of neuronal firing. Specifically, Hebb (1949) proposed a theory of perception in which neurons that respond to edges and corners of objects in the visual environment form a circuit of specific cells called cell assemblies. With repeated exposure to the sensory experience of a particular stimulus, increased neural activations of cell assemblies promote growth within the synaptic activity among neurons thereby making the perception more readily available. Elements of this theory are summed in the notion that neurons that fire together in cortex are bound together as a unified percept. Neurophysiological support for this was developed as the temporal correlation theory, which postulates that feature detection and unification occurs as function of temporal synchronicity of neurons (von der Malsburg, 1981; Singer & Gray, 1995; Eckhorn, 1999). The noise created by an overabundance of neural signals from overlapping receptive fields (Marr, 1982) is reduced by global GABAergic expression, creating an environment in which neural networks vie for dominant expression (von der Malsburg, 1981). Specifically, neurons linked by horizontal connections that are temporally correlated are more likely to overcome the inhibitory conditions and therefore be expressed to higher visual areas (Callaway, 1998).

Object form may emerge as a result of the detection and unification of orientation information into contours and ultimately shape, as objects are encoded and subsequently characterized by a synchrony of proximal and distinctive neuronal firing pattern across a large distribution of neurons and not the result of a single neuron (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Quiroga, Kreiman, Koch, & Fried, 2008). Eckhorn et al. (1988) examined whether temporal synchronicity links features of spatial consistency together. In their study, proximal
stimuli at spatially distant locations were presented to premapped receptive fields in area 17 of cat cortex. Single-cell recordings and multiple-site recordings as well as signal correlations were analyzed for coherence relative to location. Specifically, when activated by a specific stimulus feature like position, orientation, or the direction and velocity of movement, coherent neural resonances were found throughout the visual cortex when similarities existed within stimulus properties during primary encoding. These results suggest that the neural responses within layers along related visual areas were temporally coded by phase-locked neural mechanisms and therefore linked across a vertical column, between neighboring hypercolumns, and between 2 cortical areas. Therefore, Eckhorn and colleagues concluded that the neural circuitry formed from these assemblies were temporally associated and therefore encoded as a combined percept. 

In 1991, Engel and colleagues extended these finding of temporal synchrony across hemispheres (Engel, König, Kreiter, & Singer, 1991) and to extra-striate areas beyond V1 (Engel, Kreiter, König, & Singer, 1991). MT neurons in cat cortex displayed synchronized bursting patterns in both left and right hemispheric neurons to the presentation of a whole object. In contrast, the presentation of an object that was split apart produced a less synchronized oscillatory response. Using drifting grating patterns as either independent objects or parts of a solitary object, Alais, Blake, and Lee (1998) found a correlation between variations within the contrast of a grating and the firing levels in neurons specific to the grating. Thus, contrast modulations that were temporally correlated augmented perceptual coherence and presumably underlying cortical neuronal response; whereas, modulations that were uncorrelated exhibited discordance in neuronal response. Taken together, these studies suggest that the encoding and unification of an object is captured in space and time as synchronized activity of neuronal mechanisms. Blake and Yang (1997) suggested that the resulting coherence of spatial features increases the visual
system’s ability to correlate neural activations into a unified percept. Therefore, the visual system will conclude that uncorrelated activity belongs to different objects. The visual system may attribute a relationship across striate and extra-striate areas of correlated neuronal oscillations (Engel, Kreiter, König, & Singer, 1991) in order to unify features within and between visual hemifields (Engel, König, Kreiter, & Singer, 1991).

This emphasis on the visual system to parcel out huge effects from timing patterns within neural signals stems from work conducted by Hubel and Wiesel (1959, 1962, 1965) and continues into feature integration theories (Balasubramanian & Sterling, 2009). The integration of specific timing patterns within neural responses minimizes noise and diminishes the need for complicated computations. Recent theories of visual processing, for example, require more computational necessity. Ensemble perception, which suggests that the visual system inherently summarizes similar features within the visual environment, is a flexible theory that allows for the coarse representation of visual information creating a complete gist impression of the external environment (Ariely, 2001). To accomplish this, neural mechanisms underlying visual representation reflect overall statistical properties rather than individual components (Ariely, 2001). For example, it is not necessary to encode the details for each leaf on a tree. Therefore, representation of a complete veridical percept is merely an impression of the external world comprised of sets of statistical summaries for visual areas (Ariely & Burbeck, 1995; Ariely, 2001). Perceptual experiences are therefore the result of derived averages of similar components within the visual environment. Haberman and Whitney (2009a) suggest ensemble coding occurs rapidly (Haberman & Whitney, 2007; 2009a) at multiple areas along the visual pathway. Not only have ensemble mechanisms been suggested for low-level features such as size (Ariely, 2001; Chong & Triesman, 2003) and orientation (Parkes, Lund, Angelucci, Solomon, & Morgan,
2001), but Cavanagh (2001) suggest that ensemble coding may serve to drive texture perception, as deviations from uniform textures may be more readily detected, and extend to more complex objects such as faces and affective face perception (Haberman & Whitney, 2007, 2009a, 2009b, 2012). Additionally, ensemble mechanisms extract summary statistics regarding the mean of features based on frequency across time in which the representation by separate ensemble mechanisms specific for extracting various types of features are dependent on proximal relationships among visual objects in the environment (Haberman & Whitney, 2007, 2009a, 2009b; Haberman, Brady, & Alvarez, 2015). Specifically, results indicated that statistical summary characteristics were independently processed across low-level and high-level features.

The saliency of nonlinear neural networks from top-down modulation

The synchronized firing response to visual information, particularly objects, can be modulated by attention. For example, Roelfsema, Lamme, and Spekreijse (2004) found that perceptual grouping within the same object produced stronger rates of covariation of V1 neurons when mediated by cognitive factors, specifically attention. The underlying mechanisms of the visual system reflect an adaptable, complex network of properties. The complexity of neuron type in V1, where neurons early in V1 show preferential tuning to elements of a scene, such as orientation and edges (Hubel & Wiesel, 1959, 1962, 1965), to more multifaceted composites of the scene, including shape, surface textures (Landy & Bergen, 1991; Nakayama, 2005) indicates a vast ability of V1 in terms of image processing. V1 neurons are dynamic, as the response of a neuron may be enhanced, suppressed, and altered in tuning by its intra-cortical circuit (Gilbert & Wiesel, 1990; Ringach, Hawken, & Shapley, 2003; Shapley, Hawken, & Ringach, 2003). Further processing within V1 is thought to be the result of the interactions between intracortical
connections of neural circuits with varying types of modulation. Specifically, the response of a neuron in V1 may be modified by the activation of neighboring neurons (horizontal connections) within its circuit membership (Domijan, 2001) through contrast modulation (Zipser, Lamme, & Schiller, 1996), lateral inhibition (Volberg, Wutz, & Greenlee, 2013), or cross-orientation suppressive mechanisms (Allison, Smith, & Bonds, 2001). Additionally, areas outside of V1 may influence intracortical neural circuits through intercortical (vertical) connections between areas beyond the striate cortex. A vast array of research has shown that processing in V1 occurs through top-down modulation (feedback) by extra-striate areas acting upon V1. Thalamic inputs conveying primary sensory information account for approximately 35-46% of total inputs into V1 (Chung & Ferster, 1998; Paradiso, 2000). The remaining majority of inputs are from areas higher in the visual pathway that provide top-down feedback on neuronal expression in V1.

Top-down feedback directly and indirectly influences horizontal connections within neural networks in V1, in which feedback may influence mechanisms of contrast modulation, lateral inhibition, and cross-orientation suppression. Orientation information for flow extraction is provided by excitatory inputs by the LGN into V1. Given the global inhibition on noise created from overlapping receptive fields conveying similar information (von der Malsburg, 1981; Marr, 1982; Rao & Ballard, 1999; Carandini & Ferster, 2000), these inputs are broadly tuned for all orientations below threshold levels (Ringach, Hawken, & Shapley, 2003), which leads to stimulus selectivity of feed-forward striatal neurons for orientation and direction (Carandini & Ferster, 2000). This phenomenon is known as the “ice berg” effect. Intracortical connections may therefore be augmented or diminished by circuit membership from which membrane potential tuned for orientation is sharpened by lateral connections. Top-down cognitive factors, such as attention, familiarity, or affect, may serve to increase the saliency of
neuronal circuits by affecting the speed of neural activity and magnitude of neural processing (Gazzaley, Cooney, McEvoy, Knight & D’Esposito, 2005) or “sculpt” broadly tuned neurons of competing neuronal circuits above threshold (Carandini & Ferster, 2000; Ringach, Hawken, & Shapley, 2003). The dynamic nature of neurons in V1 for orientation tuning may therefore be shaped by rapid excitation and equally rapid lateral connections (Ringach, Hawken, & Shapley, 2003).

Distributed and paralleled processing of visual information as a pattern of activation across many neurons allows for great flexibility and efficacy. Feature detectors throughout the visual pathway results in a master feature map, in which different locations within the visual array are competing for saliency (Treisman & Gelade, 1980). For example, texture segmentation in V2 and object recognition in V5/V6 may be processed simultaneously for which shape recognition may precede and contribute to figure-ground processing (Peterson & Gibson, 1993, 1994). If this were more generally applied to the visual system, then the integration of information from features across visual areas specialized for specific aspects of vision would be useful as well as expedient, as top-down modulation may allow for processed information to be integrated more readily. For example, after the initial first pass of convergent information, the processing of visual information is distributed among their respective, specialized visual areas along the visual pathway. Along with information regarding experience from MLT (Kovacs, 1996), mechanisms in IT selective for concavity/convexity (Verhoef, Vogels, & Janssen, 2012) may be processed in parallel with mechanisms in V2 selective for spatial frequency, texture segmentation, and figure-ground organization (Merigan, Nealy, & Maunsell, 1993; Qiu & von der Heydt, 2005), in which the processing from higher visual areas may be used to augment or diminish the saliency of neural networks in lower visual areas.
Evidence for this top-down modulation is found in onset and response latency of visual area activation. Specifically, if there is a linear progression of activation and processing, then the onset of stimulus and response latencies should show a similar linear pattern of timing as information is processed by higher and higher levels in the visual pathway. However, Paradiso (2000, 2002) reports discrepancies in latency time periods of onset and offset neuronal activation between the dorsal and ventral pathways. For example, within the dorsal pathway, visual areas such as V1, MST, and FEF seem to be simultaneously activated, in which higher visual areas in the dorsal pathway process information faster than lower areas. In another study, Sugihara, Qiu, & Rüdiger von der Heydt (2011) utilized probability calculations to evaluate contextual integration speeds in V1 and V2 of *Macaca mulatta*. Using a direction of figure (DOF) signal task, the authors investigated whether the context of visual images (beyond the classic receptive field) of figure-ground selective neurons could be mediated by horizontal fibers within the cortex. Based on the velocities and lengths of known horizontal fibers and intercortical loops, the authors showed increased pooled response latencies of neural edge signals relative to what was predicted by horizontal signal propagation. Specifically, results suggested that the mechanism of contour integration, which is typically based on horizontal connectivity models, was temporally integrated in extra-striate areas and projected back down via intercortical feedback mechanisms, as intercortical fibers within white matter are faster in conduction velocity than horizontal intracortical fibers. Additionally, the length of intercortical fibers making circuit loops is not necessarily longer at <20mm than intracortical fibers. Finally, the outputs by V1 are reflective of sensory and cognitive influences (Li, Piëch, & Gilbert, 2004; Gilbert & Li, 2013). The implication is that perception is the result of distributed effort among sections of the visual system, which work concurrently at different velocities to integrate responses from
multiple/different areas in order to project to lower areas of the visual pathway. For higher-order processing, quicker processing times allows that visual information may be available to modulate lower areas of the visual pathway in a top-down fashion, which may increase (or suppress) the visibility of certain features (Hupé et al, 1998) coded in V1. Given the greater prevalence of intercortical inputs than thalamic inputs into V1 (Chung & Ferster, 1998; Carandini & Ferster, 2000) and the priority of neural networks over intracortical connections (Ben-Yishai, Bar-Or, & Sompolinski, 1995; Sugihara, Qiu, & Rüdiger von der Heydt, 2011), perception is prioritized by top-down modulation, in which differences in neuronal response patterns conveying orientation information may be affected (Ben-Yishai, bar-Or, & Sompolinski, 1995).

