Gradients of relative disparity underlie the perceived slant of stereoscopic surfaces

Susan G. Wardle

School of Psychology, The University of New South Wales, Sydney, Australia
Department of Cognitive Science and ARC Centre of Excellence in Cognition and its Disorders and Perception in Action Research Centre, Macquarie University, Sydney, Australia

Barbara J. Gillam

School of Psychology, The University of New South Wales, Sydney, Australia

Perceived stereoscopic slant around a vertical axis is strongly underestimated for isolated surfaces, suggesting that neither uniocular image compression nor linear gradients of absolute disparity are very effective cues. However, slant increases to a level close to geometric prediction if gradients of relative disparity are introduced, for example by placing flanking frontal-parallel surfaces at the horizontal boundaries of the slanted surface. Here we examine the mechanisms underlying this slant enhancement by manipulating properties of the slanted surface or the flanking surfaces. Perceived slant was measured using a probe bias method. In Experiment 1, an outlined surface and a randomly textured surface showed similar slant underestimation when presented in isolation, but the enhancement in slant produced by flankers was significantly greater for the textured surface. In Experiment 2, we degraded the relative disparity gradient by (a) reducing overall texture density, (b) reducing flanker width, or (c) adding disparity noise to the flankers. Density had no effect while adding noise to the flankers, or reducing their width significantly decreased perceived slant of the central surface. These results support the view that the enhancement of slant produced by adding flanking surfaces is attributable to the presence of a relative disparity gradient and that the flanker effect can spread to regions of the surface not directly above or below the gradient.

Introduction

Surfaces that are modulated in depth produce monocular perspective cues such as texture gradients and shading, and binocular information such as gradients of positional disparity. Positional (or absolute) disparity is defined as the difference in retinal position of the images in the two eyes of a given point. The first spatial derivative of absolute disparity (a linear gradient of absolute disparity) is usually identified as the stimulus for stereoscopic slant perception (e.g., Nguyenkim & DeAngelis 2003; Orban, Janssen, & Vogels, 2006; Parker, 2007; Bridge & Cumming 2008); however, several results suggest that the perception of stereoscopic slant may be more complex than a response to the magnitude of absolute binocular disparity gradients. For example, there is the well-established anisotropy between perceptual responses to horizontal and vertical disparity gradients. Perceived slant around a horizontal axis produced by vertical disparity gradients has a short latency and is close to prediction, whereas perceived slant around a vertical axis produced by horizontal disparity gradients is typically strongly underestimated, with surfaces perceived as much flatter than predicted geometrically (Gillam, Flagg, & Finlay, 1984; Fahle, & Westheimer, 1988; Mitchison & Westheimer, 1990; Gillam & Ryan, 1992; Cagenello & Rogers, 1993; van Ee & Erkelens, 1996; Pierce & Howard, 1997; Wardle, Palmisano, & Gillam, 2014). In addition, slant perception from horizontal disparity gradients is much slower than for vertical gradients (van Ee & Erkelens, 1996), emerging well after stereo fusion (Gillam, Chambers, & Russo, 1988).

The slant anisotropy indicates that positional disparity gradients per se are not very effective mediators of slant perception, since they are equally present for slant around both horizontal and vertical axes. The

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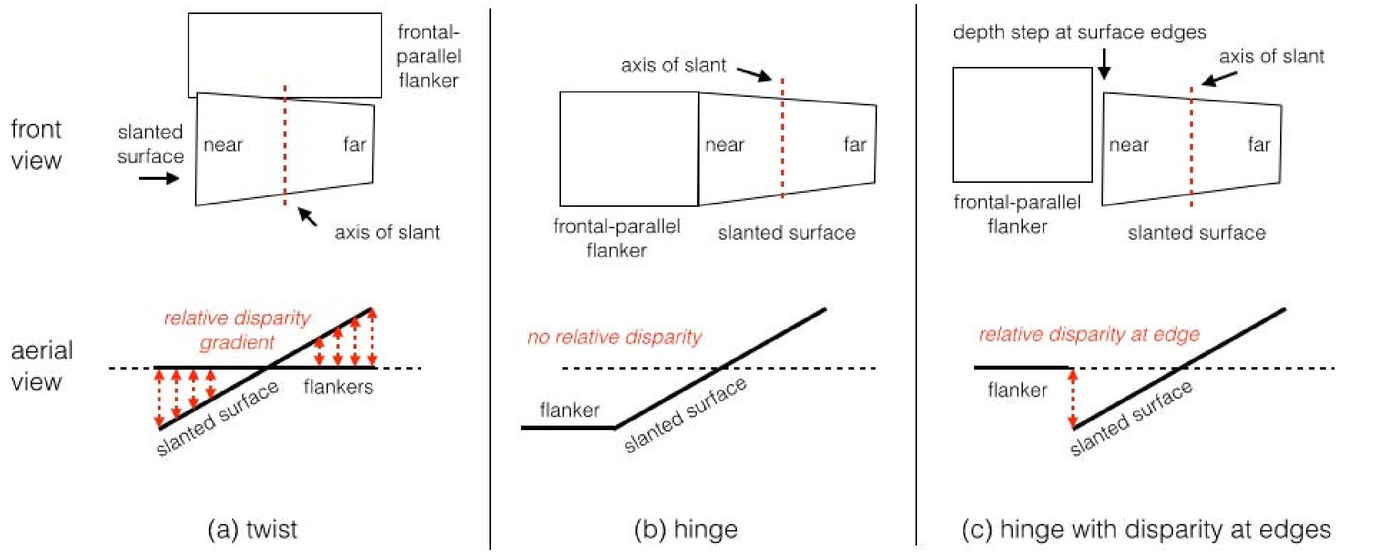

Figure 1. Three surface arrangements with different effects on horizontal slant perception. Each is shown in a front view (top row) and aerial view (bottom row). (a) In the twist configuration, the placement of the frontal-parallel flanking surface produces a relative disparity gradient along the horizontal edge of the slanted surface, and the perception of slant is enhanced. (b) In the hinge arrangement, the flanking surface is at the depth of the left or right edge of the slanted surface. It produces a change in the absolute disparity gradient at the inflexion point, but not a depth discontinuity with relative disparity. Perceived slant is not enhanced in this case. (c) If a depth step is introduced between the flanking surface and the slanted surface in the hinge, there is relative disparity at the depth discontinuity and perceived slant is increased (but not as much as in the twist).

