Vision Research 94 (2014) 41–50

Contents lists available at ScienceDirect

Vision Research

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

The role of the foreshortening cue in the perception of 3D object slant

Iliya V. Ivanov [1], Daniel J. Kramer, Kathy T. Mullen *

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec H3A 1A1, Canada

ARTICLE INFO

Article history:
Received 8 November 2012
Received in revised form 21 October 2013
Available online 9 November 2013

Keywords:
Psychophysics
Color vision
Slant
Isoluminance
3D object perception
Radial frequency

ABSTRACT

Slant is the degree to which a surface recedes or slopes away from the observer about the horizontal axis. The perception of surface slant may be derived from static monocular cues, including linear perspective and foreshortening, applied to single shapes or to multi-element textures. It is still unclear the extent to which color vision can use these cues to determine slant in the absence of achromatic contrast. Although previous demonstrations have shown that some pictures and images may lose their depth when presented at isoluminance, this has not been tested systematically using stimuli within the spatio-temporal passband of color vision. Here we test whether the foreshortening cue from surface compression (change in the ratio of width to length) can induce slant perception for single shapes for both color and luminance vision. We use radial frequency patterns with narrowband spatio-temporal properties. In the first experiment, both a manual task (lever rotation) and a visual task (line rotation) are used as metrics to measure the perception of slant for achromatic, red–green isoluminant and S-cone isolating stimuli. In the second experiment, we measure slant discrimination thresholds as a function of depicted slant in a 2AFC paradigm and find similar thresholds for chromatic and achromatic stimuli. We conclude that both color and luminance vision can use the foreshortening of a single surface to perceive slant, with performances similar to those obtained using other strong cues for slant, such as texture. This has implications for the role of color in monocular 3D vision, and the cortical organization used in 3D object perception.

1. Introduction

A sensitivity to color contrast is known to be an integral part of the ventral stream of the human visual cortex, at least up to visual area V4 and the ventral-occipital (VO) region (Brewer et al., 2005; Bushnell et al., 2011; Hadjikhani et al., 1998; Liu & Wandell, 2005; Mullen et al., 2007; Wade et al., 2002; Zeki et al., 1991). Although color vision was initially suggested to play little part in form perception (Livingstone & Hubel, 1987, 1988), subsequently, it has emerged that color contrast can be used effectively in 2-dimensional form processing providing the stimulus components are presented at sufficiently low spatial frequencies to fall within the spatial passband of color vision (Hamburger, Hansen, & Gegenfurtner, 2007; McIlhagga & Mullen, 1996; Mullen, 1985; Mullen & Beaudot, 2002; Mullen, Beaudot, & Ivanov, 2011; Mullen, Beaudot, & McIlhagga, 2000; Reisbeck & Gegenfurtner, 1998; Wuerger & Morgan, 1999).

The visual system can reconstruct 3-dimensional (3D) object form quite effortlessly from the two-dimensional (2D) achromatic retinal representation by the use of different static monocular depth cues, including perspective cues, shape from shading, and texture gradients. Emerging evidence suggests that different cues relating to object surfaces (e.g. texture, surface color) may be analysed in different areas of LOC in human visual cortex from those processing object shape and form (Cant, Arnott, & Goodale, 2009; Cavina-Pratesi et al., 2010; Tsutsui, Taira, & Sakata, 2005). One of the outstanding questions is the role that color contrast can play in recovering the 3D form of objects based on static 2D monocular cues. For perspective cues of objects, based on demonstrations, Livingstone and Hubel (1987, 1988) suggested that isoluminant chromatic stimuli do not induce the sensation of three-dimensional form: the image of a bicycle slanting away from the viewer appeared difficult to recognize at isoluminance, as did a line drawings of a collection of jumbled, overlapping 3D shapes. On the other hand, Cavanagh (1991) argued that isoluminant line drawings of very simple 3D shapes (e.g. a cube) are recognizable at isoluminance. In terms of 'shape from shading', 3D representations by definition disappear at isoluminance and so it is not surprising that there is poor object and face recognition when shaded stimuli are rendered chromatic and isoluminant (Gregory, 1977). In terms of multi-element texture gradients, Livingstone and Hubel (1988)

* Corresponding author. Address: McGill Vision Research, Department of Ophthalmology, H4.14, 687 Pine Ave West, Montreal, Quebec H3A 1A1, Canada. Fax: +1 514 843 1691.

E-mail address: kathy.mullen@mcgill.ca (K.T. Mullen).

[1] Present address: Low Vision Clinic and Research Lab, Center for Ophthalmology, University Eye Hospital, University of Tuebingen, Tuebingen, Germany.

0042-6989/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.visres.2013.10.019

reported a loss of perceived slant in line-drawn texture representations of planar surfaces at isoluminance, although this was contradicted by study using regular arrays of hard-edged rectangles to represent a receding surface (Troscianko et al., 1991). Using more complex stimuli involving the modulation of textured patterns (orientation flows of multi-element patterns) at lower spatial frequencies, however, Zaidi and Li (2006) reported that 3D modulations could be determined at isoluminance.

Here we return to the role of perspective cues in color vision in determining 3D form for single elements. We test whether color contrast can contribute to the perception of 3D form (slant) based on the projective geometry of a single cue, that of stimulus foreshortening. We investigate the perception of slant using the foreshortening cue for isoluminant chromatic stimuli, presented within the spatial passband of color vision, compared to the equivalent achromatic stimuli. Slant represents the slope of an objects' surface about the horizontal axis as it recedes away from the observer and is an important aspect of 3D vision that can potentially be determined by linear perspective cues as well as foreshortening cues. The foreshortening cue comes from the compression of a single surface (change in the ratio of width to length) in the absence of linear perspective cues (Blake, Bulthoff, & Sheinberg, 1993; Buckley, Frisby, & Blake, 1996; Cutting & Millard, 1984; Stevens, 1981).

It is unclear whether the local foreshortening cue can independently induce slant perception in single shapes, whether achromatic or chromatic. Within the context of texture perception, it has been debated whether inter-element comparisons of size and density across the surface (a global cue) or the foreshortening of individual elements (a local cue) is the predominant cause for the sensation of slant (Cutting & Millard, 1984; Knill, 1998a, 1998b; Todd, Christensen, & Guckes, 2010). Todd, Christensen, and Guckes (2010) suggest that foreshortening of elements within the context of a complete texture fail to produce slant perception, but foreshortening has yet to be investigated as a local cue on its own. We focus on whether the projective geometry of a single, non-textured cue can induce the perception of a slanted surface. This is a simple local cue that uses a single form to represent slant in the absence of the global cues present in arrays of texture elements.

Our aims are twofold: first to determine whether we can use the foreshortening cue in isolation to make 3D slant judgments of single shape stimuli. Second, by comparing our slant perception discrimination for achromatic and isoluminant chromatic stimuli, we wish to determine whether there is a role for color contrast in 3D perception from foreshortening. We apply the foreshortening cue to shapes based on radial frequency (RF) patterns, which use curved contours to represent concentric shapes. By manipulation of the local curvature and the tangent orientation along the contour in the projecting plane, we represented an object foreshortening corresponding to a particular slant. We chose RF patterns because they are well established in the literature for studying global shape perception, requiring the integration of multiple, curved, contour elements into a complete shape (Wilkinson, Wilson, & Habak, 1998; Wilson & Wilkinson, 1997). They also have the added convenience of being narrow band in the spatial frequency domain, allowing the perception of both achromatic and chromatic stimuli to be based on the same spatial frequency range. The use of narrowband stimuli also allows chromatic and achromatic stimuli to be matched in visibility, based on the contrast detection of the same spatial frequency range. If our visual system could use local compressions arising from foreshortening to support global 3D shape perception, it would suggest a single cue is adequate to induce slant perception. We show that both achromatic and isoluminant, chromatic RF patterns induce very similar slant perception and slant discrimination, demonstrating that both color and luminance vision can use the foreshortening of a surface to perceive slant, with performances similar to those obtained using other strong cues for slant, such as texture. This implies that the human visual system can use foreshortening cues with both color and achromatic contrast to determine slant and 3D form, and supports the hypothesis that the areas of the IT cortex responsible for 3D object perception based on static, monocular cues receive inputs from both color and achromatic contrast.