Emotion as top-down modulator of neural networks

Top-down mechanisms that have most dominated research inquiry of visual processes are attention, expectation, and affect. Current research on the role of emotion in visual perception focuses on the relationship between attentional mechanisms and emotion, specifically that emotion serves as an alerting mechanism to cue the brain to attend to a particular aspect within the visual array. Emotion may assist the visual system in interpreting signals in a variety of ways, as emotions may emphasize specific visual inputs. For example, perception of visual information in V1 was prioritized towards emotional content over other low-level features contained within the facial stimulus (West, Anderson, Ferber, & Pratt, 2011). As a result, response times to fear based stimuli may be faster (Lim & Pessoa, 2008). From an evolutionary perspective, emotional states are rooted in the conveyance of homogenous physiological reactions to stimuli in the environment (Dangleish, 2004), in which the expression of an
emotional state can be subsequently recognized by others as an egocentric sensory experience rather than allocentric communicative mechanism (Susskind et al., 2008). For example, fear/surprise is indicated by raised eyebrows and the opening of the eyes, which increases the visual field. The effect of this expression may serve to increase visual information. Due to the homogeneity of emotional expression, the recognition of emotional expression may assist in survival by providing the visual system context in which to organize sensory information.

Susskind et al. (2008) suggests that fear may serve to enhance visual perception through convergent mechanisms; whereas, the state of disgust diminishes sensory encoding. Therefore, the role of emotion is not just a form of social communication but may serve to run interference for sensory information for optimal adaptation (and survival) in the world. Additionally, emotion may serve to alert the brain to activate attentional mechanisms in working memory (LeDoux, 1996) in order to promote perceptual organization and to protect a particular feature from competitive masking (Grossberg & Raizada, 2000), evaluate sensory experiences as reinforcing or punishing (Rolls, 1999, 2000), or provide a contextual reference of cost to benefit framework from which the brain can evaluate sensory experience more efficiently without continued ruminations regarding consequences (Zadra & Clore, 2011).

The amygdala has been shown to play a central role in the processing of fear related stimuli (Pascoe & Kapp, 1985; Campeau et al., 1991; Davis, 1992; LeDoux 1992; Amaral, 2003). Located within the temporal lobes, the amygdaloid complex consists of approximately twelve regions with numerous sub regions (Amaral, Price, Pitkanen, & Carmichael, 1992; Davis, 1992; Stefanacci & Amaral, 2000). In response to threat, increased neural activation of the c-fos protein by the central nucleus of the amygdala has been shown (Pascoe & Kapp, 1985; Campeau et al., 1991). Lesions to the central nucleus has shown to produce the abolition of the behavioral
fear response (Davis, 1992; LeDoux, 1992; Amaral, 2003). For example, Amaral (2003) found that monkeys with destroyed amygdala regions did not show signs of the fear response when viewing pictures of snakes. In a classical conditioning paradigm, LeDoux (2000) summarized the circuitry of fear, which involves reciprocal neurochemical connections between the amygdala, medial prefrontal cortex, locus coeruleus, hippocampus, and the HPA-axis. Sensory information is sent by the thalamus to the lateral nucleus and the basal nucleus of the amygdala, which shares connections with the hippocampus that conveys information about fearful stimuli and environmental contexts (memory). The prefrontal cortex has been implicated in emotional regulation, top-down processing and object recognition, behavior planning and execution, and working memory. Top-down modulation is mediated by GABAergic connections from the medial prefrontal cortex on the amygdala (Rodrigues, LeDoux, & Sapolsky, 2009). Emotional valence and attentional mechanisms have been shown to produce similar activations and processing patterns within the pathway (Vuilleumier & Driver, 2007). Vuilleumeier (2005b) suggests that amygdalal activation may augment and therefore influence different sensory modalities, especially visual processing, in order to promote adaptive behaviors. Several studies implicate two pathways of visual processing via the amygdala – one direct and one indirect (Das et al., 2005; Vuilleumeier, 2005b) to extra-striate visual areas, which serves to enhance or diminish emotional response in the primary visual cortex. The direct, and thus faster, pathway is thought to convey coarse visual information from the thalamus to the amygdala; whereas, the indirect pathway projects more refined visual input from the thalamus to the amygdala.

Affective primes – such as those that induce fear – reliably alter the perception of visual information. Lang and colleagues, for instance, found there to be different activation sites for pleasant versus unpleasant visual stimuli within visual areas of the brain (Lang et al., 1998). In a
meta-analysis of 105 fMRI studies using Ekman and Gur face databases in affective processing spanning from 1990 to 2008, Fusar-Poli (2009) and colleagues found that the processing of fear faces compared to baselines show significant activation of neurons in the bilateral amygdala, fusiform gyrus, right cerebellum, left inferior parietal lobe, left inferior frontal gyrus, and the right medial frontal gyrus. Additionally, the amygdala has been implicated in emotional modulation to early and late stages of the visual processing (Morris et al., 1998; Lane, Chua, & Dolan, 1999). Neurons in the amygdala seem to be hierarchical in organization (Stefanacci, Suzuki, & Amaral, 1996; Stefanacci & Amaral, 2002) and show emotion-specificity in temporal synchronization of activation sites (Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2001). In a study investigating impairment by amygdalal damage, perception and recognition of fearful expressions was not shown to be affected, as amygdalal contributions to the temporal nature of fear-based processing by the visual system was established at early (≈100-150msec) and late (≈500-600msec) stages (Rotshtein et al., 2010). Activation patterns may also present spatiotemporal differences within the direct versus indirect thalamo-cortical pathways and include other regions of interest, specifically the anterior cingulate cortex. In addition to the inputs of basal ganglia conveying sensory information received from the thalamus, the anterior cingulate cortex receives direct projections regarding immediate emotional states as well as motivation. Therefore, the anterior cingulate cortex may be responsible for the mediation of cognition and emotional components of neural processing (Bush, Luu, & Posner, 2000).

Affective cues are influenced by both the expression of face perception and environmental context in which the affective face appears (Aviezer et al., 2008). Specifically, the categorization of affective expression can occur early in perception and is strongly influenced by setting context, such as body position and contexts contained within a scene. Specifically,
affective perception may be the result of the mean representation of visual information independently occurring across low-level (such as orientation and color) and high-level (such as affective expression and personal identity) features (Haberman & Whitney, 2009b; Haberman, Brady, & Alvarez, 2015). In addition, the content of emotional valence affects the neural processes at several points throughout the visual pathway (Delplanque, Lavoie, Hot, Silvert, & Sequeira, 2004). For example, Zimmer and Kovács (2011) found face adaptation aftereffects in early and late visual processing mechanisms, though activations in late ventral activations produced weaker aftereffects than earlier pathway mechanisms. In early visual areas, the emotional arousal caused by fear can enhance sensitivity to contrast (Phelps, Ling, & Carrasco, 2006) as well as enhance sensitivity to tilt of low spatial frequency patterns (Bocanegra & Zeelenberg, 2009). In addition to sensory encoding, emotion has been shown to affect perceptual experience. In a series of experiments, Stefanucci and Storbeck (2009) found that emotional arousal amplified estimates of vertical (height) but not horizontal distances (length). Specifically, when viewing a specific distance from a 2nd story balcony, the perception of distance was overestimated relative to the same distance along a corridor. Given the differences in visual cues between the two conditions – hallway (indoor) compared to balcony (outdoor), a further experiment was needed to see if the effects of the outdoor experiment could be modified. The authors found that emotional arousal could be up- or down-regulated by participants in which up-regulation led to overestimation (Stefanucci, Proffitt, Clore, & Parekh, 2008; Riener, Stefanucci, Proffit, & Clore, 2011).
Conclusions

Visual stimuli can be rather complex, as there are seemingly infinite combinations of orientation and frequency components within the space of the visual field. Research has yielded much debate over mechanisms underlying emotion and visual perception, especially in terms of binding and higher order processing. Visual perception involves the blending of “bottom-up” sensory experiences resulting from the neural signaling of light information in the environment with “top-down” non-sensory processes originating in higher areas in the brain. The ability to perceive the external environment depends on the visual system’s ability to integrate the two sources to create a unified percept, beginning with light information in the visual field being projected as a 2D image across the retina. This information is then converted to electrical signals and conveyed to higher areas along the visual pathway. Neural mechanisms early in the visual pathway have been shown to be generally selective to line orientation (Gibson & Radner, 1937; Hubel & Wiesel, 1959; Campbell & Kulikowski, 1966). Perceptual organization may result from the expression of neural networks, in which synchronized activation patterns as well as retinotopic location, might serve to delineate the belongingness of visual elements into meaningful objects from contours. The visual system’s ability to distinguish objects in the visual field stems from the recognition of object contours and boundaries, which are conveyed by neuronal activation of differences in contrast, shape, and surface texture (Humphreys, 2001). Additionally, top-down mechanisms – such as emotional state – may serve the visual system by providing contextual reference in which to efficiently interpret these electrical signals.
CHAPTER TWO

Overview of Research

Purpose of the Research

Recently, Bocanegra and Zeelenberg (2009) have shown that non-sensory neural networks – specifically the networks that are associated with the affective state of fear – may influence orientation perception in 2D images. Since orientation information has been shown to play a critical role in the perception of 3D shape (Li & Zaidi, 2001a, 2001b, 2004), it may follow that the influence of affect on 3D perceptual judgments might be explained by its influence on 2D orientation perception, specifically as a function of spatial frequency information (Winston, Vuilleumier, & Dolan, 2003; Bocanegra & Zeelenberg, 2009). Bocanegra and Zeelenberg found that orientation sensitivity for low spatial frequency patterns is increased after presentation of fearful face stimuli while orientation sensitivity for high spatial frequency patterns after fearful face stimuli is reduced. The authors suggest that there is a fear-induced enhancement of dorsal (“where/how”) processing at a cost of inhibition to the ventral (“what”) pathway (2009). Therefore, emotional cues bias visual information to be preferentially processed for both “where” versus “what type” (Bocanegra, Huijding, & Zeelenberg, 2012). If the mechanisms underlying 3D shape perception receive input from mechanisms underlying 2D pattern perception, such as the proposed extra-striate mechanisms selective for orientation flows that convey 3D shape (Li, Tzen, Yadgarova, & Zaidi, 2008; Filangieri & Li, 2009), modulations by affective state of 3D shape processing may result from feed-forward neural mechanisms and thus be predictable from modulations on 2D patterns. Specifically, the effect of fear found by Bocanegra and Zeelenberg (2009) on the perception of orientation of 2D patterns would generalize to 3D shape as conveyed by 2D orientation information. In contrast, if affective
modulation of underlying processes of 3D shape differs from 2D pattern perception, then the effect of affect may be distinct between levels within the visual pathway. However, in an orientation discrimination task using 2cpd and 6cpd Gabor stimuli, Song and Keil (2013) report that the magnocellular and parvocellular distinctions are due to contrast, as perception of spatial frequency was not affected by affective primes (De Cesarei & Codispoti, 2011; Song & Keil, 2013). Song and Keil suggest that affect may be used by early visual areas to mediate the cost for subsequent processing. Therefore, affective processing may be facilitated by the speed of perceptual processing (Lim & Pessoa, 2008), as affective response seems to strengthen vision from the moment that a visual stimulus is presented (Barrett & Bar, 2009).