anisotropy seems to be related to differences in the nature of the global configuration between the two images, which are very different for the two directions of disparity gradient. Rogers and Graham (1983), following Koenderink and van Doorn's (1976) analysis of disparity fields, pointed out that vertical disparity gradients produce a global difference in image shear, whereas horizontal disparity gradients produce a global difference in image compression. The visual system is known to be more responsive to differences in shear than to compression even in nonstereoscopic contexts, for example, motion parallax (Rogers & Graham, 1983), monocular perspective (Gillam, 1995), and visual search (Goodenough & Gillam, 1997). Subsequently, Bradshaw, Hibbard, and Gillam (2002) devised stimuli that dissociated axis of slant from type of disparity field and confirmed that the anisotropy is between shear and compression rather than between horizontal and vertical directions of slant per se.

A second result indicating that absolute disparity gradients do not adequately explain perceived slant is the finding that, lacking an effective global cue, the perception of horizontal stereoscopic slant is greatly facilitated by the presence of gradients of *relative disparity*. These gradients can occur at the depth discontinuities between neighboring surfaces of different slants in complex scenes (Gillam et al., 1984; Gillam et al., 1988), or between two superimposed transparent surfaces of different slant or curvature (Gillam & Pianta, 2005). In the present paper we explore the mechanisms underlying slant perception based on gradients of relative disparity at surface depth discontinuities.

It is well established that human depth judgments of individual objects are relative. For example, the perceived depth of a line is based on its disparity relative to that of surrounding contextual elements (Gogel, 1956, 1972; Gulick & Lawson, 1976; Westheimer, 1979a), and stereoacuity thresholds are affected by the proximity of the targets to a slanted reference plane (Glennerster & McKee, 1999; Glennerster, McKee, & Birch, 2002). Gillam and colleagues (1984, 1988) argued that just as perceived stereoscopic depth for a point or line relies on relative disparity, the perception of stereoscopic slant (in the absence of an effective global cue) relies on *gradients* of relative disparity. They argue that the difficulty in perceiving the slant of an isolated stereoscopic surface arises because it only has a gradient of *absolute* or positional disparity, which is not the primitive for stereoscopic depth. A textured slanted surface does have individual relative disparities between points at different depths on the surface. It has been proposed that stereo slant could be derived from absolute disparities by comparing the output of the disparity energy model (which encodes positional disparity) of a central point and a more peripheral point on the slanted surface (Bridge & Cumming, 2001, 2008; Nguyenkim & DeAngelis, 2003). This derivation would give the relative disparity of those two points, but it is unclear how this relative disparity would be generalized to the entire surface. The relative disparity of each successive (equally spaced) pair of points across a slanted surface is identical and does not form a relative disparity gradient. For a random dot surface this is stochastically true. Gillam et al. (1988) suggested that successive identical relative disparities across a gradient of absolute disparity could be integrated to derive slant, but the long latencies associated with seeing slant from an isolated gradient of absolute disparity suggests that if this process exists, it is inefficient. There is a much more immediate and direct response to gradients of relative disparity.

The role of relative disparity gradients in perceiving slant has been empirically supported by experiments showing that placing a frontal plane surface above and/or below a stereoscopically slanted surface significantly increases its perceived slant (Gillam et al., 1984; van Ee & Erkelens, 1996; Gillam & Blackburn, 1998; Pierce, Howard, & Feresin, 1998; Gillam & Pianta, 2005; Gillam, Blackburn, & Brooks, 2007; Serrano-Pedraza, Phillipson & Read, 2010; Gillam, Sedgwick, & Marlow, 2011) and reduces its latency (Gillam et. al., 1984; Gillam et al., 1988; van Ee & Erkelens, 1996). This arrangement of surfaces is known as the "twist" configuration (Gillam et al., 1988; Gillam & Pianta, 2005; Gillam et al., 2007; Howard & Rogers, 2012). The two surfaces in a twist configuration form relative disparity gradients along the discontinuities at the top or bottom edges of the slanted surface (see Figure 1a). In contrast, if equally proximal frontal plane surfaces are placed next to the slanted surface but in a configuration that does not create gradients of relative disparity, as in the "hinge" configuration (see Figure 1b), slant perception is not enhanced and perceptual latency is not decreased (Gillam et al., 1988; Pierce et al., 1998; Gillam & Pianta, 2005; Gillam et al., 2007). Thus, the increase in perceived slant for a surface in the twist configuration cannot be attributed to the presence of a reference surface, to slant contrast, or to the introduction of a derivative of absolute disparity (all of which apply to the hinge configuration).

However, although the standard hinge configuration (Figure 1b) does not enhance perceived slant, a modification of the hinge in which the adjacent edges of the slanted surface and the additional frontal-parallel surfaces are offset in depth in opposite directions at each end of the surface (Figure 1c) does increase slant, although not to the same extent as the twist (Gillam et al., 2007; Wardle et al., 2014). Unlike the standard hinge, this modified configuration does produce a crude gradient of relative disparity formed by disparity discontinuities at the lateral edges of the slanted surface.