2. Methods

2.1. Stimuli

Stimuli were achromatic or chromatic radial frequency patterns projected orthographically with different depicted slants, as illustrated in Fig. 1. The chromatic patterns either isolated the L/M cone opponent pathway (red–green, isoluminant) or isolated the S-cones. The radial frequency patterns were radially modulated D4s, the fourth derivative of a Gaussian (Wilkinson, Wilson, & Habak, 1998; Wilson & Wilkinson, 1997), band-limited in the spatial frequency domain, and defined by the following equations:

$$RF(r) = L_m[1 + c(1 - 4r^2 + 4r^4/3)e^{-r^2}] \quad (1)$$

$$r(x,y) = \frac{\sqrt{x^2 + y^2} - R(x,y)}{\sigma} \quad (2)$$

$$R(x,y) = R_m\{1 + A\sin[f_r \arctan(y/x) + \theta]\} \quad (3)$$

$$\sigma = \frac{\sqrt{2}}{\pi\omega_p} \quad (4)$$

where σ is the space constant of the $RF(r)$ in degrees, ω_p is the D4 peak spatial frequency (the contour, fixed at 1 cpd), $R(x, y)$ is the sinusoidal radial modulation of the D4 (defining its shape), R_m is the mean radius (2.0 deg before any applied slant). R_m is randomly varied between trials by a factor of 0.5–1 in conditions indicated in the text. f_r is the radial frequency (fixed at 4), A is the amplitude of the radial modulation fixed at 0.15, and θ is the phase of the modulation, which was randomly selected in each trial of the experiments to prevent adaptation. L_m is the mean luminance (for achromatic patterns) or mean chromaticity (for chromatic patterns) and c is cone contrast, as defined below.

We created the depicted optical slant at the centre of the stimulus by modulating the orthographic projection of the stimulus onto the screen such that:

$$\cos(\phi) = \omega/\lambda \quad (5)$$

where ϕ is the depicted physical slant, ω and λ are the width and the height of the stimulus respectively.

Stimuli were represented in the three-dimensional cone-contrast space (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1996). A linear transform was calculated to convert between the red, green and blue phosphor contrasts of the monitor and the three cone contrasts (L_C, M_C and S_C). Stimulus contrast is defined as the root mean square of the vector length in cone-contrast units (C_C):

$$C_C = \sqrt{(L_C)^2 + (M_C)^2 + (S_C)^2} \quad (6)$$

Isoluminance was estimated by a minimum motion task in the cone-contrast space (Cavanagh, Tyler, & Favreau, 1984), in which the perceived minimum motion of a Gabor stimulus (3.6 deg^2) was measured using a method of adjustment. Isoluminance was calculated as the arithmetic mean of at least 20 settings. We

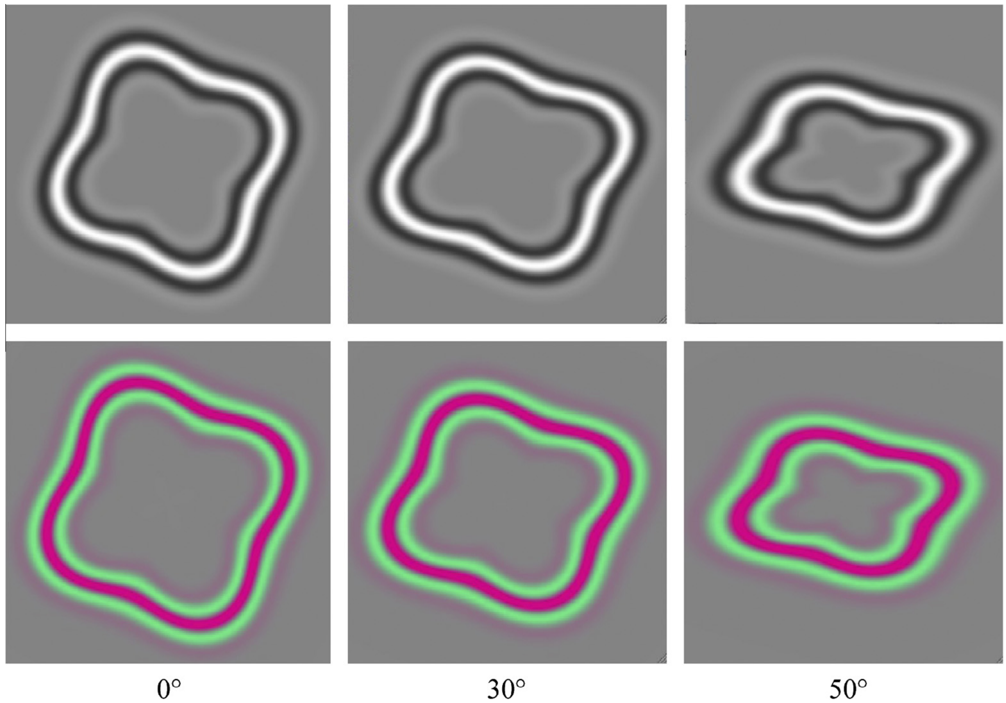

Fig. 1. Illustrations of the RF stimuli used in Experiments 1 and 2. The top three stimuli are achromatic, the bottom three show the red–green (RG) isoluminant stimuli. Isoluminance was determined for each subject. Stimuli represent 0 deg, 30 deg, and 50 deg depicted slants. Note the pictures are for illustration only and are not exact representations of the stimuli. In many of the experiments, we used a control condition in which the size (diameter) of the RF pattern was randomly varied between trials, thus de-coupling stimulus size and height from stimulus slant, as described in the text.

minimized luminance artifacts in the chromatic stimuli (Bradley, Zhang, & Thibos, 1992) by using spatially bandpass stimuli of a relatively low spatial frequency (1 cpd).

2.2. Apparatus and calibrations

Stimuli were displayed on a Sony Trinitron monitor (GDM-F500R, Sony Corporation, Tokyo, Japan) driven by a VSG 2/5 graphics board (Cambridge Research Systems, Kent, UK) with 15 bits of contrast resolution, inside a Pentium PC computer. The frame rate of the display was 120 Hz. The spectral emissions of the red, green, and blue guns of the monitor were calibrated using a PhotoResearch PR-650-PC SpectraScan (Photo Research Inc., Chatsworth, CA, USA). The monitor was gamma corrected in software with lookup tables using luminance measurements obtained from an OptiCAL gamma correction system interface with the VSG display calibration software (Cambridge Research Systems). The monitor was viewed in a dark room to prevent light contamination. The mean luminance of the display was 60 cd/m^2. The stimuli were viewed at 57 cm. Stimuli were generated online and a new stimulus was produced for each presentation.

2.3. Protocol

In all procedures, the exact location of the stimulus was varied randomly from trial to trial about the display centre by adding a positional jitter corresponding to 20% of the stimulus radius to avoid the influence of any possible after-effects. Stimulus rotation (phase) was also varied randomly between trials, so the pattern randomly changed from diamond to square-shaped, or anything in between. This varied the overall height of the stimulus from trial to trial. In addition, unless otherwise stated, the stimulus size (diameter) was varied randomly between trials by a factor of 2, so that stimulus height and size were not correlated with stimulus slant. The duration of the stimulus presentation interval was 1 s, and the overall contrast of each stimulus was Gaussian enveloped in time with a sigma of 125 ms centered on the temporal window. Auditory feedback was given after each trial for the 2-alternative forced choice (AFC) experiments. A small black fixation mark was present before and after the stimulus presentation and during the inter-stimulus interval at the centre of the display. Subjects were asked to maintain their fixation throughout the trial. Practice trials were run before the experiments commenced. All experiments were done under binocular viewing conditions, unless stated otherwise.