Research Questions

In light of the results just described, questions remain about the role of emotion on the perception of 2D patterns and the generalizability of its role from 2D patterns to 2D patterns that convey 3D shape, specifically the role of affect on the extraction of orientation. Furthermore, particular attention should be placed on determining the influence of top-down mechanisms – like emotion – on the relationship between orientation and spatial frequency in the integration of visual information contained within the environment. Therefore, the aims of this research were:

1. **To characterize the role of fear on 2D orientation detection** by examining the influence of fearful face primes on tilt perception of grating and plaid stimuli at low and high spatial frequencies (Experiment 1).

2. **To characterize the role of fear on 3D shape perception** by examining the influence of fearful face primes on 3D slant and shape perception of low and high spatial frequency
orientation flow patterns conveying surfaces slanted and corrugated in depth (Experiment 2).

3. To characterize the role of the face prime presence, paradigm differences, and ordering effects of fear on 2D orientation detection using gratings of low and high spatial frequencies (Experiment 3).

**Approach**

This research investigated the role of affective state on 3D shape detection. Specifically, we were interested in the characterizing the role of the affective state of fear on the detection of orientation, which is a low-level feature essential to the accurate perception of 3D shape. We were interested in extending previous findings by examining the effects of fear on the perception of orientation in stimuli containing one, two, and multiple orientations. Finally, we were interested in the relational contributions of orientation and spatial frequency. To address these goals, we examined how the effects of affect might generalize to different orientations, might alter the perception of orientation in more complex patterns, and might modify perception of patterns containing orientation flows conveying 3D shape. To address the relationship between orientation and spatial frequency, we measured sensitivity to changes in orientation using patterns at 2 (low and high) spatial frequencies.
**General Methods**

*Experimental Procedures*

*Participants*

Participants were generally recruited from a participant pool of university students taking an introductory psychology course. On occasion, 2 researchers (M. Fowler and E. Lockerman) served as additional participants. The research followed the tenets of the World Medical Association Declaration of Helsinki. Informed consent was obtained from each participant after explanation of the nature of the study. The research was approved by the Queens College Institutional Review Board. All had normal or corrected-to-normal vision.

*Apparatus and Presentation*

All stimuli were presented to participants on a calibrated 22 in. Mitsubishi Diamond Pro 2070 flat screen CRT monitor at a refresh rate of 100 Hz. The monitor is driven by a Cambridge Research Systems ViSaGe Visual stimulus Generator, which is controlled by a 3.2 GHz Pentium 4 PC using experimental code written in the CRS Toolbox for MatLab. Responses were recorded using a CRS CB6 infrared response box. Audio cues were provided to participants to indicate response recording.

Head positions were fixed with a chin rest in order for stimuli to be presented at eye level, 1 m away from the center of the monitor. Viewing was binocular in a dimly lit room. To minimize fatigue, participants were encouraged to take breaks as necessary in addition to a scheduled break between baseline and experimental sessions. For both baseline and experimental sessions, presented stimuli were randomized across trials.
Stimuli and Procedure

Sinusoidal gratings and plaids were viewed binocularly at 5 degrees in the periphery at a distance of 100cm. Pattern and surface shape perception were measured with and without affective face primes preceding each stimulus. In preliminary experiments (Experiment 1-2), fear versus neutral face primes were presented before single gratings (vertical and horizontal, individually) or plaid stimuli (vertical and horizontal gratings superimposed) for both planar (2D pattern) and corrugated (3D shape) surfaces. Orientation sensitivity in 2D images (Experiments 1 & 3) and sensitivity to 3D slant/curvature (Experiment 2) were measured at both low (2cpd) and high (4cpd) spatial frequencies. In replication experiments during Experiment 3, orientation sensitivity in the presence of face primes was compared to sensitivity in the absence of face primes. Affective face primes were taken from the Radboud face database (Langner et al., 2010).

Data Analysis

Data will be analyzed using repeated-measures or mixed factorial ANOVAs in IBM SPSS Statistical software, Version 22. Baseline tilt thresholds were compared for initial homogeneity in participant performance and used to determine stimuli at equivalently suprathreshold tilt levels for each participant in subsequent experimental conditions. In experimental conditions, orientation sensitivity was analyzed for mean differences as a result of the presence of affective primes. Specifically, mean differences in d-primes were evaluated for affect, orientation, and spatial frequency at α=0.05. Additional analysis was conducted for direction of tilt (positive or negative) for Experiment 1 and 3, axis of corrugation (concave and convex) for Experiment 2, and interactions for Experiments 1-3.
CHAPTER THREE: Experiment One

The role of affect on 2D orientation detection

Orientation perception is fundamental for object perception. Emotion has been shown to augment the detection of oriented visual components throughout the visual pathway (Morris et al., 1998; Vuilleumier, 2005). For example, in low-level vision, contrast sensitivity was enhanced following fearful face cues when compared to neutral face cues (Phelps, Ling, & Carrasco, 2006). In 2D pattern perception, orientation sensitivity has been shown to increase for low spatial frequency and decrease for high spatial frequency stimuli following fear face primes compared to neutral primes (Bocanegra & Zeelenberg, 2009). In the first experiment by Bocanegra and Zeelenberg (2009), participants were asked to judge whether peripherally placed Gabor stimuli appeared “tilted” or “not tilted”, and tilts were varied to determine tilt thresholds: the smallest detectable deviation in tilt from the vertical axis. Tilt thresholds, which are inversely related to sensitivity, were used to generate individual oriented stimuli that approximated 80% correct per participant at a range of spatial frequencies, 1.0cpd, 2.1cpd, 3.0cpd, 4.2cpd, and 6.0cpd. In the experimental condition, either a fearful face cue or neutral face cue from the Ekman Face Database was presented before test stimuli, which consisted of clockwise baseline tilted, counterclockwise baseline tilted, or vertically oriented Gabors, and subjects were asked to judge whether stimuli appeared tilted or not. Results showed increases in sensitivity for low spatial frequencies and decreased sensitivity for stimuli at higher spatial frequencies when stimuli were presented after fear faces relative to neutral faces. In a follow-up experiment, the benefits of emotion on low spatial frequency (2.1 cpd) and impairments of emotion on high spatial frequency (4.2 cpd) were eliminated when primes consisted of inverted
face cues (thereby minimizing emotional valence) versus upright face cues, which further bolsters previous findings (see Figure 6). The authors concluded that fear cues increase the visibility of tilt at low spatial frequency at a cost to high spatial frequency, which implies that visual processing in the dorsal pathway is enhanced at a cost to the ventral pathway.

The purpose of the first experiment was to extend the present findings by Bocanegra and Zeelenberg to other orientations and patterns, specifically horizontal gratings and horizontal-vertical plaid patterns containing more than one orientation. To accomplish this, our study employed a paradigm that is analogous to that used by Bocanegra and Zeelenberg. In their study, the authors examined the effects of emotion on the perception of orientation as a function of spatial frequency for 2D vertically oriented patterns. If the benefit of emotion to the dorsal pathway is at the cost of the ventral pathway, we expected similar findings for 2D horizontally oriented patterns as well as horizontal-vertical plaid patterns. Specifically, if differences obtained between the 2 cpd and 4 cpd spatial frequency patterns are the result of differential processing by the parvocellular and magnocellular pathways, then these differences should occur for the horizontal grating and horizontal-vertical plaid pattern, as these pathways are not thought to be selective for orientation. Therefore, enhancements and impairments between the two pathways should not be orientation specific. However, if there are differences in tilt thresholds for different spatial frequencies between oriented conditions, then we could conclude that the processing of spatial frequency is contingent on orientation of the stimulus and that affect influences neurons early in the visual pathway. If the effects of affect are not orientation specific, affective influence may occur beyond the processing of orientation information in V1.
Experimental Procedures

Participants

Twelve participants (2 authors and 10 naïve) were recruited to run 3 experimental conditions. All self-reported normal or corrected-to-normal vision.

Apparatus and Presentation

All stimuli were presented on a calibrated 22 in. Mitsubishi Diamond Pro 2070 flat screen CRT monitor with a 1024 x 768 pixel screen. The monitor was driven by a Cambridge Research Systems ViSaGe Visual Stimulus Generator at a refresh rate of 100 Hz and controlled by a 3.2 GHz Pentium 4 PC. Experimental code was written using the CRS Toolbox for Matlab. Responses were recorded on a CRS CB6 infrared response box.

Head positions of participants were fixed using a chin-rest positioned 100cm from the stimulus monitor so that the visual angle for all presented stimuli was 6.5 degrees. The monitor was elevated such that the center of the screen was level with participant’s eyes. The mean luminance was 54 cd/m². All stimuli were presented 5 degrees from the center of the screen, which was marked with a central fixation point. Viewing was binocular. An audio cue was given to provide feedback to indicate the participant’s response as recorded. The experiment took place in a dimly lit room. In order to minimize fatigue, participants were encouraged to take breaks as needed in addition to a scheduled break between baseline and experimental sessions. Stimuli were randomized across trials.
**Stimuli and Procedure**

Participants were given verbal instructions, including background and purpose, regarding the nature of the experiment. Consent was obtained prior to task description. In order to assist in familiarization with the task, examples of visual stimuli were shown to participants, followed by time for participant questions and verbalizations of the task to confirm their level of understanding.

To measure sensitivity to orientation, sinusoidal luminance gratings were mapped onto a planar surface at 2 spatial frequencies for 3 pattern types: 2 cpd and 4 cpd for vertical (0° tilt), horizontal (90° tilt), and plaid (superimposed horizontal-vertical grating), respectively (see Figure 7). Using the method of constant stimuli, the tilt threshold, or minimum degree of tilt required for detection of deviation from horizontal or vertical axes, was determined for both positive (counterclockwise) and negative (clockwise) tilts. Sensitivity is inversely related to threshold, where higher threshold values indicate lower sensitivity (or reduced ability to detect). To determine baseline detection, stimuli were presented at tilt angles between 1-10 degrees in 1.0 degree intervals in either the positive or negative direction. Using a 2-alternative forced choice paradigm, participants were tasked with judging stimuli as tilted or not tilted while maintaining central fixation. After a practice session, participants ran the baseline session for both directions of tilt for each spatial frequency. For each session, after an initial 60s adaptation phase to the mean grey background, each of the test stimuli were presented either to the left or right of fixation for 40ms with a 10ms inter-stimulus interval (ISI) for a total of 10 times per tilt angle. Using a Weibull function curve-fit, baseline tilt thresholds were determined for correct detection at 80% for each spatial frequency, direction of tilt, and oriented pattern type per participant. In establishing reliable baseline measurements, initial ranges presented to participants were 1-10
degrees, from which smaller ranges may have been utilized for subsequent baseline measurements. For example, Figure 8 shows the Weibull function with a tilt range of 1-5 degrees for both positive and negative curve fittings. Baseline sessions were blocked per spatial frequency to include both directions of tilt; each spatial frequency was tested for each of the 3 pattern conditions.

Test stimuli were generated using baseline tilt thresholds for both the positive and negative tilt thresholds per spatial frequency per participant. All prime and test images were presented on a mean grey screen with a cross constantly displayed in the middle of the screen to serve as the point of fixation. Following a 60s fixation period during which participants adapted to the mean grey background, fearful or neutral face primes from the Radboud Database (3 male model pairs in total) were presented simultaneously in periphery 5° to the left and right of the point of fixation for 70ms prior to either a pattern at baseline tilt threshold or a non-tilted pattern presented randomly 5° to either the right or left of the point of fixation. Figure 9 is a schematic of the experimental timeline per trial. For each oriented condition per spatial frequency, each of the stimuli were presented 12 times per 3 pairs of fear-neutral primes for each of the 4 test pattern conditions for a total of 288 trials. Test pattern conditions consisted of a positively tilted stimulus, a negatively tilted stimulus, and a vertically oriented (not tilted) stimulus, that latter of which was presented twice as many times as the tilted stimuli per session so that the number of trials in which the stimulus was tilted equaled the number of trials in which the stimulus was not tilted. This design is required in paradigms used to extract d-prime (d’), the metric we used to measure sensitivity. D-prime was measured for each of the tilt conditions per face cue. D-prime is the difference between the z-transformation of correctly identifying a test as being tilted when the stimulus is actually tilted (hit) and the z-transformation of incorrectly a test as being tilted
when the stimulus is actually not tilted (false alarm), i.e. $d' = z(\text{hits}) - z(\text{false alarms})$. Response feedback was given per trial as 2 different tones.