A feature of the stereoscopic slant anisotropy is the asymmetrical role of cue conflict for horizontal versus vertical axis slant. Conflicting perspective cues have a greater influence on slant around a vertical axis than on slant around a horizontal axis (Gillam & Ryan, 1992; Ryan & Gillam, 1994). Gillam (1968) showed that the effectiveness of a cue in eliciting perceived slant in isolation predicts its domination in a cue conflict (see also Todd, Christensen, & Guckes, 2010). Other authors have found a relationship between cue dominance and cue reliability (Hillis, Watt, Landy, & Banks, 2004). Consequently, the observation that horizontal axis slant is more resistant to perspective sources of cue conflict than vertical axis slant is consistent with the idea that the former has a more effective source of stereo slant information (global shear), and that this is weighed more heavily than compression when in conflict with monocular cues such as linear perspective. However, Gillam et al. (1984) found that the strong attenuation of stereo surface slant when in conflict with perspective (in the form of a rectangular grid) was eliminated by adding fronto-parallel flanking surfaces to the stereo slanted surface in the twist configuration. Under these conditions the perceived surface slant is close to the degree predicted by its degree of horizontal magnification. The observation that relative disparity gradients provide a sufficiently strong stereoscopic slant cue to override even very strong conflicting perspective information in the stimuli further underscores their significance. Unsurprisingly, in studies using random dot or line stimuli (Gillam et al., 2007; Wardle et al., 2014), which provide weaker conflicting perspective cues than grid patterns (Gillam & Ryan, 1992), introducing a twist configuration also eliminates any effect of cue conflict.

In sum, there is now substantial evidence that absolute disparity gradients (the first spatial derivative of positional disparity) are much less effective in the perception of slant about a vertical axis than relative disparity gradients (Figure 1a). We present here two experiments with stimulus manipulations designed to probe the mechanisms underlying the operation of disparity gradients in stereoscopic slant perception. In the first experiment we compared the magnitude of perceived slant for outlined surfaces with textured surfaces for both single slanted surfaces and surfaces embedded in a twist configuration. This comparison allowed us to investigate the importance of both an explicit linear gradient of absolute disparity in the perceived slant of single surfaces, and an explicit gradient of relative disparity in the perceived slant of surfaces in a twist configuration. To anticipate our findings, we found that perceived slant for single surfaces did not differ for surfaces defined by an outline versus those defined by a texture. In contrast, for the twist configuration, textured surfaces were perceived as

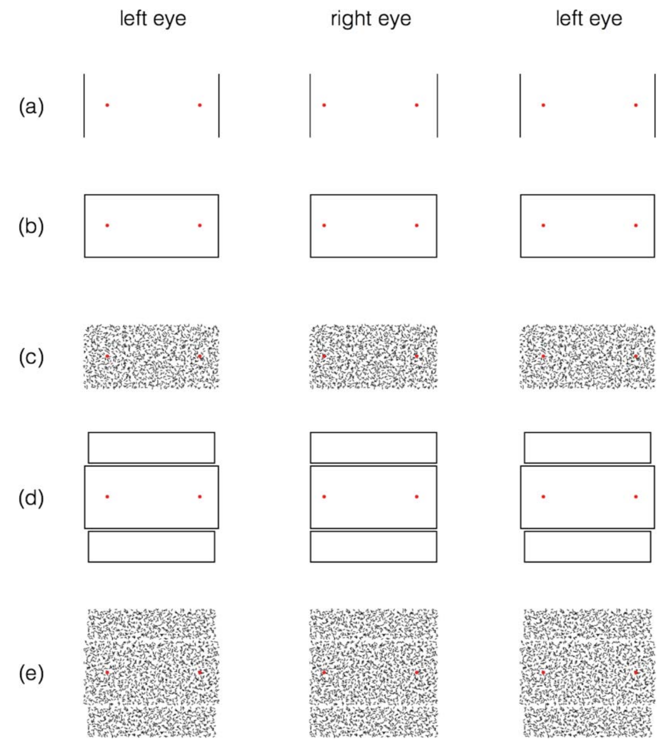

Figure 2. Example stimuli from Experiment 1 (6% slant to the right, drawn to scale). The red dots on each image are the probes used to measure perceived slant. The experimental conditions are (a) vertical lines at a relative depth equivalent to the near and far edges of the slanted surface, a single slanted surface defined by (b) outline only or (c) random line texture, and a 'twist' stimulus defined by (d) outline only or (e) random line texture. Only the texture conditions (c and e) contain disparity gradients across the slanted surface: an *absolute* disparity gradient for both surfaces (c and e), and in addition, a *relative* disparity gradient for the surface in the twist configuration (e). The two panels on the left are for divergent fusion; the two panels on the right are for crossed fusion.

more slanted than outlined surfaces of the same horizontal magnification. This observation suggested that perceived slant depends on the quality of the relative disparity gradient. In a second experiment we tested this by varying the quality of relative disparity gradients in a twist configuration using three different manipulations: reducing texture density, adding variable degrees of disparity noise to the flankers, and varying flanker width. We found no effect of texture density, but adding disparity noise to the flankers or shortening the flanker width significantly reduced perceived slant.

Experiment 1

In Experiment 1 we used slant stimuli (see Figure 2) that were either constructed from random line textures (and had a disparity gradient across the entire surface) or were simple outlines (and thus lacked an explicit disparity gradient, except at the vertical surface edges). The stimuli were either isolated stereoscopically slanted surfaces, or the same surfaces with additional frontal plane flanking surfaces placed above and below in a "twist" configuration. We included a further condition in which only the two vertical lines corresponding to the near and far edges of the slanted outline stimulus were present. This control was to compare the effect on the probe bias of the disparity of the lines alone (i.e., the difference in depth between the vertical edges) with the effect when the lines are completed into a slanted surface (i.e., by connecting the two vertical lines with horizontal lines to form a rectangle), which does not add any disparity information.

To measure perceived slant, we used a probe bias task that has been used successfully in previous experiments (Gillam et al., 2011; Wardle et al., 2014). The task exploits the observation that when two dots are positioned at the same depth in front of an isolated stereoscopically slanted surface, they appear to be at different depths. This is because the depths of the dots relative to the surface are perceived correctly, but the slant of the surface is underestimated, introducing a bias in the apparent depths of the dots relative to each other (Mitchison & Westheimer, 1984). Thus the degree of offset in depth between the two dots (bias) can be used as a proxy for the degree to which slant is misperceived.

Methods

Observers

Eleven observers with normal or corrected-to-normal vision participated in Experiment 1. One additional observer was excluded because of poor performance on the practice task and being unable to complete the experiment in the allocated time. Observers were recruited from within the School of Psychology at the University of New South Wales and the department's paid participant pool and were naive with regards to the experimental aims and hypotheses. Stereo vision was assessed using a practice task (see Procedure for details). All experiments were conducted in accordance with the guidelines set out in the Declaration of Helsinki and with the approval of the university's ethics committee.