In order to be able to express the contrast of both achromatic and chromatic stimuli in multiples of stimulus detection thresholds and to control for the differences in contrast sensitivity for the band-limited chromatic and achromatic patterns (Mullen, 1985) we acquired contrast detection threshold for the stimuli. Detection thresholds were measured using a 2AFC staircase method. Two intervals were presented, one with a blank mean luminance and the other with a stimulus, and the subject picked the interval with the stimulus. The contrast of the stimuli decreased by a factor of 12.5% after two correct responses, and increased by a factor of 25% after every incorrect response. The first contrast change was 50%, before the first reversal. Each session was terminated after six reversals, and the detection threshold was computed from the mean of the last five reversals.

2.3.1. Two methods of slant matching

In the first experiment, we used two different methods to measure perceived slant. One method was visual, in which subjects viewed a black line presented on the display screen and could vary its orientation between horizontal and vertical to match the perceived slant of the RF stimulus. This method has been used previously as a metric for slant perception for multi-element patterns and is illustrated in Figs. 5 and 6 of Todd, Christensen, and Guckes (2010). One of eight RF stimuli with a depicted slant varying between 0 and 70 deg was randomly selected and presented. Once the subject had viewed the depicted slant of the RF stimulus, s/he would switch screens using a toggle and adjust the rotation of the line on the screen, in steps of 0.5 deg between horizontal and vertical, until the angle of the line was judged to matched the perceived slant of the RF stimulus. Subjects were allowed to switch freely between the stimulus and the line until they felt they had accurately matched the two. This task was repeated 20 times for each depicted slant for both the chromatic and achromatic stimuli. This experiment aimed to provide a perceptual metric for the subjects' perception of slant in the RF stimuli.

The second method of slant matching was a non-visual, manually-based lever method. A smoothly functioning mechanical lever was attached to the laboratory bench, whose slant could be adjusted manually by rotation about the horizontal axis. Its slant was calibrated and its slant-angle could be read from the subject's lever settings by the experimenter. The subject did not look at the lever while making the slant matches and could not see the scale for the lever. Subjects were instructed to rotate the lever by hand until its slant perceived manually through the subject's hand position matched the visually perceived slant of the RF patterns on the screen. Fifteen to twenty slant matches were made for each depicted slant (between 0 and 70 deg) and a mean calculated, following the same protocol as for the line-adjustment task. Overall, 8 subjects performed both line and lever methods of slant matching.

In order to avoid the possibility that the subject makes a direct height match to the stimulus on the screen by rotating the line or adjusting the lever we used a control condition in which the size (diameter) of the RF pattern was randomly varied between trials, thus de-coupling stimulus size and height from stimulus slant, as described above. Two complete data sets were collected with size-variation (six subjects) and without (six subjects), with some performing both conditions. In addition, the random variation in the rotation (phase) of the RF pattern between trials decouples stimulus height and slant. Finally, the adjustable the lever on the bench could not be viewed during the experiment making direct visual comparisons impossible.

We calculated the correlation between line- and lever-adjusted slants using Pearson's correlation coefficient for both size-constant and size varying conditions. For brevity, only the data for the size-varying condition are plotted Fig. 2A, although the statistics are reported below for both conditions. The slant matches based on lever- and line-adjustments were highly and significantly correlated with Pearson's correlation coefficient of 0.85 for the size varying and 0.84 ($p < 0.001$) for the size-constant condition. We used a Bland–Altman analysis (Bland & Altman, 2007) to examine the agreement between the line- and lever-adjustment tasks, with results for the size-varying condition plotted (Fig. 2B). The difference (the lever minus the line slant settings) was plotted against the mean of the two measurements. The limits of agreement were calculated as the mean difference with ±2 standard deviations used to assess the precision, as described in Bland and Altman (2007). The mean difference between lever- and line-adjusted slants was small at 0.6 deg with 95% upper and lower confidence limits of 28.2 and −29.6 deg for the size varying condition (Fig. 2B), and 6.9 deg with 95% upper and lower confidence limits of 39.7 and −25.8 deg, respectively for the size-constant condition. The points are scattered about the means and do not show any systematic trend in the data that would indicate a significant deviation of one method from the other, such as a proportional error or significant absolute difference. The data points converge towards the (0,0) origin of the plot but this reflects the fact that settings below 0 could not be made with either method. This analysis indicates that both line and lever methods are measuring the same thing, the perceived slant of the RF shape.

2.3.2. Slant discrimination method

In the second experiment, we used a 2AFC method of constant stimuli to measure the discrimination of slant. In one interval a fixed reference stimulus appeared and in the other interval a stimulus of greater slant was presented, selected from 4 to 5 possible slants ranging from equal to the reference stimulus to a depicted slant of up to 30 deg steeper. The subject indicated by pressing the appropriate button which of the two stimuli had the least slant. At least 80–100 trials were collected for the discrimination of each of the 5 stimulus pairs, and a psychometric (logistic) function was fitted to the data. Psychometric functions were fitted using the psignifit toolbox (version 2.5.6) for Matlab (see http://bootstrap-software.org/psignifit/), which implements the maximum-likelihood method described by Wichmann and Hill (2001). We took the discrimination threshold as the threshold difference in slant from the reference stimulus corresponding to 75% correct. We measured slant discrimination thresholds as a function of 5 different reference slants from 0 to 60 deg to create a function for slant discrimination threshold vs. depicted slant. In a control experiment, we collected an additional set of data for this experiment comparing binocular and monocular viewing conditions on one subject with achromatic stimuli. Data sets were collected under both size-constant and size-varying conditions as indicated in the text. Six subject participated in this experiment.

2.4. Observers

Twelve observers were used in the study: the three authors and nine additional subjects naive to the purposes of the study (NN, AY, MG, RB, AD, LL, RW, SK and YJK). All had normal or corrected to normal vision, and had normal color vision according to the Farnsworth–Munsell 100 Hue-Test.

3. Results

We used a single, orthographically projected shape to determine whether an objects' foreshortening cue can induce the perception of slant and allow us to discriminate between different slants. In the first experiment, we aimed to measure the subjects' ability to perceive slant by asking the subject to make slant estimations, as explained in Section 2. If the visual system can access the pattern's foreshortening as a local cue for perceived slant, we would expect that the perceived slant estimations would vary with the depicted slant of the stimulus and be reliable. If, however, the foreshortening of a single element fails to induce the perception of slant, we would expect there to be no perception of slant from the orthographically projected single stimulus, only the impression of a change in shape. In this case, the subject may fail to match perceived slant, or make random matches producing large errors and no distinct pattern.