**Data Analysis**

Baseline tilt thresholds computed as correctly identified at 80% as a function of tilt were recorded per participant. The mean baseline tilt threshold per direction of tilt, spatial frequency, and pattern type was compared to evaluate homogeneity of baseline thresholds (of generated images without affective influence) prior to the experimental paradigm. For the experimental conditions, $d'$ was averaged across each of the participants per face cue as a function of spatial frequency for each of the oriented pattern types. Data were analyzed using a repeated-measures factorial ANOVA in order to look at mean $d'$ differences between orientation, spatial frequency, affect, and their interactions at $\alpha=0.05$.

**Results**

**Experiment 1A:** In order to characterize the role of fear on orientation sensitivity for gratings at 2 orientations and 2 spatial frequencies.

Computed baseline tilt thresholds at 80% accuracy were evaluated for initial consistency in task performance across 12 participants for tilt direction (positive and negative tilts), spatial frequency (2cpd and 4cpd), and orientation (vertical versus horizontal gratings) without affective influence. Using a 2x2x2 repeated-measures factorial ANOVA, no significant effects or interactions were observed, $p>0.05$.

In the experimental condition, affective primes (both fear and neutral faces) were presented prior to individually generated grating stimuli for each computed tilt threshold.
obtained in the baseline condition. Participant d-primes (n=12) were recorded for each tilt direction (positive or negative), spatial frequency (2cpd and 4cpd), and affective face condition (fear and neutral) per orientation. Data were analyzed in a 4-way repeated-measures ANOVA. No significant overall main effects were found for tilt direction, orientation, affect, or spatial frequency. However, a significant interaction was found for orientation and spatial frequency, $F(1,11) = 4.968, p = 0.048$. Additionally, there were two 3-way interactions: affect, orientation, and spatial frequency, $F(1,11) = 6.491, p = 0.027$ and affect, orientation, and direction of tilt, $F(1,11) = 5.314, p = 0.041$. Figure 10 shows these results, in which tilt sensitivity is averaged across tilt direction per participant. The mean d' per affective cue and spatial frequency is plotted per orientation. No other significant effects were observed.

Separate 3-way repeated-measures ANOVAs were performed in order to characterize simple main effects for spatial frequency, direction of tilt, and affect as a function of each pattern of orientation. Similar to Bocanegra and Zeelenberg (2009), there was a significant interaction for spatial frequency and affect, $F(1,11) = 9.213, p = 0.011$ in the vertical condition. However, significance was not found for spatial frequency or affect, individually. In the horizontal condition, sensitivity for the 2cpd pattern ($M = 3.248, SEM = 0.518$) was significantly higher than the 4cpd pattern ($M = 2.399, SEM = 0.339$), $F(1, 11) = 5.015, p = 0.047$. For both conditions, no other significant effects were found. Thus, while the interaction found by Bocanegra and Zeelenberg (2009) was replicated for spatial frequency and affect for the vertical condition, we did not find this effect in the horizontally oriented condition.
Experiment 1B: In order to characterize the role of fear on orientation sensitivity for a pattern containing 2 orientations for 2 spatial frequencies.

Similar to Experiment 1a, a 2x2x3 repeated-measures factorial ANOVA was conducted on computed baseline tilt thresholds to evaluate homogeneity of sensitivity to tilt without affective influence for direction, spatial frequency, and oriented patterns (vertical, horizontal, and combined horizontal-vertical plaid). Significant differences were not found, $p > 0.05$.

Using the same participants (n=12) from Experiment 1A, d-primes were analyzed for the vertical, horizontal, and combined horizontal-vertical orientation conditions using a 4-way repeated-measures ANOVA. Data analysis showed an overall main effect for orientation, $F(2, 22) = 6.502, p = 0.016$. Using the Bonferroni procedure, post-hoc analysis revealed significantly greater orientation sensitivity for the vertical ($M = 2.587$, SEM = 0.415, $p = 0.036$) as well as the horizontal ($M = 2.823$, SEM = 0.395, $p = 0.018$) conditions than the horizontal-vertical combined ($M = 1.991$, SEM = 0.351) condition, where differences between the vertical and horizontal conditions were not significant, $p = 1.000$. Finally, there was a significant interaction between tilt and spatial frequency, $F(1, 11) = 4.918, p = 0.049$ (see Figure 11).

Given the result irregularities within the 3 pattern conditions, subsequent data analysis was performed to narrow these results with regards to number of components contained within oriented patterns. The d-primes were averaged per participant across vertical and horizontal patterns to compare to the horizontal-vertical pattern. However, findings were consistent with the previous analysis. An overall effect of sensitivity to averaged patterns containing one oriented component ($M = 2.705$, SEM = 0.387) were significantly higher than patterns containing 2 oriented components ($M = 1.991$, SEM = 0.351), $F(1, 11) = 14.286, p = 0.003$. No other overall main effects were found. Furthermore, no simple main effects or interactions were
revealed in a 3-way ANOVA performed for either the 1-component condition or the 2-component condition.

**Summary**

Results for this experiment show that orientation sensitivity differed across orientation conditions for single grating patterns. This finding is inconsistent with the suggestion by Bocanegra and Zeelenberg (2009) that the enhanced processing of the dorsal pathway (low spatial frequency information) is at a cost to the processing in the ventral pathway (high spatial frequency information). The results found by Bocanegra and Zeelenberg for the vertical oriented pattern were replicated but did not extend to horizontal orientation condition in this study. Therefore, the effects of affect seem to be orientation specific, which indicates that affective influence may occur in V1, where neural mechanisms have been shown to distinctly code for orientation. Our results show that sensitivity to tilt at different spatial frequencies changes as a function of the affective influence on orientation. We have shown in previous studies that the processing of orientation is influenced by the number of oriented components present (Fowler & Li, 2013). As the presence of both oriented components contained within the plaid pattern did not yield discernable differences for different spatial frequencies nor were the plaid pattern results analogous to results obtained by either single oriented grating condition, this suggests that visibility of orientation information is a target feature of affective influence over spatial frequency.
CHAPTER FOUR: Experiment Two

The role of affect on 3D shape perception

In 2D planar surfaces, perception of spatial frequency has been found to be contingent on orientation information (Webster & De Valois, 1985), such that the vertical orientation sensitivity differed for low versus high spatial frequency as a function of affective cues (Bocanegra & Zeelenberg, 2009). It has been proposed that monocular neural mechanisms extract orientation flows from images of curved surfaces for correct 3D shape perception (Li & Zaidi, 2001a, 2001b, 2004). In 3D shape perception, reliance on spatial frequency information in isolation may lead to misperception of 3D shape (Li & Zaidi, 2000, 2004). To test the generalizability of previous findings of fear on oriented components within a 2D planar surface to orientation flows created from 3D surface mappings, we used the same paradigm as Experiment 1. However, test stimuli were planar surfaces slanted away from the fronto-parallel plane along the z-axis (with slant angle being varied) as well as curved surfaces corrugated in depth along the z-axis (with amplitude of curvature being varied). Slanted and corrugated surfaces were patterned with vertical or horizontal gratings. Correct slant and curvature perception rely on the visibility of orientation flows that run parallel to the axis along which depth changes. Specifically, in the slanted surfaces, vertical gratings produce the necessary flow for floor/ceiling slants for which depth is changing along the vertical axis (see Figure 12 top, planar slants). Similarly, horizontal gratings produce the requisite flow in left/right slants for which depth is changing along the horizontal axis (Figure 12 bottom, planar slants). Similarly for horizontally corrugated surfaces for which depth changes along the vertical axis (see Figure 12, top, corrugated), vertical gratings produce the requisite flows, and for vertically corrugated...
surfaces for which depth changes along the horizontal axis, requisite flows are produced by the horizontal grating (see Figure 12, bottom, corrugated).

We expected that the vertical and horizontal conditions would produce findings similar to those findings in Bocanegra and Zeelenberg (2009), as we expect our results for the vertical patterns to mirror results obtained by Bocanegra and Zeeleberg and subsequently replicated in Experiment 1. Furthermore, we do not have apriori reasons to believe that the horizontal patterns would yield specific differences. Specifically, if the effects of affect on spatial frequency are the result of a benefit/cost by dorsal/ventral pathway processing, then we should see an interaction between spatial frequencies for each of the oriented conditions, as differences in spatial frequency between oriented patterns are not expected due to differential processing in the parvocellular and magnocellular pathways. However, if affect influences spatial frequency differently per orientation, then the differences between the vertical and horizontal oriented conditions should reflect any differences found in Experiment 1. Therefore, differences in amplitude thresholds between 2 cpd and 4 cpd stimuli per orientation would suggest that affective influence may modulate the extraction of orientation with respect to spatial frequency by early visual areas (Experiment 1) as well as continued processing of spatial frequency information with respect to orientation in mid-level vision where orientation flows for 3D shape are extracted. If no similarities are found in orientation conditions as a function of 2D and 3D surfaces, then the influence of affect on the processing of orientation information is different for 2D and 3D surfaces.
**Experimental Procedures**

**Participants**

Forty-eight participants were recruited for 4 experimental conditions (n=12 per condition). All self-reported normal or corrected-to-normal vision.

**Apparatus and Presentation**

All equipment, including hardware, software, and response box, as well as viewing conditions matched those used in Experiment 1.

**Stimuli and Procedure**

All participants were given verbal instructions regarding the nature of the experiment and shown images of visual stimuli. Participants were asked to verbalize their comprehension of the task as well as provided the opportunity to ask questions. Consent was obtained.

Vertical and horizontal grating stimuli were generated at 2 cpd and 4 cpd for 2 different 3D surface conditions: slanted planar and corrugated surfaces (see Figure 12). Patterns were mapped onto these surfaces using a volumetric texture mapping, which minimized the occurrence of frequency modulations in the surface texture (see Li & Zaidi, 2004). In this mapping, either a vertically or horizontally oriented grating was repeated along the depth axis to simulate a volumetric solid. From this solid, planar slanted or sinusoidal carving along the depth axis were rendered and the carved surfaces were projected in perspective. In the projected image, the orientation flows conveying 3D shape are generated by the horizontal grating for surfaces slanted to the left or right along the horizontal axis or for surfaces vertically corrugated in which the surface modulates in depth about the horizontal axis. For slanted floor/ceiling
surfaces or horizontally corrugated surfaces for which depth modulates along the vertical axis, the orientation flows conveying 3D shape are generated by the vertical grating. Frequency modulations are associated with surface depth and not surface slant (Li & Zaidi, 2003) and thus remain a poor indicator of shape in the absence of orientation information. The use of texture mapping via carved volumetric solids allowed that orientation flows be projected in the perspective into the image plane while minimizing frequency modulations (Li & Zaidi, 2000, 2003, 2004).

Slanted planar stimuli were created for both 2 cpd and 4 cpd for both vertical (floor/ceiling) and horizontal (left/right) slants at a mean luminance of 54 cd/m². Initial ranges of slanted planar stimuli began at 10-60 degrees in 10 degree intervals for both floor and ceiling slants. In a 2-alternative forced choice paradigm, participants were asked to determine whether the stimulus appears to be slanted or not slanted while maintaining central fixation. Baseline sessions were blocked by planar slant, in that participants either ran the vertical (floor/ceiling) slants for both 2 cpd and 4 cpd or horizontal (left/right) slants for both 2 cpd and 4 cpd. Using the method of constant stimuli, slant amplitude threshold was obtained per participant per spatial frequency and used to generate stimuli for the experimental conditions. The same paradigm and procedures used in Experiment 1 during baseline tilt threshold acquisition and experimental extraction of d’ were used in for slanted planar conditions.