Stimuli and apparatus

Experimental stimuli were generated on a MacPro computer with custom-written scripts using MATLAB (The MathWorks) and additional functions from the Psychtoolbox (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). Stereoscopic images were displayed using a mirror stereoscope and two identical LCD monitors (Dell U2412M) to display separate images to the left and right eyes. The resolution of both monitors was set to 1920 × 1200 pixels. Stimuli were viewed from a distance of 84 cm. The experimental apparatus and several stimulus parameters were identical to that used for experiments 2 and 3 in Wardle et al. (2014).

Examples of the experimental stimuli are shown drawn to scale in Figure 2. The stimuli were surfaces stereoscopically slanted around a vertical axis, with the exception of one condition in which only the near and far vertical edges of the slanted surface were visible (Figure 2a). The disparity of the two vertical lines in this stimulus matched the disparities of the near and far edges in the slanted stimuli. Slanted stimuli were either a single surface (Figure 2b, c) or a "twist" stimulus (Figure 2d, e), which had additional frontal-parallel flanking surfaces above and below the slanted surface. The slant stimuli were either pseudorandom line textures (Figure 2c, e) or a rectangular outline of the same dimensions (Figure 2b, d; H: 1.95° × W: 3.90°). The random line textures were constructed from small lines (4 × 1 arcmin) with random orientations drawn from a uniform distribution (0°–360°). Each pattern was generated by randomly allocating 3 lines to each 7 × 7 arcmin region of the pattern in order to produce a texture with even density. A new line pattern was randomly generated on each trial. To produce the perception of slant in the textured stimuli, the horizontal screen positions of the lines were magnified from the center of the stimulus boundaries in one eye. Slant was produced in the outline stimuli by horizontally elongating the rectangular outline in one eye's view. Thus, in the outline conditions, slant was only specified by a width difference between the two eye's views. In contrast, in the textured stimuli, slant was specified both by a width difference and by a horizontal disparity gradient across the surface. For all conditions, two levels of stimulus magnification were used, 3% or 6%, which corresponded to surface slants of 21° and 36° respectively (using Equation 1). Equation 1 (Ogle, 1950/1964, p.162, equation 8) shows the conversion of magnification (M in the form, e.g., 1.03 for 3%) to slant (θ) where y is viewing distance (84 cm), and a is half the interocular distance (6.5/2 = 3.25cm).

$$\tan(\theta) = \frac{M-1}{2M} \times \frac{y}{a} \tag{1}$$

Procedure

Prior to the main experiment, observers completed a practice task that involved matching the depth of two vertical black bars (H: 64 × W: 4 arcmin, horizontal separation: 0.7°). This was necessary because the majority of observers had not previously participated in a stereo experiment. The relative disparity of the bars at the start of each trial varied between 2 and 7 arcmin (in increments of 1 arcmin), with either the left or right bar nearer to the observer (6 relative disparity steps × 2 bar depth orderings = 12 trial types). Observers used the keyboard to adjust the depth of both bars to appear equal (in steps of 0.5 arcmin). Pressing the up arrow key moved the left bar forward in depth and the right bar backward. The directions were reversed for the down arrow key. There was no time limit, and when observers judged the depth of the bars to be equal, they pressed the space bar to initiate the next trial. Each set of bars were displayed for a minimum of 3 seconds before the space bar would proceed to the next trial, to prevent accidental key presses. Observers completed the first 12 trials with feedback. The bars turned orange when their relative disparity was within 2 arcmin, and green when it was within 0.5 arcmin. This was followed by 24 practice trials (each of the 12 trial types was repeated twice per observer in random order) without feedback. A correct response for each trial on the practice task would be a relative disparity of 0 arcmin, indicating that the observer had accurately positioned both bars at the same depth (absolute disparity). In calculating the mean offset between the bars for each observer and starting relative disparity, the absolute value of the probe settings was used to determine the relative depth difference between the bars regardless of sign (i.e., regardless of which bar (left or right) was in front of the other). If observers matched the depth of the bars perfectly, the mean of their responses for every trial type would be 0 arcmin (relative disparity of the two bars). The group mean from all 24 practice trials (averaged across all 11 observers and 12 conditions) was 1.55 arcmin ($SD = 2.09$ arcmin), indicating that observers generally performed well on the practice task.

In the experiment, observers matched the relative depth of two red probes positioned in front of the slanted surface (see Figure 1). The disparity probes used to measure perceived slant were two small red circles (diameter: 6 arcmin) horizontally separated by a distance of 2.8°. When the probes were set to the same depth (zero relative disparity), they were located 7 arcmin in front of the slanted surface. This standing disparity was necessary to allow the depth of the probes to be adjusted in the matching task. At the start of each trial, the relative disparity of the probes was randomly selected between ±4 arcmin. Observers adjusted the relative depth of the probes by using the keyboard to change their relative horizontal disparity as in the practice task. The upper and lower bounds of the probe were set at ±30 arcmin to prevent observers accidently moving the probe too far in either direction (which

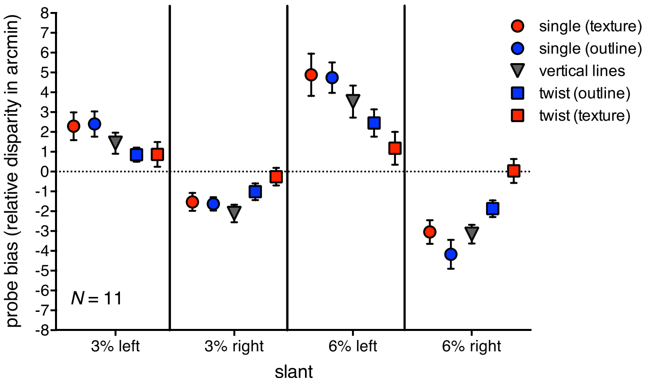

Figure 3. Results from Experiment 1. Each plotted point shows the mean probe bias averaged over all eleven observers for different conditions: single surfaces (circles), surfaces in a twist configuration (squares), and vertical lines only (triangles), which are at a depth equivalent to the near and far edges of the slanted surfaces in the single and twist conditions. The bias was measured in each of the five conditions for two magnifications (3% and 6%) and two directions of slant (left and right), grouped on the *x* axis. Error bars are between-subjects *SEM*, and thus cannot be used to infer statistical significance.