The results of the perceptual matching task are shown in Fig. 3a–f. All the data in this figure were collected using the size-varying stimulus. The black, red and blue lines without symbols represent the average slant matches to the achromatic, isoluminant RG, and S-cone isolating chromatic stimuli, respectively, made using the manual lever match. The small symbols without connecting lines represent the average slant matches for achromatic stimuli (black symbols), and chromatic stimuli (RG isoluminant, red symbols) made using the visual line match, which was used on all six of the subjects. The dashed black line represents settings of a theoretical observer whose matching is veridical to the depicted slant. All observers show a monotonic increase in slant settings as a function of the depicted slant of the stimulus. No observer matched the depicted slant veridically. Four systematically under estimated slant (RW, AY, LL, YJK) and the other two tended to overestimate slant (MG, SK). Although somewhat variable between subjects, within subjects the perceived slants were very consistent throughout the trials. All our subjects reported that they

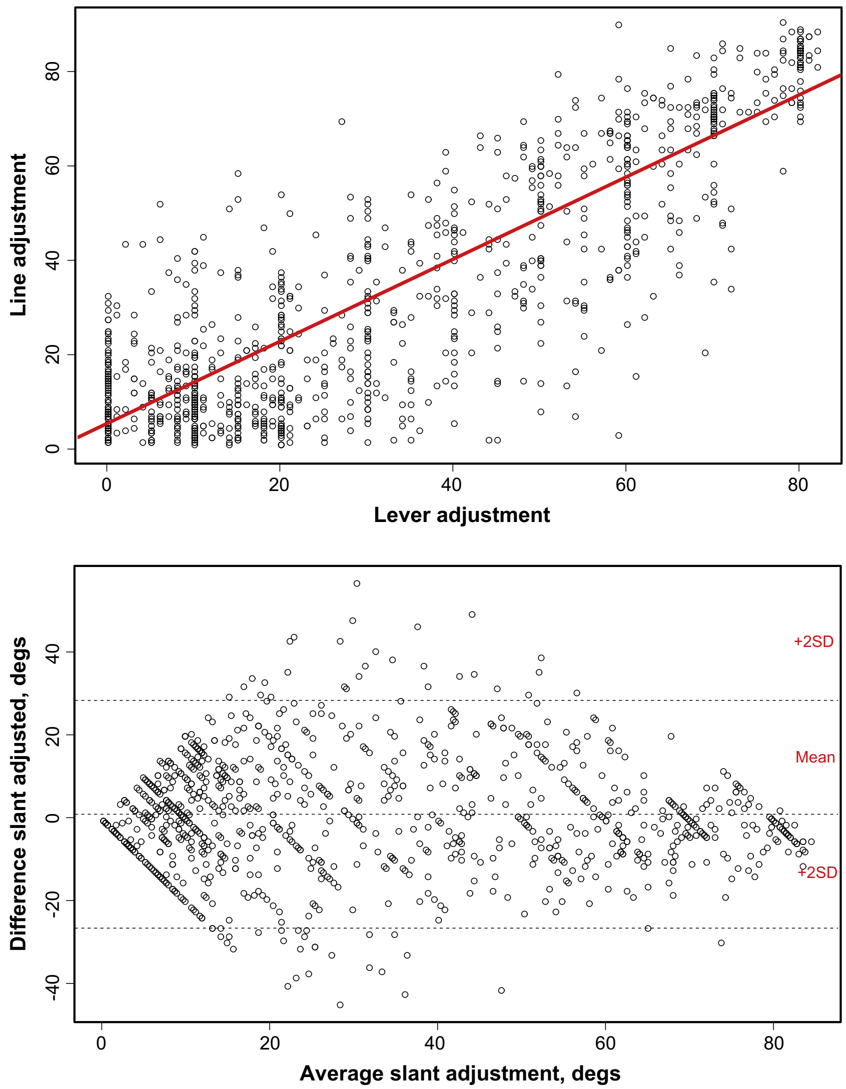

Fig. 2. (A) Pearson's correlation between line- and lever-adjusted slants. Slant matches obtained from the visual line adjustments are plotted as a function of the matches obtained from the manual lever adjustments. Data for color and achromatic stimuli are included. Line adjustments as a function of lever adjustments are highly correlated, with correlation coefficient of 0.84 and 95% confidence interval between 0.81 and 1. (B) Bland–Altman plot of agreement between line and lever adjustments. The middle horizontal line represents the mean difference (lever-adjusted match minus line-adjusted match) between settings made by the two methods, plotted against the mean of the two measurements (lever- and line-adjusted matches). The mean difference of the two is 0.6 deg with 95% upper and lower confidence limits of 28.2 and −29.6, respectively (dotted lines). Data in (A) and (B) are for the size varying condition. Data for the size constant condition are not shown but are similar with a mean of 6.9 deg and the 95% upper and lower limits are 39.7 and −25.8 deg, respectively.

experienced the RF pattern as slanted, perceiving it as a "four-cornered" RF pattern with unity aspect ratio leaning away from them.

We used two slant matching methods, visual matching by line adjustment and manual lever matching, and results for these were in close agreement. The correlation analysis and Bland Altman analysis performed across all subjects (see Section 2) indicate that both methods are measuring the same thing, a perceptual match of slant. A two-way within subjects ANOVA on our entire data set for the achromatic and RG isoluminant stimuli with factors of depicted slant, method (line or lever) and contrast type (achromatic or RG color) on all observers showed a significant main effect of depicted slant ($F = 92.3$, $p < 0.001$), while factors contrast type ($F = 0.011$, $p = 0.92$) and method ($F = 0.015$, $p = 0.909$) were not significant. This analysis confirms the results of the Bland Altman analysis reported in Section 2 showing that the method used (lever or line) does not affect the results obtained.

In Fig. 3, the shapes of the functions plotting perceived slant as a function of depicted slant all show an initial flat section up to 20–30 deg, in which differing slants are perceived as similar, followed by a rise in the function indicating that different slants are perceived. In the absence of slant perception, we would expect that the matching function in our method of adjustment task would remain flat at 0 deg, or relatively scattered, as has been found previously for slant judgments made using the foreshortening cue for textured patterns (see Fig. 7 of Todd, Christensen, and Guckes (2010). For low slants (0–20 deg), the matches are flat and fall between 3 and 20 deg, indicating that subjects cannot distinguish between the different slants presented. For the rising part of the function (above 20–30 deg), consistent perceptual slant matches can be made by all subjects. These effects are predictable from the results of the next experiment on slant discrimination, as discussed later.

For the perceptual matching data shown in Fig. 3, we performed a main effects analysis on the five subjects who performed all three conditions (Ach, RG and S-cone isolating). The analysis showed no significant effect of contrast type (RG and S-cone isolating color contrasts vs. Ach) for any of the subjects in the manual lever matching settings at the $p < 0.05$ level ($F = 0.323$, $p = 0.6$). Using