In order to extend our examination to more complex, curved surfaces, vertical and horizontal gratings of 2 cpd and 4 cpd were mapped onto sinusoidally corrugated surfaces using the same volumetric carved mapping for both centrally convex and concave surfaces. Similar to the slanted planar condition, orientation flows are created by the grating component that is parallel to the axis along which depth is changing. For the vertical corrugations in which the
depth modulates along the horizontal axis, the orientation flows that convey 3D shape are generated by the horizontal grating. In the horizontally corrugated surfaces in which depth changes along the vertical axis, the orientation flows conveying 3D shape are generated by the vertical grating. Employing the method of constant stimuli, initial baseline corrugated depth amplitude thresholds were measured from a range of 2-20 centimeters with 2.0 centimeter intervals. In a 2-alternative forced choice paradigm, participants were tasked with determining whether the stimulus looked corrugated or not corrugated. All other paradigm and procedures used were analogous to Experiment 1 and the slanted planar condition of Experiment 2.

**Data Analysis**

For all slanted and corrugated conditions, baseline slant and curvature thresholds computed at 80% correct identification were recorded per participant. Similar to Experiment 1, mean amplitude baselines per direction, spatial frequency, and pattern orientation were used to quantify differences without affective influence. D-prime data were then averaged per experimental condition and analyzed using an independent factorial ANOVA for mean differences between orientation, spatial frequency, affect, and potential interactions at $\alpha=0.05$.

**Results**

*Experiment 2A: In order to characterize the role of fear on sensitivity to 3D slant for 2 pattern orientations for 2 different spatial frequencies.*

Using a 2x2x2 mixed factorial ANOVA (N=24), baseline slant thresholds computed for 80% correct identification were used to evaluate differences in slant thresholds for slant direction, as positive or negative, as a function of orientation (vertical versus horizontal) and
spatial frequency (2cpd versus 4cpd). For the 2 independent samples recruited for each orientation (n=12), no significant differences in baseline thresholds or interactions were observed for slant direction or spatial frequency, $p > 0.05$.

D-primes were assessed using a 4-way mixed factorial ANOVA for direction of slant, orientation, spatial frequency, and affective influence, in which independent samples were recruited per orientation (see Figure 13). Findings include a significant overall main effect of spatial frequency. Specifically, sensitivity to the 2cpd pattern ($M = 2.563$, SEM = 0.250) was significantly higher than the 4cpd pattern ($M = 1.905$, SEM = 0.220), $F(1, 22) = 24.080$, $p < 0.001$. A significant 3-way interaction between tilt, affect, and spatial frequency was found, $F(1, 11) = 4.984$, $p = 0.036$. No other significant effects were observed.

Finally, separate 3-way repeated-measures ANOVAs were run per orientation sample. In both the vertical condition containing floor/ceiling slants and the horizontal condition containing left/right slants, significantly greater sensitivity was found for 2cpd patterns (vertical: $M = 2.439$, SEM = 0.389; horizontal: $M = 2.688$, SEM = 0.314) over 4cpd patterns (vertical: $M = 2.038$, SEM = 0.339; horizontal: $M = 1.772$, SEM = 0.279), $p = 0.041$ and $p = 0.001$, respectively.

**Experiment 2B:** *In order to characterize the role of fear on sensitivity to 3D curvature for 2 patterns of corrugated gratings for low and high spatial frequencies.*

Thirteen participants were recruited for each of 2 orientation conditions, vertical and horizontal, for 2 spatial frequencies and 2 axes of corrugation. A mixed 3-way factorial ANOVA (N=26) yielded no significant differences in baseline curvature amplitudes for the independent-measure of orientation (vertical versus horizontal), the repeated-measure of spatial frequency (2cpd versus 4cpd), or the repeated measure of corrugation (concave versus convex), $p > 0.05$. 
A 4-way mixed factorial ANOVA was used to analyze results of affective influence on orientation, spatial frequency, and axis of corrugation. Significance was achieved for the overall main effect of affect, $F(1, 24) = 5.293$, $p = 0.030$, in which sensitivity to curvature amplitude was significantly diminished following fear face cues ($M = 3.354$, SEM = 0.315) than neutral face cues ($M = 3.562$, SEM = 0.350). A significant interaction was observed for affect and orientation, $F(1, 24) = 6.192$, $p = 0.020$. No other significant findings were found (see Figure 14).

Per orientation, separate 3-way repeated-measure ANOVAs were conducted. A significant result for affect was found within the horizontal condition, $F(1, 12) = 7.991$, $p = 0.015$. Specifically, sensitivity to curvature amplitude was diminished in horizontal corrugations following fear face cues ($M = 2.951$, SEM = 0.456) compared to following neutral face cues ($M = 3.382$, SEM = 0.556). No other significant effects were attained.

**Summary**

These findings suggest that affective influence on the perception of 2D surfaces is not generalizable to the perception of 3D surfaces, which bolsters previous findings that the general cost/benefit effect of affect in the dorsal/ventral pathways proposed by Bocanegra and Zeelenberg was not supported. In addition to this finding that affective influence on orientation processing is different for 2D and 3D surfaces, this study shows that affective influence on orientation processing is different between 3D surfaces, as well. Specifically, the differences between spatial frequency and relationship between affect and spatial frequency suggest that affective influence seems to modulate the extraction of orientation in slanted planar surfaces. In
corrugated surfaces, affective influences were dependent on orientation, in which fear seemed to hinder sensitivity to orientation in the horizontal condition.
CHAPTER FIVE: Experiment Three

The role of ancillary factors on affective influences and orientation detection

It has been shown that neuronal response for spatial frequency is orientation specific (Webster & De Valois, 1985). Bocanegra and Zeelenberg (2009) found changes in tilt sensitivity as a function of spatial frequency in 2D vertically oriented stimuli as a function of affective priming. Specifically, Bocanegra and Zeelenberg found that there was an influence of fear face cues on neuronal mechanisms for subsequent processing. Pizlo (1994) found that unreliable tilt cues (deviations around the horizontal-vertical plane) harm 3D shape perception more than slant cues (deviations in depth from fronto-parallel). In the previous experiments, we wanted to explore how affect might influence subsequent processing in the extraction of orientation information and therefore orientation flows necessary for 3D shape. In viewing the results of previous experiments, a clear relationship between affect has been shown for orientation and spatial frequency. Specifically, affective influence is orientation-specific; and, tilt sensitivity for different spatial frequencies changes as a function of affective influence on orientation. One possible application of spatial frequency and orientation is in processing 3D shape. In viewing the changes in spatial frequency in regards to orientation processing for accurate shape perception, we used different surface shapes, in which orientation information contributes to particular aspects of the visual scene and therefore is processed in different visual areas. Our findings were consistent with this, as the affective influence of changes in spatial frequency were linked to processing of orientation information by visual region. In considering our results, the paradigm we used was analogous to the paradigm used by Bocanegra and Zeelenberg (2009). However, there were a few considerations that we must consider in our inability to replicate
initial findings across orientations. For example, Bocanegra and Zeelenberg randomized spatial frequency (2.1 cpd and 4.2 cpd) within one session. However, in our studies, Experiment 1 and 2 were blocked by both orientation and spatial frequency to minimize participant fatigue. Therefore, order effects might have played a role in our ability to obtain desired results. Secondly, we were interested in whether the presence of the affective prime in itself might produce effects. Although Bocanegra and Zeelenberg did run a complimentary study using inverted faces, which did not produce affective affects, we sought to evaluate whether the mere presence of any affective prime would change our results. Other considerations included the use of the d’ metric by Bocanegra and Zeelenberg. Though the d’ metric is used to control for response bias during the experimental phase, we were interested in evaluating affective influence on sensitivity in order to view differences in homogeneity during baseline measurements as well as to ascertain the robustness of the effects of affect within another sensitivity paradigm. To accomplish this, we adapted the method of constant stimuli paradigm used for obtaining baseline measurements with our affective cues (fear face, neutral face, and non-face) to evaluate how affect might directly influence tilt sensitivity. Finally, in previous experiments, the visual acuity of recruited participants was self-reported, in which verification of corrected-to-normal vision was not determined. As a precaution, participants were given a visual acuity test prior to participation.

In this study, we sought to examine the relationship between spatial frequency and orientation in planar surfaces in order to evaluate ancillary contributions of our research paradigm on previous findings. Specific considerations for investigation were the contribution of order effects, the presence of an affective prime (as interference), and finally the utilization of
the d’ metric. We did not expect these variables to produce observable differences from current results.

**Experimental Procedures**

**Participants**

A total of 80 participants were recruited for 5 experimental conditions (n=16). All had normal or corrected-to-normal vision, as determined by acuity screening prior to participation.

**Apparatus and presentation**

All equipment, including hardware, software, and response box, as well as viewing conditions matched those used in Experiment 1 and Experiment 2.

**Stimuli and Procedure**

As in Experiments 1 and Experiment 2, all participants were given verbal instructions regarding the nature of the experiment, shown images of visual stimuli, and given a chance to ask questions. Consent was obtained following instructions. For the following 2 experiments, a Precision Vision ETDRS visual chart was used to verify the visual acuity of participants to be within a range not to exceed 2 diopters, or an approximate Snellen score equal to 20/40 or higher. Participants were blocked for order effects by spatial frequency, in which one-half of the participants viewed the 2 cpd gratings first while the second half initially viewed the 4 cpd gratings first. Additionally, the presence of an affective prime was investigated by the simultaneous inclusion of a non-face condition so that within each session, before each test grating, there was a fear face cue, a neutral face cue, or no face presented. To test the utility and
generalizability of the d' metric, the first experiment (3A) evaluated affective differences within these parameters using the d' metric, whereas the second experiment evaluated affective influences directly on tilt threshold.

In parallel to Experiment 1, vertical and horizontal gratings were generated at 2 cpd and 4 cpd onto planar surfaces in order to evaluate differences in tilt sensitivity due to presence of an affective prime using the d' metric. Using a 2-alternative forced choice paradigm with the method of constant stimuli, participants were asked to determine whether a stimulus looked tilted or not tilted. For baseline sessions, gratings ranging in orientation from -10 to +10 in 1.0 degree intervals were randomly presented 5 degrees to the left or right of the point of fixation for a total of 12 times per grating, or 240 trials per session. The Weibull function curve-fit was employed to determine sensitivity to changes in tilt at 80% correctly identified per condition. For each participant, individual test gratings were generated per tilt threshold (positive and negative) per spatial frequency (2 cpd and 4 cpd) to serve as test stimuli in the experimental condition. In the experimental conditions, affective cues (fear face, neutral face, or no face cue) were presented prior to the test grating for a total of 480 trials per session. All further baseline and experimental paradigms and procedures followed in parallel with Experiment 1, except for the addition of a no face prime condition during the experimental phase. Experimental blocking per sample was by orientation, in which grating patterns for both vertical and horizontal orientations were presented 12 times per 3 pairs of fear-neutral primes plus a no face prime condition for both 2 cpd and 4 cpd for a total of 432 trials per session. Spatial frequency conditions were counterbalanced for order effects across both the vertical and horizontal orientations experimental conditions.

In order to further investigate the impact of the non-face prime relative to the fear face and neutral face cues as well as the generalizability of results from previously obtained d'
measurements, affective primes were integrated into the previously used baseline tilt threshold procedure in order to evaluate differences in tilt sensitivity due to presence of an affective prime. Participants were blocked to view either vertical or horizontal grating patterns at orientations spanning 1-10 degrees either positively tilted or negatively tilted in intervals of 1.0 degree. Conditions were counterbalanced for spatial frequency. Using a 2-alternative forced choice procedure, participants judged whether the grating appeared tilted or not tilted following exposure to an affective prime. Affective primes were presented randomly and contained either a fear face cue, neutral face cue, or no cue across 720 trials per session. The Weibull function curve-fit was used to determine tilt thresholds for each of these cues at both 2 cpd and 4 cpd. All remaining paradigm procedures were consistent with Experiment 1 and Experiment 2.