causes diplopia and a loss of perceived depth, making it difficult to correct). In the experiment there were two magnifications (3% and 6%), two directions of slant (left and right), two types of surface (texture or outline) and two surface configurations (single surface or "twist" stimulus with flankers). This produced 16 conditions in a factorial design. The addition of the extra control condition with the vertical lines (Figure 1a) produced a total of 20 conditions, which were repeated six times in random order, for a total of 120 trials per observer. Observers completed the experiment at their own pace, but the stimuli were shown for a minimum of 3 s on each trial before they could enter their response. Short (30 s) breaks were provided every 30 trials, and observers were encouraged to take additional breaks as needed.

Results and discussion

The mean probe settings for each condition in Experiment 1 are shown in Figure 3. The probe bias is quantified by the relative disparity between the two probe dots; a relative disparity of zero means the depth of the probes was accurately matched and slant was perceived veridically. If slant is misperceived, the predicted direction of the bias is to perceive the probe that is further from the surface (i.e., the probe in front of the side of the surface which is slanted away) as nearer than the probe that is closer to the surface (i.e., the probe in front of the nearest side of the slanted surface). The direction of the bias is coded as positive for leftward slant (right probe perceived nearer than left probe) and negative for rightward slant (right probe perceived further than left probe). As can be seen in Figure 3, the magnitude of the bias varied strongly across stimuli.

The results were analyzed in a repeated-measures ANOVA. Before statistical analysis, the data were recoded so that the predicted direction of the bias was positive for both leftward and rightward slant (the data for rightward slant were multiplied by -1 to invert the sign). The main effects of slant type, $F(4,40) = 30.758$, $p < 0.001$, and magnification, $F(1,10) = 21.492$, $p < 0.01$, were significant; but there was no effect for the direction of slant, $F(1,10) = 0.430$, $p > 0.05$. There were significant interactions between slant type and magnification, $F(1.9, 18.997) = 8.679$, $p < 0.01$, and for magnification and direction, $F(1,10) = 8.839$, $p < 0.05$. The sphericity assumption was violated for the interaction effects of slant type and magnification (Mauchly's test; $\chi^2(9) = 21.945$, $p < 0.05$), so the Greenhouse–Geisser correction was applied to the degrees of freedom.

Planned contrasts with the error rate controlled at $\alpha = 0.05$ using the Bonferroni correction were conducted to test for the differences of interest between the conditions. For this analysis the results were collapsed across the direction of slant (left or right), as this main effect was not significant in the ANOVA. Across magnification and surface type (outline or textured), there was a significantly greater probe bias for the single surface than for the twist stimulus, $F(1,10) = 89.791$, $p < 0.05$. This is consistent with previous results showing that the presence of flankers in a twist configuration enhances perceived slant (Gillam et al., 1984; Gillam et al., 1988; Gillam et al., 2007; Wardle et al., 2014) and reduces the probe bias (Gillam et al., 2011; Wardle et al., 2014). For the single surface, there was no significant difference in the magnitude of the bias (across both magnitudes) when the surface was a simple outline compared to when it was composed of random texture with an absolute disparity gradient, $F(1,10) = 1.423$, $p > 0.05$. This is further evidence that the absolute disparity gradient (present only in the textured surface) does not contribute much to the perception of slant of an isolated surface (Gillam et al., 1988).

For the twist stimulus, there was a significantly greater probe bias (across both magnifications) for the outline stimulus compared to the textured surface, $F(1,10) = 9.370$, $p < 0.05$) indicating that stereoscopic slant was enhanced for the textured surface in the twist configuration compared to the outlined surface. The magnitude of slant perceived for the textured twist surface was close to veridical (as predicted by the amount of horizontal magnification), which is shown by a mean probe bias close to zero across all magnifications and directions of slant (Figure 3). This result provides additional support for the idea that it is the relative disparity gradient across the slanted surface in the twist configuration that increases its perceived slant (Gillam et al., 1988). Further, our results show that the visual system is not able to extrapolate the depth gradient along a continuous line effectively enough in the outline condition to equal the condition in which the relative disparity gradient is explicitly specified along the horizontal edges of the surface by a random texture pattern. These results suggest that the degree of perceived slant is related to the quality of the relative disparity gradient, which will be explored further in Experiment 2.

Finally, the magnitude of the probe bias was significantly reduced for the control condition with the vertical lines alone compared to the single surface outline, $F(1,10) = 23.407$, $p < 0.05$. As the relative disparity between the vertical lines is equal in these conditions (see Figure 2a, b), the only difference between them is the addition of two horizontal lines that connect the vertical lines to form a rectangular surface in the outline condition (Figure 2b). The fact that the surface condition produced a significantly greater bias than when only the vertical edges were present suggests that the relative depth of the near and far edges is perceived differently (i.e., underestimated) when the edges are connected to form an isolated slanted surface. These results are related to previously reported effects of closure on subthreshold and suprathreshold depth discrimination (Westheimer 1979b; McKee, 1983; Mitchison and Westheimer, 1984, Zalevski, Henning, & Hill, 2007; Deas & Wilcox, 2014), which will be addressed in the General discussion.

Experiment 2

The results of Experiment 1 suggest that the magnitude of slant enhancement in the twist configuration is related to the degree to which the relative disparity gradient is specified. This suggests that degrading the quality of the relative disparity gradient in the twist will also reduce the amount of slant perceived for the central surface. In Experiment 2 we test the effect of degrading the strength of the relative disparity gradient in the twist stimulus using three methods: (a) by reducing texture density, (b) by reducing the width of the flanking reference surfaces, and (c) by adding disparity noise to the flanking surfaces. Reducing density reduces the number of points forming the relative disparity gradient, whereas reducing the flanker width reduces the portion of the slanted surface that is supported by the gradient. It is possible that the resolution of the slant for this portion of the surface is extrapolated to the rest of the surface, in which case an equivalent magnitude of probe bias would be expected regardless of flanker width. It was expected that adding disparity noise would make the relative disparity signals more difficult to extract, and thus reduce the benefit of adding flanking surfaces in the twist. For comparison, we measure perceived slant in these conditions relative to that perceived for a single slanted surface and an unaltered twist stimulus. Comparison of the different surface manipulations in Experiment 2 will reveal how the quality of the relative disparity gradient influences perceived slant and to what degree depth specified by the relative disparity gradient in the twist can be extrapolated across the slanted surface.