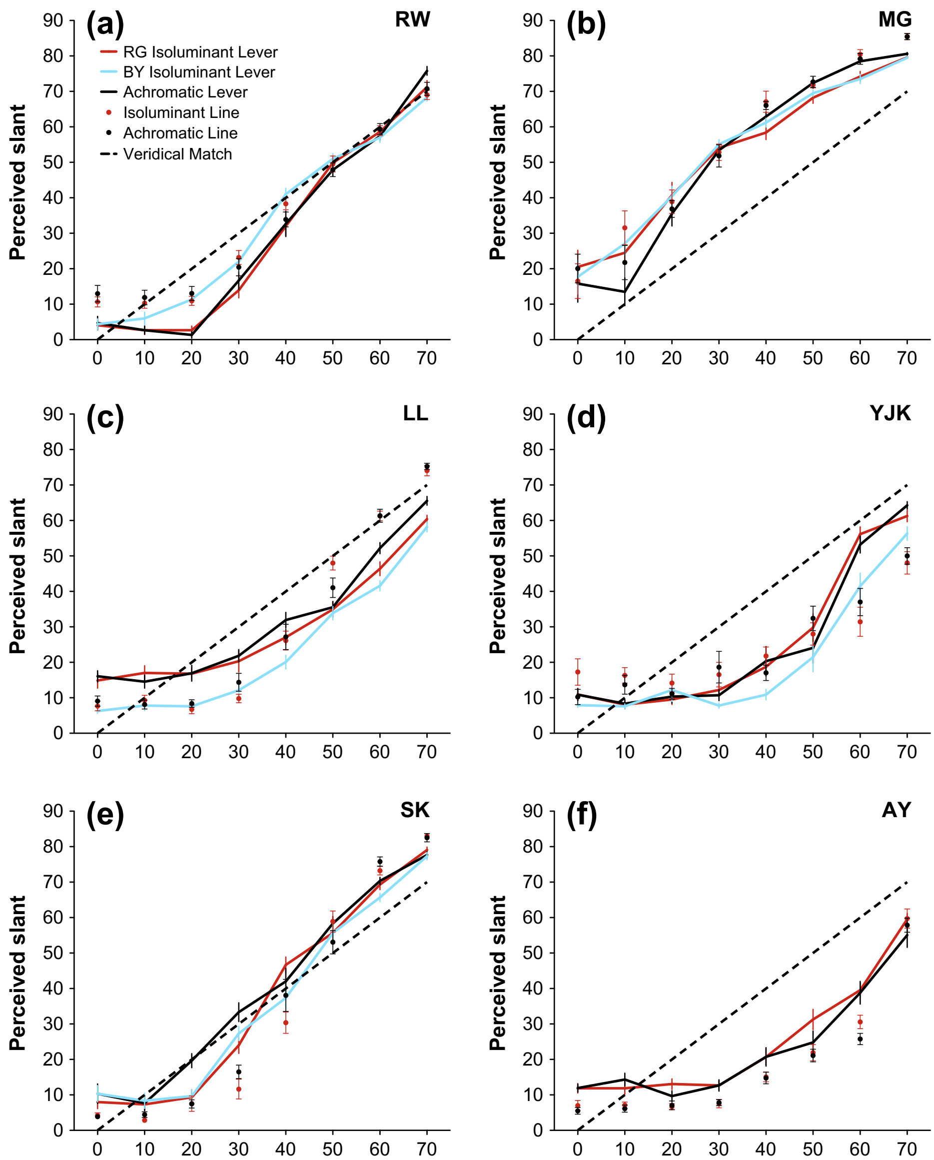

Fig. 3. Perceived slant measured by the methods of lever- or line-adjustment for 6 subjects (panels a–f). Each data point represents the average settings based on 20 trials. The solid lines with no symbols show results obtained using the lever adjustment method, and the unconnected symbols show results using the line-adjustment method. Red indicates results for RG chromatic stimuli, blue for S-cone isolating stimuli, and black for achromatic stimuli, presented at relatively high suprathreshold cone contrasts of 6%, 30% and 40%, respectively. The black dashed line shows the theoretical match for a veridical observer. See text for statistical analyses. All data shown in this figure used size-varying stimuli. Data collected using size constant stimuli are not shown (for brevity) but all the analyses are described in the text.

individual analyses, there were no significant differences in the matches using achromatic and RG stimuli ($p > 0.05$) in any observer. In one observer (LL), matches for the S-cone isolating stimuli were significantly different from the achromatic ($p = 0.002$). Overall, however, the data suggest that both RG isoluminant and S-cone isolating color contrasts can be used to make consistent slant judgments that are as precise as those based on luminance contrast. This demonstrates that the local foreshortening cue of a single stimulus can induce similar perceptions of slant in both the achromatic and color pathways.

We also collected a complete data set using size-constant stimuli (six subjects) for RG isoluminant and achromatic stimuli. For brevity these data are not plotted, but very similar results were obtained to those in Fig. 3 using the size-varying stimuli. A main effects analysis showed no significant effect of contrast type (color vs. luminance) for any subject at the $p < 0.05$ level, with one exception (AY had significantly higher lever settings for the RG isoluminant stimuli). When this condition was repeated on the same subject using the size-varying stimuli the effect no longer occurred.

We also made an overall comparison of the results for slant matching with and without size-variation using a two-way within subjects ANOVA. This showed no significant difference between data sets ($F = 7.111$, $p = 0.288$). This shows that the subjects are not making a direct height or size match in the slant matching experiment as they make similar slant matches with or without these cues. We conclude that the slant discrimination is not based on estimations of the stimulus size or height, indicating that the aspect ratio is the more important cue.

In Experiment 2, we measured slant discrimination thresholds as a function of different base slants using a method of constant stimuli, as described in Section 2. In Fig. 4a–f, we plot discrimination thresholds as a function of the base slant for the achromatic stimuli (shown in black) and chromatic stimuli (RG isoluminant in red, S-cone isolating in blue). In all cases, the slant discrimination thresholds decrease as the slant increases, reaching an asymptote. This finding is broadly similar to previous work using achromatic textures that showed discrimination thresholds decline as slant increases (Knill, 1998a; Fig. 3), suggesting that slant discrimination is as strong for single elements as it is for textured patterns. The discrimination thresholds for chromatic and achromatic stimuli are similar in both form and magnitude. Three subjects had very similar thresholds for the chromatic and achromatic stimuli (DK, IVI and RW), whereas two showed some visible differences with NN and KTM showing slightly poorer discrimination thresholds for the chromatic stimuli. A 2-way ANOVA, however, revealed no difference in thresholds between the achromatic and RG isoluminant or S-cone isolating stimuli for any of the five subjects (DK, $p = 0.9115$; IVI, $p = 0.6605$; NN, $p = 0.5318$; KTM, $p = 0.79$; RW, $p = 0.1$), but did show an effect of depicted slant indicating the thresholds varied across slant. This indicates that slant can be discriminated equally well based on either chromatic or achromatic contrast and that slant perception has a very similar dependence on base slant.

In a control experiment, we compared monocular and binocular viewing conditions for achromatic stimuli, and the data set is shown in Fig. 4d (subject AY). This was done to control for the influence of any possible conflict between a stereo cue present binocular viewing and the monocular perspective cue. There is no significant difference between the data sets for monocularly and binocularly viewed stimuli, which verifies that the presence of any stereo information in the binocular viewing conditions does not influence slant discrimination thresholds. Finally, we note that data in panels a–d were collected using the size constant condition, and data in panels e–f were collected using the size varying condition. A comparison of the results for slant discrimination with and with out the size variation of all five observers showed no significant difference between the data sets ($F = 0.008$, $p = 0.929$) (AY not included as he did not do the color conditions). This shows that slant discrimination in the size constant condition is not influenced by the discrimination of stimulus height of area and indicates that the cue of aspect ratio is the salient one.

In these stimuli, the cue to the object's slant is the shape compression resulting from foreshortening, corresponding to a change in the aspect ratio of the stimulus. Note that linear perspective cues (convergence of parallel lines) are not present in these orthographically projected stimuli. We have argued that the ability to