**Data Analysis**

Similar to Experiment 1 and Experiment 2, an independent factorial ANOVA was used to compare baselines computed at 80% correct identification per participant per spatial frequency in order to analyze differences in affective influence on task performance in orientation and spatial frequency sensitivity. Additionally, these differences were evaluated with respect to order effects and the absence of affective cues.

**Results**

Experiment 3A: *In order to investigate the role of affective influence on orientation sensitivity for 2 gratings of 2 different spatial frequencies using face cues and no face controls,*

A 2x2x2 mixed factorial ANOVA (N=32) was used to evaluate computed baseline tilt thresholds at 80% correct identification for differences in tilt thresholds for tilt direction, as
positive or negative, as a function of orientation (vertical versus horizontal) and spatial frequency (2cpd versus 4cpd). For the 2 independent samples (n=16) recruited for each orientation, no significant differences or interactions were observed in baseline thresholds for slant direction or orientation, \( p > 0.05 \). However, greater sensitivity for 2cpd (\( M = 4.842, \text{SEM} = 0.223 \)) was observed than for 4cpd stimuli (\( M = 5.814, \text{SEM} = 0.235 \)), \( F(1, 30) = 30.930, p = 0.000 \).

In the experimental condition, affective primes consisting of either a fear face cue, neutral face cue, or no face cue were randomly presented prior to either the positively tilted or negatively tilted test stimuli generated per participant at 2cpd and 4cpd. Independent groups were recruited per orientation and d-primes were calculated within each group per direction of tilt (positive or negative) and spatial frequency (2cpd and 4cpd) for each cue affective condition (fear, neutral, or none). A 4-way mixed ANOVA was used to analyze results to compare the presence of affective facial cues to the no cue condition. Significant overall main effects were achieved for both affect, \( F(2, 60) = 5.365, p = 0.007 \), and spatial frequency, \( F(1, 30) = 6.636, p = 0.015 \) (see Figure 15a). Post hoc comparisons using the Bonferroni correction found that sensitivity for tilt was significantly decreased in the fear face condition (\( M = 2.517, \text{SEM} = 0.130 \)) relative to the neutral face condition (\( M = 2.826, \text{SEM} = 0.163, p = 0.043 \)) and the no face cue condition (\( M = 2.832, \text{SEM} = 0.157, p = 0.011 \)), in which there were no significant differences between the neutral face and no face cue conditions, \( p = 1.000 \), (see Figure 15b). As found in the baseline tilt thresholds, tilt sensitivity remains higher for 2cpd gratings (\( M = 2.920, \text{SEM} = 0.189 \)) than 4cpd gratings (\( M = 2.530, \text{SEM} = 0.115 \)), (see Figure 15c, left bottom panel). Finally, a significant interaction was found between affect and orientation, \( F(2, 60) = 3.118, p = 0.023 \). No other overall or interactions achieved significance.
Two 3-way repeated-measures ANOVAs were conducted per independent oriented condition to investigate the relationship between affect and orientation. For the vertically oriented stimuli, no significant effects were observed. However, a significant overall main effect in tilt thresholds was found for affect in the horizontally oriented condition, $F(2, 14) = 5.291, p = 0.019$. Bonferroni pairwise comparisons revealed a significant difference between the fear face cue ($M = 2.628, SEM = 0.159$) and the no face cue ($M = 3.097, SEM = 0.232$), in which sensitivity to tilt decreased following the fear face cue.

In subsequent data analysis, the role of counterbalancing conditions between participants that viewed the 2cpd then 4cpd and participants that initially viewed the 4cpd condition then the 2cpd condition was examined. D-primes were averaged across direction of tilt and organized between groups for orientation and order effects as well as within groups for affect and spatial frequency. A 4-way mixed factorial ANOVA was conducted to evaluate the differences in findings between Experiment 1a and Experiment 3a. No significant overall main effects or interactions were found as a result order effects, $p > 0.05$.

Experiment 3B: In order to investigate the generalizability of affective influence from the d-prime paradigm to the baseline constant stimuli paradigm for orientation sensitivity for gratings at 2 different spatial frequencies using face cues and no face controls,

Tilt thresholds were found using the method of constant stimuli paradigm utilized in the baseline collection procedures from previous experiments. The face cues (fear and neutral) and no face controls were presented prior to a range of test gratings either positively tilted or negatively tilted. Tilt thresholds were calculated using a Weibull fit at 80% correct identification following the presentation of the fear face cue, neutral face cue, or no face cue. Data analysis
was conducted to determine the role of affective face cues on baseline tilt thresholds for 2 oriented patterns (vertical and horizontal) at 2 spatial frequency gratings (2cpd and 4cpd). Using a 4-way mixed factorial ANOVA, overall main effects were found for spatial frequency as well as affect. Given the inverse relationship of threshold to sensitivity, sensitivity to 4cpd gratings ($M = 4.957$, SEM $= 0.244$) was significantly higher than 2cpd gratings ($M = 4.485$, SEM $= 0.230$), $F(1, 30) = 11.328$, $p = 0.002$. Post hoc analysis using the Bonferroni procedure yielded a significant difference between the 3 affective cues: fear face ($M = 4.770$, SEM $= 0.219$), neutral face ($M = 4.827$, SEM $= 0.229$), and no face cue ($M = 4.567$, SEM $= 0.248$), $F(2, 60) = 4.756$, $p = 0.012$. Of these pairwise comparisons, tilt sensitivity was significantly lower following neutral face cues than no face cue, $p = 0.033$ (see Figure 16a). Additional results showed significant interactions for affect and tilt direction, $F(2, 60) = 4.389$, $p = 0.017$ as well as affect and orientation, $F(2, 60) = 3.7279$, $p = 0.045$ (see Figure 16b, left bottom panel).

**Summary**

Despite adding the no face condition to the d-prime paradigm, results are still indicative of affective influence on visual information. Specifically, no differences were shown between the neutral and no face condition, but fear decreased overall sensitivity to visual information of orientation and spatial frequency. In further analysis, affect was shown to influence visual processing as a function of orientation but not spatial frequency. This finding was also shown in the constant stimuli paradigm, as affective differences were found as a function of orientation and direction of tilt (positive and negative tilt). Finally, no differences were found as a result of order effects.
Experiment One: To characterize the role of fear on 2D orientation detection by examining the influence of fearful face primes on tilt perception of grating and plaid stimuli at low (2 cpd) and high (4 cpd) spatial frequencies.

Our findings were consistent with previous findings by Bocanegra and Zeelenberg (2009) indicating that for vertically oriented patterns, orientation sensitivity of high spatial frequency patterns (4 cpd) is diminished following exposure to fear face primes while orientation sensitivity to low frequency patterns (2 cpd) is augmented following fear face primes. However, we found that this is not generalizable to horizontally oriented patterns or to patterns containing both vertical and horizontal components. Therefore, the conclusion by Bocanegra and Zeelenberg (2009) that affective influence serves to enhance dorsal pathway processing at a cost to processing within the ventral pathway is not supported by our findings, as orientation is low-level feature and should not be differentially influenced by affect (Hubel & Wiesel, 1959, 1962, 1965; Campbell & Kulikowski, 1966). In other words, the differential influence of affect on the two extra-striate pathways should not be orientation specific; however, our results suggest that they are.

The differences in how affect influenced tilt thresholds at different spatial frequencies was found to depend on the orientation of the pattern. Therefore, since affective influence appears to be orientation specific, it likely acts differentially on the orientation- and frequency-specific mechanisms in V1 (Hubel & Wiesel, 1959, 1962, 1965; Campbell & Kuliskowski, 1966;
Webster & De Valois, 1985). Therefore, differences in sensitivity found between spatial frequencies are the result of affective influence on visual processing of orientation information.

**Experiment 2:** To characterize the role of fear on 3D shape perception by examining the influence of fearful face primes on 3D slant and shape perception of orientation flow patterns conveying surfaces slanted and corrugated in depth at low (2 cpd) and high (4 cpd) spatial frequencies.

Consistent with results from Experiment 1, effects of affect were also not generalizable to areas beyond V1, where mechanisms that extract orientation flows for 3D shape perception may reside. Specifically, differences were found in how affect influences the perception of 2D versus 3D surfaces as well as different 3D surface shapes. Therefore, the suggestion by Bocanegra and Zeelenberg (2009) that a cost/benefit relationship as a function of spatial frequency within the dorsal/ventral pathway exists was not upheld beyond V1. In 2D images of 3D shape, changes in spatial frequency might serve to signal changes in depth in regards to determining the dimensions of object shape, relationships between objects, or establishing figure-ground. For example, smaller objects or parts of an object (which will contain higher spatial frequencies in the image) may be interpreted as farther away in depth from the observer. Additionally, 3D shape is generally considered to be processed in intermediate areas of the visual pathway, beyond V1. Therefore, our results are consistent with the notion that affective influence may differ in regards to processing level. As visual information is processed, then affective influence may also change to account for the increased complexity of constructed visual information of a percept from components along the visual pathway.
In considering the differences found between 3D surfaces, our data are consistent with our previous results in Experiment 1. Affect influences the processing of orientation information as a function of spatial frequency. Corrugated surfaces (used in Experiment 2b) may be viewed as being comprised of multiple planar slants (used in Experiment 2a). In particular, results of Experiment 2a translate to Experiment 2b, when viewed from the framework of processing complexity along the visual pathway. Namely, the processing of orientation, which affect might modulate, from V1 to higher areas would produce perceptual differences between spatial frequencies depending upon the specificity to a particular visual area. In other words, as visual information increases in complexity from 2D gratings to 2D images conveying 3D shape, higher level visual areas are recruited in processing this information. Affect may then differentially influence processing of orientation information of different spatial frequencies in regards to visual area. Our results did not indicate significant effects in slanted surfaces for affective cues or for a relationship between spatial frequency and orientation, suggesting that affective influence was limited to fronto-parallel planar and corrugated surfaces. However, we found a significant 3-way interaction in the slanted condition between direction of slant, affect, and spatial frequency (See Figure 17). In parceling out these effects, we found similarities in orientated conditions (vertical and horizontal) per spatial frequency (i.e. – vertical LSF looks like horizontal LSF; vertical HSF is similar to horizontal HSF), which is consistent with our finding no overall main effects of orientation. Given the lack of relationship between spatial frequency and affect, then the influence of affect seems to influence spatial frequency in terms of direction of slant. Moreover, the differences between spatial frequencies per orientation found in Experiment 1 are consistent with this experiment. However, in Experiment 1, fear decreased sensitivity to high spatial frequencies and only for vertical orientations. In Experiment 2, fear
seems to hamper sensitivity to low spatial frequencies. Furthermore, affective influence seems to prioritize direction of slant of the oriented flows relative to spatial frequency, which indicates a different processing level than V1, for both orientations.

In corrugated surfaces, the influence of affect on orientation was found to be clearly distinctive, as significant differences were found for horizontally patterned (vertically corrugated) surfaces while the role of spatial frequency decreased as more visual information was contained in the stimuli. When evaluating differences in surface information between slanted and corrugated surfaces, this switch in affective influence in processing spatial frequency for the extraction of orientation can be traced to the image complexity, as mechanisms processing the image are assembled from 2D to 3D perception. Thus, our results show that affect may differentially influence visual processing for orientation at multiple areas along the visual pathway.

**Experiment 3:** To characterize the role of the face prime presence, paradigm differences, and ordering effects of fear on 2D orientation detection using gratings of low (2 cpd) and high (4 cpd) spatial frequencies.