Methods

Observers

Nine of the observers who participated in Experiment 1 also participated in Experiment 2. All observers were naive to the experimental aims and hypotheses and were not debriefed on the aims of the experiment until Experiment 2 was completed.

Stimuli and apparatus

The experimental setup and stimulus parameters were identical to those in Experiment 1, with the following modifications. In Experiment 2, all of the slant stimuli were pseudorandom line patterns with slant specified by a gradient of horizontal disparity (see Experiment 1, Methods). Only one magnification (6%) was used as it produced the greatest magnitude of effect in Experiment 1. Three factors were varied: the density of the line pattern, the length of flankers in the twist stimulus, and the amount of noise in the flankers in the twist stimulus. In the density conditions, three texture densities were used to construct the single surface and twist stimuli (Figure 4): low (7 lines/deg^2), medium (26 lines/deg^2), and high (178 lines/deg^2); the highest density was identical to that used for the texture conditions in Experiment 1. For the flanker width comparison, two additional twist stimuli were used with flanker widths shorter than the central slanted surface: 2/3 (2.6°) and 1/3 (1.3°) of the original width of 3.9° (Figure 5c, d) . Finally, in the noise conditions, disparity noise was added to the upper and lower frontal-parallel flankers in the twist configuration (the central slanted surface contained no noise). The disparity noise was drawn from a normal distribution with a mean of 0 and a standard deviation of 5.3 (low noise, Figure 5e) or 10.6 (high noise, Figure 5f) arcmin.

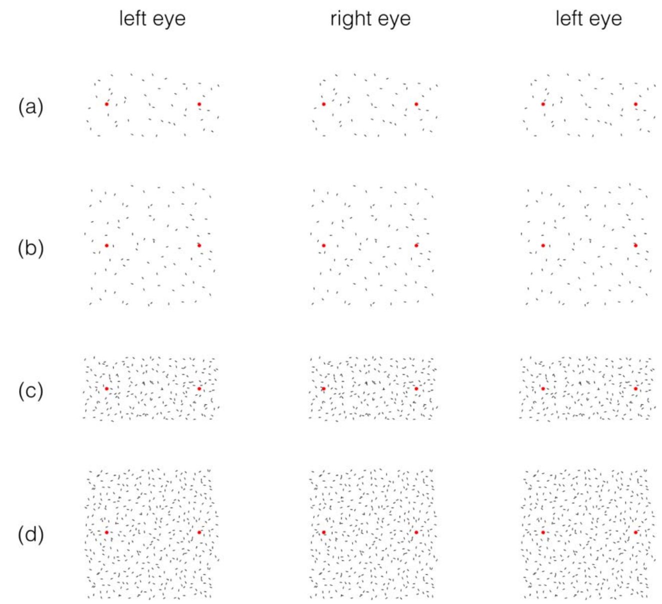

Figure 4. Example density stimuli from Experiment 2. Three densities were used; two are shown here: the low density (7 lines/deg^2) stimulus for (a) a single surface and (b) the 'twist' stimulus, and the medium density (26 lines/deg^2) stimulus for (c) a single surface and (d) the 'twist' stimulus. The high density (178 lines/deg^2) stimuli are shown in Figure 5 in panels (a) for the single surface and (b) for the twist, and matched the density used in Experiment 1. Red dots are the probes. Stereograms may be viewed with crossed (right two panels) or divergent (left two panels) fusion.

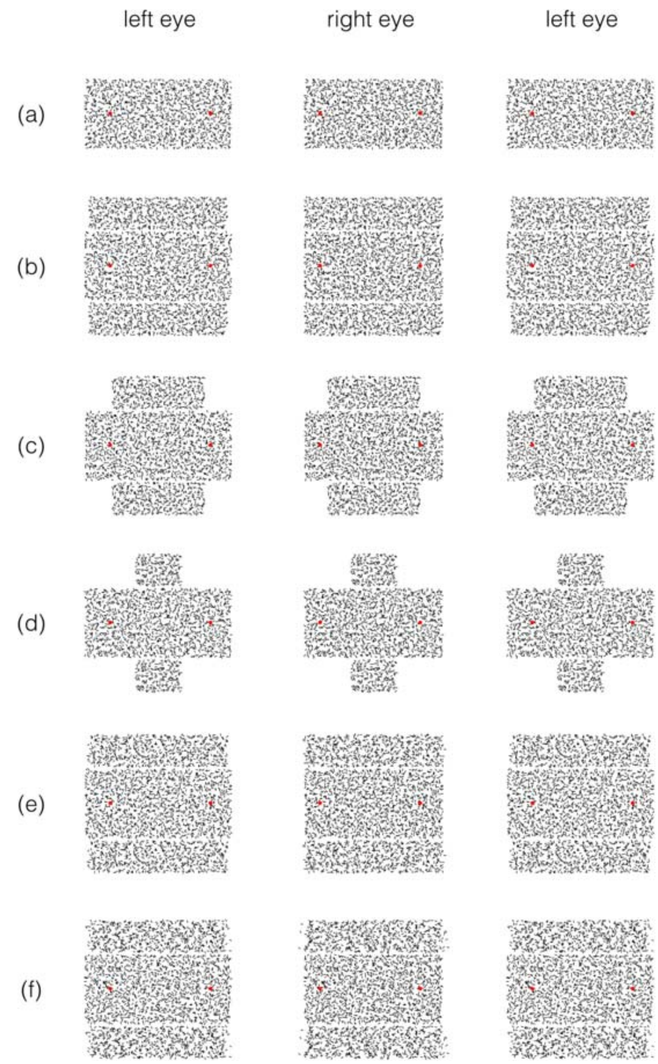

Figure 5. Example stimuli from Experiment 2 for the width and noise conditions. A single slanted surface (a) and a standard twist stimulus (b) were used as the reference conditions. In the width conditions, stimuli had either (c) 2/3 or (d) 1/3 the flanker length of that used in the standard twist stimulus. In the noise conditions, either a (e) low ($SD = 5.3$ arcmin) or (f) high ($SD = 10.6$ arcmin) level of disparity noise was added to the twist flankers (but not the slanted surface). Red dots are the probes. Stereograms may be viewed with crossed (two columns on the right) or divergent (two columns on the left) fusion.