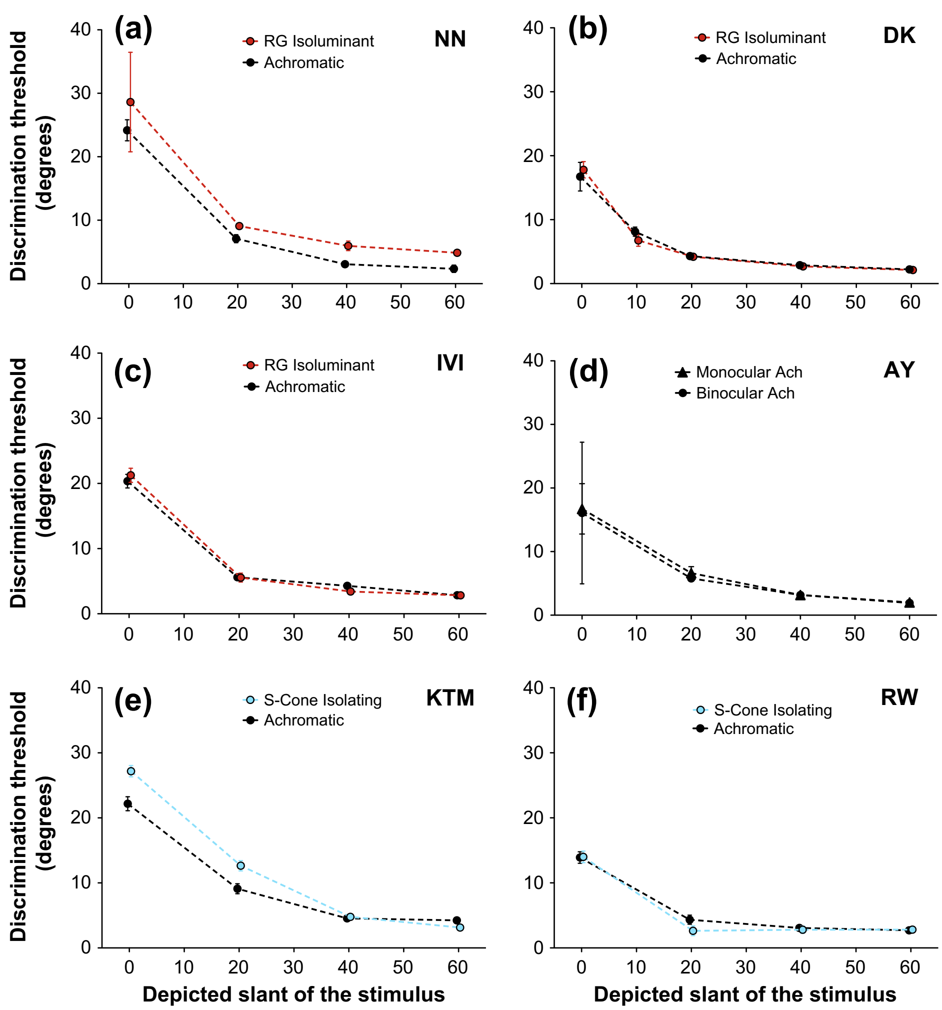

Fig. 4. Slant discrimination thresholds (in deg) measured as a function of the base slant of the stimulus for achromatic, RG isoluminant and S-cone isolating chromatic stimuli for 5 subjects as marked (panels a–c, e–f). The contrast was 5× the contrast detection threshold for each subject and presentations were binocular. There were no significant differences between chromatic and achromatic thresholds for any subject. Panel (d) shows results for a control experiment in which slant discrimination was compared for monocular and binocular stimulus presentations for achromatic stimuli. There was no significant difference between the two. The error bars show ±1 SD. In pannels (a)–(d) stimulus size did not vary and in pannels (e)–(f) stimulus size varied between trials. There was no significant difference between the size varying and size constant conditions (see text). (Note AY's variance at 0 deg is high because of his difficulty in doing this particular discrimination.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

discriminate this underlying change in aspect ratio (shape) is limiting the subject's ability to discriminate between different slants. If this is correct, we predict that the form of the function for slant discrimination vs. base slant will be limited by the change in the aspect ratio as a function of slant. As base slant increases, the aspect ratio increases from unity following a cosine function, as seen in Eq. (5). To test the prediction that slant discrimination thresholds (Δ slant) are limited by the detection of a fixed incremental change in stimulus aspect ratio, we calculated a model discrimination function based on the derivative of Eq. (5). This is plotted in Fig. 5 as solid lines for both achromatic and chromatic stimuli (see legend for further details). We used the chi-squared statistical test to compare observed data with the model fit. For both color and luminance stimuli the differences between observed and expected data are no greater than expected from chance variation ($\chi^2_{\text{blue.}} = 0.4$, Df = 2, $p > 0.8$; $\chi^2_{\text{red.}} = 0.8$, Df = 2, $p > 0.5$; for the achromatic and isoluminant stimuli respectively).

We show in Fig. 5 that the threshold discrimination of slant seems to be limited by a criterion detectable change in the aspect ratio of the stimulus. Aspect ratio is nonlinearly related to slant and we argue this accounts for the shape of the slant discrimination functions: slant discrimination is poor at low base slants, but is more precise as base slant increases. This is likely to account for why the measurements of slant perception in Fig. 3 were relatively flat at low base slants, when the subjects did not have the perceptual accuracy to see differences between their selected slants. The similarity of the results for achromatic and chromatic stimuli suggests that that shape discriminations can be equally well supported to the same degree of accuracy by color contrast as by achromatic contrast under the conditions used here.

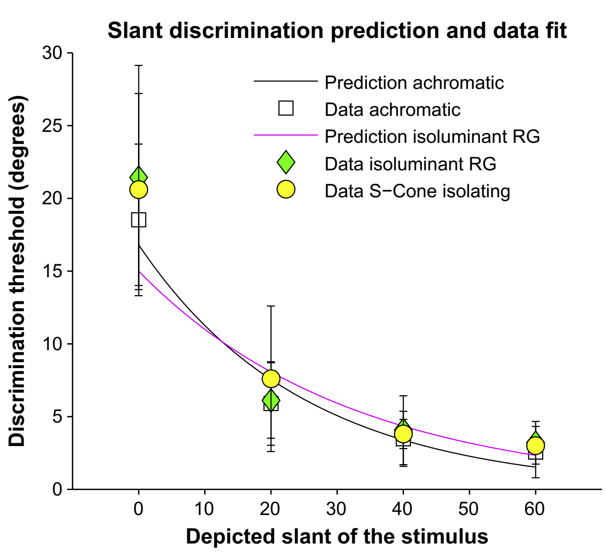

Fig. 5. A model fit to the slant discrimination data (solid lines). The data points represent the average slant discrimination thresholds of the observers data in Fig. 4: achromatic (open squares), red–green (green diamonds) and S-cone isolating stimuli (yellow circles). The model fits are based on data for the three subjects (NN, DK and IVI) who competed both achromatic (black line) and RG chromatic (red line) conditions. Data points are plotted for the S-cone isolating condition (average of 2 subjects). The model curves show the predicted discrimination thresholds (T) assuming that threshold slant discrimination as a function of base slant is determined by the detection of a criterion change in the stimulus aspect ratio. The slant discrimination threshold for any given base slant is determined by the following equation: $T \propto \frac{\sigma/(d\psi)}{(d\phi)}$ where σ is the standard deviation of the observers' slant judgments, ψ is the perceived slant, φ is the physical slant, and $\frac{(d\psi)}{(d\phi)}$ is the slope of the psychometric function at that base slant. The model is an acceptable fit to the data (see text). The error bars show ±1 SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

In this paper we investigated whether the visual system can use the foreshortening cue to perceive slant and whether isoluminant color contrast can be used to determine the slant of an object. We compared perceived slant and slant discrimination thresholds of achromatic and isoluminant chromatic radial frequency patterns projected orthographically. Radial frequency patterns are well established in the literature for studying shape and form perception (Hess, Wang, & Dakin, 1999; Mullen & Beaudot, 2002; Mullen, Beaudot, & Ivanov, 2011; Wilkinson, Wilson, & Habak, 1998; Wilson & Wilkinson, 1997). These stimuli are confined to a narrow band of spatial frequencies and allow us to isolate and compare the responses to achromatic and chromatic contrast for stimuli matched in spatial content and visibility. Since color vision has a low pass contrast sensitivity function (Mullen, 1985) we used a mid-spatial frequency (1 cpd) for the contour, which is close to peak contrast sensitivity for both the red–green chromatic and achromatic systems. We have shown that for a single shape the foreshortening cue is sufficient to produce the perception of slant for both chromatic and achromatic stimuli. In the experiments, the size of the stimuli was randomly varied to decouple stimulus height and size from slant ensuring that slant matching and discrimination thresholds are based on the discrimination of the foreshortening cue (stimulus aspect ratio). For both achromatic and isoluminant chromatic stimuli, we find that perceptual judgments of slant are very similar under our conditions, demonstrating that the visual system can use color contrast as effectively as achromatic contrast to determine the slant of an object. We do not know whether using a higher contour spatial frequency would improve slant discrimination in the bandpass achromatic system, although the similarity of our slant discrimination threshold to those obtained using other types of achromatic stimuli (Knill, 1998a) suggests that our achromatic slant thresholds are fairly typical.