Results from Experiments 1 and 2 have highlighted the robust relationship between orientation and affect in 2D and 3D surfaces. In this study, we wanted to further investigate the role of affective influence on orientation sensitivity in regards to previous limitations from Experiment 1. In this study, the role of affect was shown to influence visual processing as a function of orientation but not spatial frequency for both the d’ and tilt threshold paradigms, which was consistent with Experiment 1. Furthermore, the inclusion of a no prime condition showed no differences in orientation sensitivity when compared to face primes, which rules out
the possibility that there is any general interference caused by the presence of the faces. In the d-prime condition, the overall effect of fear hampered sensitivity, as the neutral face and the no face cues did not differ. In contrast, only neutral faces seemed to differ from fear and no face cues in the constant stimuli conditions. Again, this similarity in fear and no face cues suggests that differences are due to affective influence and not the presence or absence of a cue conducive with interference of a cue.

However, the results of the d-prime paradigm were inconsistent with previous findings showing a relationship between affect and spatial frequency for vertical orientations. Specifically, as a result of the inclusion of the no face condition, the interaction between emotion and spatial frequency was eliminated. In evaluating the possible source for this disparity between Experiment 1a and Experiment 3a, systematic changes for this paradigm include the inclusion of the no face prime as well as differences in baseline measurements. Specifically, baseline threshold measurements used for test stimuli during the experimental phase were compared for homogeneity. In Experiment 1a, there were no significant differences in spatial frequency; whereas, there were significant differences in baseline threshold measurements between the 2 spatial frequencies (2 cpd and 4 cpd) in Experiment 3a. A major advantage of the d-prime paradigm is that it controls for bias. Therefore, homogeneity of baseline variance was not assumed to be of consequence in our research design, as differences in baselines would be equated for experimental sessions. However, in considering our paradigm across all experiments, Experiment 3a was the only experiment to show heterogeneity in baseline measurements. Given the consistency of findings in affect and orientation but not affect and spatial frequency, this disparity is likely due to these initial differences in spatial frequency during baseline acquisition. To investigate this suggestion further, empirical differences in
spatial frequency as a function of affect between the d-prime paradigm (see figure 14c, bottom panel) and the constant stimuli paradigm (see figure 15b, bottom panel) were considered. In Experiment 3b, all 3 face conditions were directly interleaved into the constant stimuli paradigm used in baseline acquisition, where homogeneity in tilt thresholds across spatial frequencies might be more variable because both sub- and supra-threshold tilts are presented. Specifically, we hypothesized that any perceptual differences in baseline tilt thresholds as a result of spatial frequency might yield differential results as a result of inherent sensitivities to the stimuli, such as contrast. Namely, the graphical representation of this interaction would produce lines that did not overlap as a function of our interaction between affect and spatial frequency. However, in Experiment 3b, our results were not only equal for affect when collapsed across orientation for spatial frequency, but the interaction between fear and neutral returned. Given that the overall visual information between 2 cpd and 4 cpd contains both perceived contrast differences as well as differences in the number of oriented bars, perceptual differences between 2 cpd (higher perceptual contrast, lower number of oriented bars) and 4 cpd (lower perceptual contrast, higher number of oriented bars) might reflect homogeneity in initial baseline measurements of tilt threshold necessary for data interpretation. As our results produced no significant effects for either ordering effects or the addition of the no face condition for either Experiment 3a or 3b, the lack of an interaction from Experiment 1a to Experiment 3a is likely the result of participant differences. Taken together, the results of Experiment 3a and 3b are consistent with results from Bocanegra and Zeelenberg as well as our findings in Experiment 1a to show the robust nature of the affective influence of fear on the relationship between spatial frequency and orientation, as the role of no face primes, paradigm differences, and ordering effects produced no effects in the detection of 2D orientations.
CHAPTER SEVEN

Final Remarks

Conclusions

The results of these studies indicate that top-down modulation of affect influences orientation perception differentially at multiple areas along the visual pathway. As a result of affective influence, we found differences in sensitivity to tilt for 2D images between the vertical and horizontal orientations as well as differences in sensitivity along the visual pathway as orientation is processed from 2D to 3D shape. In general, affective influence of fear was shown to modulate sensitivity to spatial frequency information, but this effect was dependent on orientation. Specifically, in tracking differences in spatial frequency across 2D images and 2D images conveying 3D shape, affective influence of fear was orientation specific for 1) vertically oriented patterns on 2D fronto-parallel surfaces and 2) 3D corrugated surfaces for which oriented flows around vertical conveyed 3D shape. Planar surfaces slanted in 3D space showed spatial frequency specific sensitivity in regards to direction of surface slant for both floor/ceiling and left/right surfaces. Taken together, this suggests that affective influence impacts the role of spatial frequency information within orientation processing across different visual areas (V1 for 2D patterns and beyond for 3D shapes).

The dominance of orientation specificity may serve to set a framework, from which changes in spatial frequency may signal changes within the visual array. For 2D patterns, our results indicated that changes in tilt sensitivity as a function of spatial frequency for vertically oriented stimuli may be the result of affective influence on V1, where neural mechanisms of orientation processing for the detection of edges underlie the identification of object boundaries.
As we move up the visual pathway beyond V1 to extra striate areas, orientation information contributes to 3D shape perception via the extraction of orientation flows (Li & Zaidi, 2001a, 2001b, 2004). Our results show different interactions between affect and spatial frequency for different 3D stimuli: namely, slanted versus corrugated surfaces. In considering the differences between these two surfaces, there is an increase in visual information from slanted to corrugated surfaces. Specifically, corrugated surfaces contain multiple slants. For the slanted stimuli, the role of affect on spatial frequency is distinguished by differences between low and high spatial frequencies. However, the effect of spatial frequency was not orientation specific for slanted surfaces. Of greater interest is how spatial frequency is different between our patterns due to affective influence than in the overall effect of spatial frequency. The significance of this 3-way relationship between direction of slant, spatial frequency, and affect points towards affective influence in processing spatial frequency in regards to directionality of orientation information conveyed by the slant, as floor/ceiling measurements were similar to left/right measurements. As stimulus complexity increases with the number of slanted components for corrugated surfaces, our results indicate spatial frequency decreases in importance for orientation processing. Specifically, in corrugated surfaces, the role of fear showed orientation specificity in vertically corrugated surfaces patterned with horizontally oriented surface patterns.

There are two things to consider in light of these results: processing along the visual pathway and texture segmentation by spatial frequency. Affect may influence spatial frequency as it is processed at different areas along the pathway depending on its contributions to orientation. As orientation processing progresses up the pathway to provide information in regards to edges (V1) to shape (beyond V1), then affect will influence the processing of...
corresponding information regarding spatial frequency. In early visual areas (V1), this relationship will be directed towards determining edges and size, particularly for determining vertically aligned orientations. Higher level processing of orientation for shape might be directed towards determining spatial relationships, like depth. In considering locations in space, spatial frequency has been shown to encode depth, or distance from the viewer (Li & Zaidi, 2003), where modulations in spatial frequency were correlated with perceived changes in depth. Additionally, spatial frequency has been shown to contribute to processing figure-ground relationships (Qiu & von der Heydt, 2005). V2 of the visual pathway has been implicated in spatial relationships regarding figure-ground organization (Merigan, Nealy, & Maunsell, 1994; Pizlo, 1994; Qiu & von der Heydt, 2005). In texture segmentation, spatial frequency has been shown to help establish figure-ground relationships, in which spatial frequency information can be coded as either figure (Wong & Wiesstein, 1985; Kylmenko & Wiesstein, 1986; Brown & Wiesstein, 1988) or ground (Frisby & Mayhew, 1979; Schor & Howarth, 1986). Spatial frequency was shown to be perceived as depth modulation, or distance to viewer, and not changes in slant or shape (Li & Zaidi, 2003). As effects of fear on sensitivity to tilt for different spatial frequencies was not orientation specific, the relationship between orientation and spatial frequency may not contribute directly to determining shape but rather towards determining directionality of oriented flows that encode shape, and the relationship may change with differential processing of visual areas specialized towards spatial arrangements, or depth. Area V4 of visual cortex has been implicated in contour processing (Pasupathy & Connor, 2002; Habak, Wilkinson, Zakher, & Wilson, 2004; Dumoulin & Hess, 2006), while area IT in monkeys has been shown to be selective for convex and concave surfaces, as conveyed in our corrugated condition (Verhoef, Vogels, & Janssen, 2012). Therefore, the lack of contribution by spatial
frequency on orientation flows for either vertical or horizontal conditions for our slanted or corrugated stimuli suggests that differences found between our slanted surfaces and corrugated surfaces may exist due to differences in orientation processing at different points along the visual pathway.

Spatial frequency may be treated independently along the visual pathway relative to processing of orientation information. In considering these differences in the treatment of spatial frequency towards orientation as we move from lower visual areas to higher visual areas, our results indicate a switch in affective influence from 2D vertical patterns on planar surfaces to 3D corrugated surfaces for which vertical patterns convey surface curvature. Spatial frequency may be coding for spatial relationships. Therefore, changes in spatial frequency of vertically oriented stimuli (of figures) seems consistent with the processing of 3D shape from texture cues, as perceptual organization of spatial frequency information from V1 to V2 has been shown to have differential results dependent on the presence of other oriented components. In 2D images, affective influence might serve to differentially increase the saliency of particular features relative to spatial frequency for discerning spatial relationships along the depth axis contained within the visual array. Specifically, spatial frequency may be used to code objects as closer or further away. In 2D images conveying 3D shape, affective influence might increase the saliency of spatial frequency of orientated components for depth configuration as it relates to orientation information. Specifically, fear might serve to hinder the perception of higher spatial frequencies (or lower contrast) and depth of 2D images. In the perception of shape, however, affect might serve to influence saliency of spatial frequencies in regards to providing cues towards directionality of oriented features in earlier visual areas processing shape and then differentially hinder orientation processing in higher visual areas coding for convex/concave shape perception.
**Limitations**

Perceptual judgments were made by human participants with normal or corrected-to-normal vision. We assume that data collected were produced from participants with the ability to detect and extract orientation information for visual stimuli. However, it was possible that participants selected from the participant pool may have been unable to effortlessly extract visual information from presented stimuli due to an unknown type of visual impairment affecting this ability or possessed outdated corrective wear. Additionally, cognitive factors that could impact participant fatigue or well-being (such as high levels of sleep deprivation, stress, emotionality, or mental exhaustion) were not assessed. Due to the copious amount of hours needed during data collection, a purely repeated-measures design was not feasible across all experiments.

Sets of visual stimuli were computer-generated using single grating and plaid patterns along the two primary axes – vertical and horizontal. Although orientation sensitivity was measured in references to a primary axis, oblique axes were ignored. Only two spatial frequencies (2 cpd and 4 cpd) were used. Additionally, gratings and plaids were limited in number of components. Therefore, the data collected reflect a simplistic representation of a vastly diverse amount of possible visual components that could be contained within the visual field. Images were generated in grey-scale, consisting of luminance values ranging from white to dark. Therefore, we cannot generalize findings to visual information requiring normal color vision. Finally, in regards to our affective primes, we used a limited number of models depicting a limited number of affective expressions: fearful versus neutral facial expressions. Generalizations cannot be made for other negative affective expressions or for positive facial expressions.
**Future Directions**

Although this series of experiments has highlighted the robust role of affective influence in orientation extraction, questions remain regarding the limitations of this finding. Future research is needed to extend these findings in regards to current understandings of this relationship and theories regarding 3D shape perception.