Results and discussion

As in Experiment 1, for the analysis the direction of the bias is coded as positive for leftward slant (right probe perceived nearer than left probe) and negative for rightward slant (right probe perceived further than left probe). The results for texture density were analyzed with a repeated-measures ANOVA. There was a significant main effect for surface type (single vs. twist), $F(1, 8) = 36.781$, $p < 0.001$, but no effect of texture density or slant direction. No interactions were significant after applying the Greenhouse–Geisser correction for violating Mauchly's test of sphericity. The mean probe bias averaged across all observers is plotted in Figure 6. Given that our other manipulations were successful (see results below), the most likely reason why texture density did not have an effect is because this manipulation did not have the intended effect of degrading the disparity gradient. This implies that a gradient of relative disparity does not need to be constructed from many elements. The increased slant perceived for the twist even at low texture densities suggests that extrapolation across a stereoscopic surface from relative disparity gradients at the surface edges does not require many elements. One possible reason for this result may have been that not many texture elements are required in order to perceive a smooth stereoscopic surface (e.g., Hillis et al., 2004; appendix A). In Figure 7 the effects of flanker width and disparity noise on the probe bias are shown in separate panels. For flanker width, there is a significant linear decrease in the probe bias across flanker width from a single surface to a full twist stimulus, $F(1,8) = 16.493$, $p < 0.05$. This indicates that

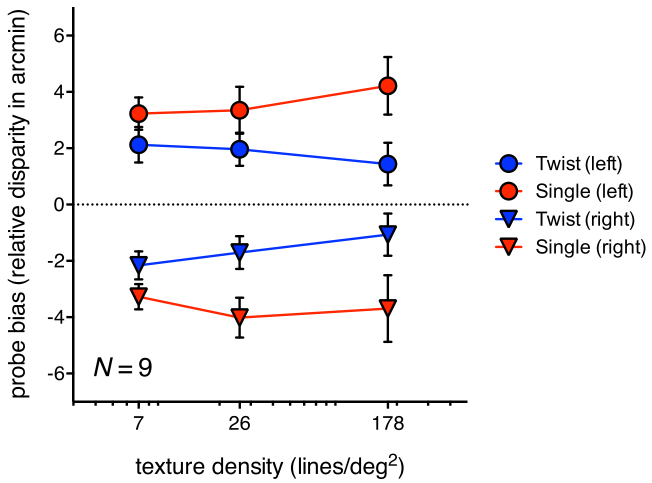

Figure 6. Results of Experiment 2 for variations in texture density (group means). Each point shows the mean probe bias averaged over all nine observers. Error bars are *SEM*.

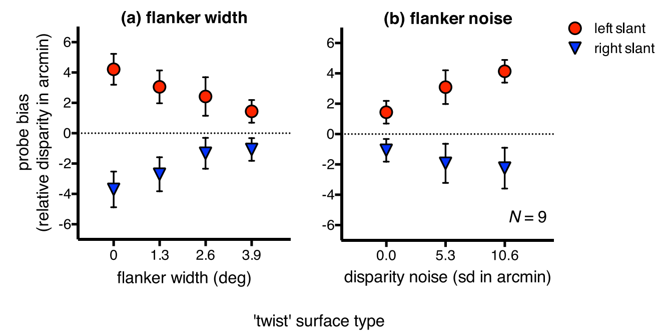

Figure 7. Results of Experiment 2 for variations in flanker width (left panel) and disparity noise (right panel) in the "twist" slant stimulus. Each point shows the mean probe bias averaged over all nine observers. Note that the points plotted as 3.9° in panel (a) and as $SD = 0$ in panel (b) are identical and are for the standard twist stimulus of full width and without noise (Figure 5b). The single surface (Figure 5a) is plotted in panel (a) as width $= 0°$ for comparison across flanker width. All plotted points were used in the linear trend analysis (as absolute values averaged across direction). Error bars are *SEM*.

perceived slant increased as a function of how far the relative disparity gradient extended across the slanted surface. Similarly, there is a significant linear increase in the probe bias as noise is increased in the twist flankers, $F(1,8) = 26.396$, $p < 0.05$. This relationship shows that degrading the relative disparity signal between the central surface and the twist flankers decreased the magnitude of slant perceived for the central surface. In both cases, degrading the relative disparity gradient by adding noise or reducing the flanker width reduced the magnitude of perceived slant. These results provide further evidence for the importance of relative disparity gradients in stereoscopic slant perception.

To further examine the effect of flanker width on perceived slant, we also tested whether there was a significant difference in the probe bias for each of the three sizes of flanker width in the twist compared to the isolated surface. Each of the three flanker widths produced a significant reduction in the probe bias relative to the isolated slanted surface condition: 1/3 width $F(1,8) = 26.521$; 2/3 width $F(1,8) = 22.517$; full width $F(1,8) = 16.066$, all $p < 0.05$, Bonferroni correction applied for multiple comparisons. This shows that although the magnitude of perceived slant systematically increases as the width of the frontal parallel flankers extends along the edges of the slanted surface, even a small flanker at the central axis of slant produces a significant increase in perceived slant. This is suggestive of a process of depth interpolation occurring across the slanted surface. This result is also important because it shows that a reduction in the probe bias is possible even when the probes are not directly below the frontal-parallel flankers (see also Gillam et al., 2011).