4.1. Local foreshortening cues for slant perception

Our thresholds for slant discrimination are broadly similar to those found by Knill (1998a), who used textured multi-element surfaces with perspective, indicating our stimuli produce the perception of slant with an accuracy similar to that obtained from other slant producing cues, including linear perspective and the global cues found in textures such as element density. Our stimulus, however, does not contain linear perspective cues or global texture because it is a single object that is orthographically projected. In our stimulus, the only cue to induce the perception of slant is the projective geometry, the compression of the stimulus shape, which has previously been argued to be insufficient for slant judgments (Todd, Christensen, & Guckes, 2010). Along with this, it has been shown that for texture, orthographic projections alone do not induce the perception of slant (Todd, Christensen, & Guckes, 2010). The discrepancy between our findings and those of Todd, Christensen, and Guckes (2010) demonstrates that multi-element texture patterns need to have linear perspective on both a local and global scale for the perception of slant, but for individual shapes or elements, the local foreshortening cue (orthographic projection) in the absence of linear perspective can be sufficient.

The performance on perceptual matching (Fig. 3) indicates that the slant perceptions were consistent within subjects but varied between subjects. The results were similar for achromatic and isoluminant chromatic stimuli. Interestingly, slant perceptions are initially underestimated and become more accurate at steeper slants. This finding is consistent with the data of Todd, Christensen, and Guckes (2010) who also find that perceived slant is initially underestimated, though they used textured stimuli. Although slant perceptions varied between subjects, shallower slants (below 20–30 deg) were all perceived as similar, producing an initial flat section in the matching function, whereas steeper slants (above 30 deg) were more accurately distinguished as different. The slant discrimination experiments (Fig. 4) show that threshold discrimination in this range is generally smaller than 5 deg. Our modeling (Fig. 5) suggests that the shape of the slant discrimination function is determined by the foreshortening cue (change in stimulus aspect ratio), which is reduced at low slant values, but increases at higher slants. This finding confirms that the foreshortening of a single surface can induce slant perceptions.

Our slant judgment data represent the perception of slant of single objects (Proffitt et al., 1995) whereas previous studies have investigated texture (Todd, Christensen, & Guckes, 2010). Todd, Christensen, and Guckes (2010) showed that slant perceptions depend on how the stimulus was presented to the subject. Using an orthographically projected textured pattern, there was no perception of slant, whereas projecting the stimulus at a camera angle of 60 deg produced slant perceptions veridical to the actual slant. This was used to show that the foreshortening cue, which is the only cue available for orthographical projections, was not capable of inducing slant perception. It also reveals interesting differences between textures and single shapes. A question arising from this is why the stimulus foreshortening (shape compression) produces the perception of an object of fixed shape slanted in depth, indicating object constancy across viewpoint, rather than the perception of a 2D object undergoing a shape change. In other words, the subjects all perceived the shape as a radial frequency pattern with unity aspect ratio viewed at different angles of slant. One possible answer is that a familiarity with the RF stimulus, which typically has unity aspect ratio, could have lead to the assumption of object constancy. A more likely answer is that 2D shape changes consistent with foreshortening, even in unfamiliar objects, lead to the interpretation of a change in 3D projection, since this is likely to happen in the real world, where object view-point changes continuously. For a textured surface to induce slant, there needs to be both linear cues and global scaling cues. A textured pattern projected orthographically without global scaling cues does not induce slant perception (see Fig. 5 of Todd, Christensen, and Guckes (2010)). With contour based shape constancy, no such cue conflict exists and the surface appears to simply be changing viewpoint, creating the sensation of slant.

4.2. The role of color vision in slant perception

Both slant discrimination thresholds and slant perceptions are very similar for the chromatic (RG and S-cone isolating) and the achromatic stimuli under our conditions. This demonstrates that the foreshortening cue can generate a 3D perception of slant in color vision, similar to that found for achromatic vision. This is surprising because several early studies have claimed that isoluminant color contrast is unable to support the perception of 3D form based on static monocular depth cues (Cavanagh, 1991; Cavanagh, Adelson, & Heard, 1992; Livingstone & Hubel, 1987, 1988). Early studies postulated that the perception of color is distinct from form perception, and suggested that color contrast plays little to no role in form and shape perception (Gregory, 1977; Tansley & Boynton, 1978). Livingstone and Hubel (1987) also claimed the perception of depth is lost at isoluminance when depth is induced by occlusion or perspective, implying a segregation of color perception from 3D form perception. These findings, along with the absence of 'shape from shading' in color vision, supported the presumption that color contrast at isoluminance cannot contribute to the perception of 3D form. Many of these findings, however, were observational and have not been tested thoroughly. More recent results, as reported in the Introduction, have tended to support a role of color in 3D form in texture arrays (Troscianko et al., 1991; Zaidi & Li, 2006). Our results demonstrate that color contrast alone can be used to generate a perception of 3D slant of a single object based on foreshortening cues. Natural scenes typically contain combinations of color and achromatic contrast and how these are used to provide 3D object shape is an area of future study.

More recent studies have concluded that color vision plays a role in 2D form perception and contour processing for both RG and S-cone isolating stimuli (Beaudot & Mullen, 2005; McIlhagga & Mullen, 1996; Mullen & Beaudot, 2002; Mullen, Beaudot, & Ivanov, 2011; Mullen, Beaudot, & McIlhagga, 2000). It was noted previously that the foreshortening cue comes from the changing aspect ratio, the shape, of the stimulus. We have shown that the perception of depth from this foreshortening cue, which takes its cue from changes in object form, can arise from isoluminant color contrast. This task requires that color vision can both detect the change in shape, and then use this information to create a 3D representation of form.

FMRI results in human vision suggest that there are different brain regions with response preferences for the surface (material) properties of objects, such as texture and color, as opposed to the geometric properties of an object embodied in its form or shape (Cant, Arnott, & Goodale, 2009; Cavina-Pratesi et al., 2010; Tsutsui, Taira, & Sakata, 2005). Each of these regions potentially makes contributions to global 3D vision; using texture-based as well as shape-based cues our visual cortex can re-construct the 3D properties of an object. Color vision is an interesting case because it may have an input into both of these brain areas, providing crucial information about the material properties of an object from its surface color as well as delineating its shape based on its color differences from the surround. In this paper, we have investigated a single geometric cue to 3D form perception, and we have shown that color vision can utilize 2D form information to perceive object slant, demonstrating a chromatic input into 3D shape processing areas and the global network of 3D object analysis. Our use of a single shape was designed to activate the shape-based object areas of the brain as opposed to visual areas responsive to surface properties, which would have been recruited if we had used multiple elements forming textures. This is important as these two types of task, based on object shape vs. surface texture, may differ in their reliance on color contrast for 3D perception.

Ultimately the perception of 3D form requires the linking of multiple depth cues. Tsutsui, Taira, and Sakata (2005) have shown evidence in macaques that the CIP (central intra-parietal) combines different depth cues from several areas. There are selective neurons with large receptive fields that are tuned to particular slants irrespective of the slant cue. Cavina-Pratesi et al. (2010) showed there is surface and geometric specific processing in different regions of the human brain. The LOC (lateral occipital cortex) responds to shape and the geometric properties of a 3D surface, whereas the pCoS (posterior collateral sulcus) responds to texture and surface properties in 3-dimensions. Our data provide corroborating psychophysical evidence for foreshortening sensitive neurons in the brain that can respond to the slant of a surface using just its projective geometry and regardless of whether the contrast is chromatic or achromatic. We further suggest that orthographic projections in textured stimuli do not induce slant perceptions because the brain region specific for texture may not be not tuned to the geometry of the individual elements but only global, texture-based cues.