Continued research is needed in terms of image complexity. Specifically, given our consistency in finding affect differentially influences the relationship between spatial frequency and orientation, the discrepancy in results between the 2D single grating patterns and 2D plaid patterns may be related to cross orientation suppression mechanisms by vertically aligned and horizontally aligned orientations, in which the visibility of each orientated component suppressed the saliency of the orthogonal orientation (Morrone, Burr, & Maffei, 1982; Bonds, 1989; De Angelis, Robson, Ohzawa, & Freeman, 1992; Petrov, Carandini, & McKee, 2005; Meese & Holmes, 2007; Roeber, Wong, & Freeman, 2008; Li & Zaidi, 2009). As affect influences orientation perception, then the overall decrease in sensitivity to patterns containing both orientations suggests that saliency of one orientation is needed for affective effects. Experiments geared towards varying either contrast or spatial frequency of one of the components would reduce the cross orientation suppression produced by the orthogonal components and increase the saliency of one component. Within 2D images, this can be directly tested in a series of experiments designed to 1) increase the visibility of one orientation in the presence of its orthogonal orientation and 2) evaluate differences in spatial frequency in the presence of its orthogonal orientation. In the first series of experiments, visual stimuli of one orientated component may be reduced in contrast by various amounts. For example, the d-prime paradigm may be utilized to investigate vertically oriented stimuli at full contrast values superimposed
onto horizontally oriented stimuli rendered at half contrast. Despite the presence of the horizontal grating, we would hypothesize that results would resemble those found in Experiment 1a, in which an interaction would be found between spatial frequencies. Horizontally oriented stimuli at full contrast superimposed onto vertical stimuli at half-contrast would be expected to produce the same effects shown in Experiment 1a, i.e. no interaction of frequency and emotion. Furthermore, the method of constant stimuli might be used to look at affective differences in tilt sensitivity as a function of varying degrees of contrast in the orthogonal orientation (i.e. – full contrast vertical orientation superimposed onto a horizontal oriented grating ranging in contrast from 50% to 100% in intervals of 10%). Results should show systematic differences between the contrasted stimuli, in which 100% contrast should replicate findings shown in our data and 50% should resemble those in the extension study. While this proposed experiment looks at the role of contrast for affective influence on the relationship between spatial frequency and orientation, the second set of experiments would focus on the role of spatial frequency.

Specifically, this set of experiments would parcel out the effects of spatial frequency in the presence of oriented information of different spatial frequency information. We found that there were no affective effects on spatial frequency and orientation when 2 cpd vertical was superimposed on 2 cpd horizontal or 4 cpd vertical was superimposed on 4 cpd horizontal gratings. Using a double-disassociation design, the effects of spatial frequency on orientation sensitivity might be better reflected by pairing 2 cpd vertical grating onto a 4 cpd horizontal grating as well as 4 cpd vertical mapped onto a 2 cpd horizontal grating. From this, orientation sensitivity could be measured, as saliency of a particular orientated feature is increased with the release from cross orientation suppression mechanisms. Typically, the lower spatial frequency component will be more salient (Li & Zaidi, 2009). Although these experiments may be
rudimentary and highly predictable in nature, they are necessary in order to understand affective influence on V1 in order to properly generalize findings shown in this work.

Furthermore, findings should be considered in regards to 3D shape, in which plaid patterns are mapped onto planar slanted and corrugated 3D surfaces. Additionally, other types of plaids may also be investigated, such as the octoplaid pattern utilized in Fowler and Li (2013). In this pattern, oriented components may be systematically evaluated for orientation sensitivity – including oblique – angles as a result of affective influence. As surfaces are slanted or varied in depth from frontoparallel, cross orientation suppression mechanisms are released, thereby increasing the visibility of certain orientation and spatial frequency information. In systematically evaluating differences in 2D plaid patterns as a function of investigating the roles of spatial frequency and contrast, these findings may be used to consider the effects of affective influence in more complex images in order to generalize findings to more naturalistic viewing conditions, which remains an eventual goal in determining top-down cognitive factors on 3D shape perception.
Figure 1. Schematic of magnocellular and parvocellular projections of ipsilateral (red) and contralateral (blue) projections originating in the retina of the eye to thalamic layers (of the LGN), V1, and dorsal (purple) and ventral (green) pathways.
Figure 2. Depiction of the classic receptive field proposed by Hubel and Wiesel, in which adjacent flanking inhibitory regions (in black) oppose the center region (in white).
Figure 3. Depiction of the classic receptive field, in which adjacent regions oppose the center region, which is excited by light to code oriented borders within a visual scene.
Figure 4. Changes in spatial frequency and orientation of sinusoidal gratings. From left to right, spatial frequency increases while orientation changes in tilt by 45° increments from a vertically oriented pattern to horizontally oriented pattern with oblique orientations in the center.
Figure 5. Accurate 3D perception depends on the visibility of orientation flows. For vertically corrugated surfaces shown here, the requisite orientation flow is created by the horizontal component for 2 types of plaid patterns. For plaids containing 2 components (left panel, superimposed components vary by 90°) and 8 components (middle panel, superimposed components vary by 22.5°), the subtraction of the horizontal component (right panel) produces incorrect shape perception (Li & Zaidi, 2001b).
Figure 6. Results depicted by Bocanegra and Zeelenberg (2009) showing an interaction in tilt sensitivity (d') between spatial frequency and affective cue. The authors conclude that affective fear face cues increase sensitivity to lower spatial frequency (2.1 cpd) information but decrease sensitivity to higher spatial frequency (4.2 cpd) information.
Figure 7. Sinusoidal gratings used at 2 cpd for vertically oriented (left), horizontally oriented (middle), and plaid (right) experimental conditions. Bottom panel depicts each test grating at -5 degrees tilt.
Figure 8. Sample baseline data for an individual participant illustrating the extraction of tilt threshold using a Weibull fit. For each spatial frequency per orientation, measurements will be concurrently obtained for positive and negative tilt thresholds at 80% correct identification tilts ranging from 1.0 to 5.0 degrees. Each tilt stimulus will be presented 10 times for a total of 200 trials.
Figure 9. Schematic of timeline per trial. For each of our 6 experimental conditions, positive and negative tilted stimuli at baseline tilt threshold levels were generated per participant to serve as test stimuli. For each condition, test stimuli were randomized for tilt among negative tilt threshold grating, the positive tilt threshold grating, or a non-tilted grating and randomized for location to either the left or right of the point of fixation. Taken from the Radboud face database (bottom left panel), affective face cues (either fearful - left or neutral - right) were presented for 70ms followed by the 40ms presentation of the test grating.

**Per trial:**

- Preadapt = 60s
- Face = 70ms
- ISI = 40ms
- Test = 40ms

**Experimental Conditions:**
- Vertical – 2cpd
- Vertical – 4cpd
- Horizontal – 2cpd
- Horizontal – 4cpd
- Plaid – 2cpd
- Plaid – 4cpd
Figure 10. Results of Experiment 1a. Mean d' for 12 participants for both vertical and horizontal experimental conditions. Error bars represent the standard error of the mean.

N=12

**VERTICAL**

<table>
<thead>
<tr>
<th>Spatial Frequency</th>
<th>2cpd (LO)</th>
<th>4cpd (HI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>d-prime (d')</td>
<td>1.5</td>
<td>2.0</td>
</tr>
</tbody>
</table>

**HORIZONTAL**

<table>
<thead>
<tr>
<th>Spatial Frequency</th>
<th>2cpd (LO)</th>
<th>4cpd (HI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>d-prime (d')</td>
<td>3.0</td>
<td>2.5</td>
</tr>
</tbody>
</table>

Fear

Neut
Figure 11. Results for Experiment 1b. D-primes averaged across 12 participants for vertical, horizontal, and vertical-horizontal plaid conditions. Error bars represent the standard error of the mean.
Figure 12. Schematic of oriented stimuli at 2 cpd. Modulations to orientation patterns (middle panel) are shown for planar surfaces (left panels) and corrugated surfaces (right panels). Positive direction of slant and curvature amplitude (top panels) and negative direction of slant and curvature amplitude (bottom panels) are also indicated. For both types of surfaces, the critical orientation flow essential to conveying 3D slant and shape is created by orientation modulations around the axis along which depth is changing. For vertically oriented stimuli (top set of stimuli), the requisite flows are created by orientation modulations around the vertical axis, creating perceptible changes in amplitude of slant (floor/ceiling) or corrugation (convex/concave). For horizontally oriented stimuli (bottom set of stimuli), the necessary flows are generated by orientation modulation around the horizontal axis, creating perceptible changes in amplitude of slant (left/right) or corrugation (convex/concave).
Figure 13. Results of Experiment 2a. D-prime averaged across 12 participants for each experimental condition of grating orientation (vertical and horizontal) for slanted surfaces. Error bars represent the standard error of the mean.

N=24

VERTICAL (n=12)

HORIZONTAL (n=12)
Figure 14. Results of Experiment 2b. Mean d' for 13 participants (N=26) for both vertical and horizontal grating conditions mapped onto corrugated surfaces. Error bars represent the standard error of the mean.

N=26
Figure 15. Results of Experiment 3a. A.) Mean d’ for 16 participants for both vertical and horizontal experimental conditions (N=32), including no face cue (None). Error bars represent the standard error of the mean. B.) Mean d’ for affect, in which spatial frequency and orientation is collapsed across participants. C.) Mean d’ of orientation (top panel, left) and spatial frequency (bottom panel, left), in which right panels depict the effects of affect on orientation (top right) and spatial frequency (bottom right).

A.)

N=32

VERTICAL (n=16)

HORIZONTAL (n=16)

Spatial Frequency

Spatial Frequency

2cpd (LO) 4cpd (LO)

2cpd (LO) 4cpd (LO)

- Fear
- Neut
- None
B.)

Mean Effect of Affect on Tilt Sensitivity (N=32)

![Graph showing the mean effect of affect on tilt sensitivity with categories FEAR, NEUT, and NONE. The graph indicates a decrease in d' (sensitivity) as affect decreases.]
C.)

**Mean Effect by Orientation**

- Vertical orientation: d' approximately 3.2
- Horizontal orientation: d' approximately 2.8

**Affect on Orientation**

- Vertical orientation: FEAR > NEUT > BLNK
- Horizontal orientation: FEAR > NEUT > BLNK

**Mean Effect by Spatial Frequency**

- 2cpd (LO) orientation: d' approximately 3.0
- 4cpd (HI) orientation: d' approximately 2.5

**Affect on Spatial Frequency**

- 2cpd (LO) orientation: FEAR > NEUT > BLNK
- 4cpd (HI) orientation: FEAR > NEUT > BLNK
Figure 16. Results of Experiment 3b. Mean tilt thresholds are plotted for 13 participants for both vertical and horizontal experimental conditions. Error bars represent the standard error of the mean. A.) Mean tilt threshold for affect, in which spatial frequency and orientation is collapsed across participants. B.) Mean tilt threshold of orientation (top left panel) and spatial frequency (bottom left panel), in which right panels depict the relationship between affect on orientation (top panel, right) and spatial frequency (bottom panel, right).

A.)

Mean Effect of Affect on Tilt Sensitivity (N=32)

<table>
<thead>
<tr>
<th>Tilt Threshold (deg)</th>
<th>Fear</th>
<th>Neut</th>
<th>None</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
<td>5</td>
<td>4.5</td>
</tr>
</tbody>
</table>

Affective Face Prime
B.)

**Mean Effect by Orientation**

![Graph showing mean effect by orientation with tilt threshold on the y-axis and orientation on the x-axis.]

**Affect on Orientation**

![Graph showing affect on orientation with affective face prime on the x-axis and tilt threshold on the y-axis.]

**Mean Effect by Spatial Frequency**

![Graph showing mean effect by spatial frequency with tilt threshold on the y-axis and spatial frequency on the x-axis.]

**Affect on Spatial Frequency**

![Graph showing affect on spatial frequency with affective face prime on the x-axis and tilt threshold on the y-axis.]

- **VERTICAL**
- **HORIZONTAL**
- **Fear**
- **Neut**
- **None**
- **2cpd (LO)**
- **4cpd (HI)**
Figure 17. Three way interaction results of Experiment 2a. Mean d' for participants for both vertical and horizontal experimental conditions (columns) for both the low (2 cpd) and high (4 cpd) spatial frequencies (rows). Error bars represent the standard error of the mean.
References


Qiu, F. T., & Von Der Heydt, R. (2005). Figure and ground in the visual cortex: V2 combines stereoscopic cues with Gestalt rules. *Neuron, 47*(1), 155-166.


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