Acknowledgments

This study was funded by a CIHR Grant (MOP-10819) and an NSERC Grant (RGPIN 183625-05) to K.T. Mullen. The authors thank Luis Garcia Suarez, Mina Gheiratmand, Niia Nikolova, Ahmad

Yoonessi, Raiju Babu, Yeon Jin Kim, Shaleeza Kaderali, Lauren Libenson and Roy Waknin for their help as subjects. We thank Mina Gheiratmand, Shaleeza Kaderali, Yeon Jin Kim and Roy Waknin for assistance in the laboratory.

References

Beaudot, W. H., & Mullen, K. T. (2005). Orientation selectivity in luminance and color vision assessed using 2-d band-pass filtered spatial noise. *Vision Research, 45*, 687–696.

Blake, A., Bulthoff, H. H., & Sheinberg, D. (1993). Shape from texture: Ideal observers and human psychophysics. *Vision Research, 33*, 1723–1737.

Bland, J. M., & Altman, D. G. (2007). Agreement between methods of measurement with multiple observations per individual. *Journal of Biopharmaceutical Statistics, 17*, 571–582.

Bradley, A., Zhang, X., & Thibos, L. (1992). Failures of isoluminance caused by ocular chromatic aberrations. *Applied Optics, 31*, 3657–3667.

Brewer, A. A., Liu, J., Wade, A. R., & Wandell, B. A. (2005). Visual field maps and stimulus selectivity in human ventral occipital cortex. *Nature Neuroscience, 8*, 1102–1109.

Buckley, D., Frisby, J. P., & Blake, A. (1996). Does the human visual system implement an ideal observer theory of slant from texture? *Vision Research, 36*, 1163–1176.

Bushnell, B. N., Harding, P. J., Kosai, Y., Bair, W., & Pasupathy, A. (2011). Equiluminance cells in visual cortical area v4. *Journal of Neuroscience, 31*, 12398–12412.

Cant, J. S., Arnott, S. R., & Goodale, M. A. (2009). FMR-adaptation reveals separate processing regions for the perception of form and texture in the human ventral stream. *Experimental Brain Research, 192*, 391–405.

Cavanagh, P. (1991). Vision at equiluminance. In J. J. Kulikowski et al. (Eds.). *Vision and visual dysfunction: The limits of vision* (Vol. V, pp. 234–250). Boca Raton, FL: CRC Press.

Cavanagh, P., Adelson, E. H., & Heard, P. (1992). Vision with equiluminant colour contrast: 2. A large-scale technique and observations. *Perception, 21*, 219–226.

Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 1*, 893–899.

Cavina-Pratesi, C., Kentridge, R. W., Heywood, C. A., & Milner, A. D. (2010). Separate channels for processing form, texture, and color: Evidence from FMRI adaptation and visual object agnosia. *Cerebral Cortex, 20*, 2319–2332.

Cole, G. R., Hine, T., & McIlhagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space. *J Opt Soc Am A, 10*, 38–51.

Cutting, J. E., & Millard, R. T. (1984). Three gradients and the perception of flat and curved surfaces. *Journal of Experimental Psychology: General, 113*, 198–216.

Gregory, R. L. (1977). Vision with isoluminant colour contrast: 1. A projection technique and observations. *Perception, 6*, 113–119.

Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. (1998). Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience, 1*, 235–241.

Hamburger, K., Hansen, T., & Gegenfurtner, K. R. (2007). Geometric-optical illusions at isoluminance. *Vision Research, 47*, 3276–3285.

Hess, R. F., Wang, Y.-Z., & Dakin, S. C. (1999). Are judgements of circularity local or global? *Vision Research, 39*, 4354–4360.

Knill, D. C. (1998a). Discrimination of planar surface slant from texture: Human and ideal observers compared. *Vision Research, 38*, 1683–1711.

Knill, D. C. (1998b). Ideal observer perturbation analysis reveals human strategies for inferring surface orientation from texture. *Vision Research, 38*, 2635–2656.

Liu, J., & Wandell, B. A. (2005). Specializations for chromatic and temporal signals in human visual cortex. *Journal of Neuroscience, 25*, 3459–3468.

Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience, 7*, 3416–3468.

Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240*, 740–749.

McIlhagga, W. H., & Mullen, K. T. (1996). Contour integration with colour and luminance contrast. *Vision Research, 36*, 1265–1279.

Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology, 359*, 381–400.

Mullen, K. T., & Beaudot, W. H. (2002). Comparison of color and luminance vision on a global shape discrimination task. *Vision Research, 42*, 565–575.

Mullen, K. T., Beaudot, W. H., & McIlhagga, W. H. (2000). Contour integration in color vision: A common process for the blue–yellow, red–green and luminance mechanisms? *Vision Research, 40*, 639–655.

Mullen, K. T., Dumoulin, S. O., McMahon, K. L., de Zubicaray, G. I., & Hess, R. F. (2007). Selectivity of human retinotopic visual cortex to S-cone-opponent, L/M-cone-opponent and achromatic stimulation. *European Journal of Neuroscience, 25*, 491–502.

Mullen, K. T., Beaudot, W. H., & Ivanov, I. V. (2011). Evidence that global processing does not limit thresholds for RF shape discrimination. *Journal of Vision, 11*(3), 1–21.

Proffitt, D. R., Bhalla, M., Gossweller, R., & Midgett, J. (1995). Perceiving geographical slant. *Psychonomic Bulletin & Review, 2*, 409–428.

Reisbeck, T. E., & Gegenfurtner, K. R. (1998). Effects of contrast and temporal frequency on orientation discrimination for luminance and isoluminant stimuli. *Vision Research, 38*, 1105–1117.

Sankeralli, M. J., & Mullen, K. T. (1996). Estimation of the L-, M- and S-cone weights of the post-receptoral detection mechanisms. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 13*, 10.

Stevens, K. A. (1981). The visual interpretation of surface contours. *Artificial Intelligence, 17*, 47–73.

Tansley, B. W., & Boynton, R. M. (1978). Chromatic border perception: The role of red- and green-sensitive cones. *Vision Research, 18*, 683–697.

Todd, J. T., Christensen, J. C., & Guckes, K. M. (2010). Are discrimination thresholds a valid measure of variance for judgments of slant from texture? *Journal of Vision, 10*, 1–18 (article no. 20).

Troscianko, T., Montagnon, R., Le Clerc, J., Malbert, E., & Chanteau, P. L. (1991). The role of colour as a monocular depth cue. *Vision Research, 31*, 1923–1929.

Tsutsui, K., Taira, M., & Sakata, H. (2005). Neural mechanisms of three-dimensional vision. *Neuroscience Research, 51*, 221–229.

Wade, A. R., Brewer, A. A., Rieger, J. W., & Wandell, B. A. (2002). Functional measurements of human ventral occipital cortex: Retinotopy and colour. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, 357*, 963–973.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*, 1293–1313.

Wilkinson, F., Wilson, H. R., & Habak, C. (1998). Detection and recognition of radial frequency patterns. *Vision Research, 38*, 3555–3568.

Wilson, H. R., & Wilkinson, F. (1997). Evolving concepts of spatial channels in vision: From independence to nonlinear interactions. *Perception, 26*, 939–960.

Wuerger, S. M., & Morgan, M. J. (1999). Input of long- and middle-wavelength-sensitive cones to orientation discrimination. *Journal of the Optical Society of America A: Optics Image Science and Vision, 16*, 436–442.

Zaidi, Q., & Li, A. (2006). Three-dimensional shape perception from chromatic orientation flows. *Visual Neuroscience, 23*, 323–330.

Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience, 11*, 641–649.