General discussion

Our results build on previous studies showing that relative disparity gradients are much more effective than absolute disparity gradients in eliciting stereoscopic slant around a vertical axis. It is striking that for single surfaces there was no increase in perceived slant for the textured surface compared to the outline surface (Experiment 1), even though only the textured surface contains the linear gradient of absolute disparity that is generally considered the basis of stereo slant perception. This finding reinforces previous reports of poor slant response to absolute disparity gradients in a horizontal direction (Gillam et al., 1984; Fahle & Westheimer, 1988; Mitchison & Westheimer, 1990; Cagenello & Rogers, 1993; van Ee & Erkelens, 1996; Pierce & Howard, 1997; Wardle et al., 2014). However, for the twist configuration, there was a significant reduction in the probe bias (and hence an increase in slant magnitude) for the textured surface compared to the outline, since in this case the textured surface contains both absolute and relative disparity gradients. These data indicate that the presence of linear gradients of *relative* disparity across the entire horizontal surface edges has a greater effect on perceived stereoscopic slant than extrapolation along the outline contours of depths from edge discontinuities.

Even for outline surfaces, the presence of the flanking surfaces in the twist configuration enhanced the slant of the central surface to a significant extent, although not to the same degree as for textured surfaces. This suggests that another possible cue to slant, the graded depth separation of the horizontal edges of slanted and flanking outline surfaces respectively, has some effect although it is much less effective than an explicit relative disparity gradient carried by texture. Additionally, the slant enhancement for the outline surfaces in a twist may indicate some extrapolation of the depth differences at the proximal edges of the flanker and central surfaces across the lines. Variations in the texture density of two surfaces in a twist configuration (Experiment 2) did not have an effect for the densities we used, indicating that gradients of relative disparity operate effectively with only minimal components. Only sparse texture elements seem to be required in order to perceive a coherent, solid stereoscopic surface (e.g., see stereograms in Figure 4).

In Experiment 2 we found that degrading the quality of the relative disparity gradient by adding disparity noise to the flankers reduced the magnitude of slant perceived for the slanted surface as a function of the amount of noise added. It is clear that although the density of the gradient is not important, its consistency is. The effectiveness of the relative disparity gradient is diminished if it is interspersed with random disparities that are not consistent with a linear gradient. Changing the width of the frontal plane flankers in the twist also had an effect. The increase in perceived slant produced by the narrowest flankers was not as great as for flankers extending across the whole width of the slanted surface. However, our results also show that horizontal slant based on a relative disparity gradient can be extrapolated to horizontal parts of the surface beyond the extent of the gradient. Flankers forming a twist configuration but with a width spanning only the central third of the slanted surface (see Figure 4d) still significantly reduced the bias of the probes positioned at the outer ends of the slanted surface relative to a surface without flankers. There is evidence for an analogous *vertical* interpolation of depth across a slanted surface from frontal-parallel flankers in the twist configuration. Gillam et al. (2011) found that increasing the height of the central slanted surface in the twist configuration (thus increasing the distance between the flankers and the probes, which were in line with the center of the slanted surface) reduced the magnitude of perceived slant (measured by an increase in the probe bias). However, even at fairly large heights of the central surface (4.4°), the probe bias was reduced for the twist configuration compared to an isolated surface, suggesting that depth propagated vertically across the central surface for a considerable distance from the locations of the relative disparity gradients.

Our finding in Experiment 1 that the probe bias was reduced when the two horizontal lines connecting the vertical lines into a rectangle were removed (i.e., leaving only the vertical lines at the near and far edges) is consistent with previous results of the effect of closure on depth discrimination (Westheimer, 1979b; McKee, 1983; Mitchison & Westheimer, 1984; Deas & Wilcox, 2014). Depth discrimination thresholds are increased when horizontal lines are added to a pair of vertical lines to form a closed rectangle, compared to when only the vertical lines are present (McKee, 1983; Mitchison & Westheimer, 1984). Similarly, Deas and Wilcox (2014) used a suprathreshold depth estimation task and found that the relative depth of two vertical lines was underestimated when they were connected by horizontal lines to form a closed object, compared to when the lines were either isolated or connected to form two separate closed objects. Experiment 1 confirms this result using a substantially different method (the probe bias task) to estimate perceived depth. Stevens and Brookes (1988) attribute the effect of closure to the formation of a surface, which is then processed for slant cues deriving from its shape. Interestingly, Zalevski et al. (2007) found that adding consistent perspective cues to the configuration by changing the shape of the outlined rectangle to be consistent with the implied slant did partially reduce the attenuation of depth perceived when the vertical lines were joined, but not to a level equivalent to when the lines were separate. Thus, the effect of closure cannot be completely accounted for by cue conflict between disparity and perspective. Our results additionally show that for isolated surfaces, an enclosed outline figure and a fully textured figure of the same area and shape produce the same slant, suggesting that the depth attenuation produced for closed figures is not produced by the box outline configuration itself, but by a more general problem in deriving surface slant around a vertical axis.

Although cue conflict exists in our stimuli, it cannot explain our results. Possible conflicting cues in our RDSs include a homogenous texture gradient and the linear perspective defined by the regular rectangular shapes. Although these cues conflict with the disparity information (which specifies a slanted surface), the strength of the twist configuration is powerful enough to negate any conflicting depth information from these cues (e.g., Gillam et al., 1984; Gillam & Blackburn, 1998). In a previous series of experiments we found the perceived slant of our basic random line twist stimulus to be approximately veridical (Wardle et al., 2014; see Figure 4). In addition, the disparity noise and flanker width manipulations in Experiment 2 were only made to the flanking surfaces, with the slanted surface (and hence any conflicting cue information) identical between comparisons. Although the density manipulation was applied to both slanted and flanking surfaces, it would be likely to reduce the strength of any conflicting monocular cues from texture or linear perspective, as there are far fewer texture elements and a less defined border in the monocular images for the stimuli with the lowest density (see Figure 4a, b). Indeed, we found that although the probe bias was reduced for the twist stimulus, this did not vary reliably as a function of density as would be expected from the reduction in cue conflict with lower density stimuli.

Although behavioral results have shown that relative disparity gradients are important in the perception of stereoscopic slant about a vertical axis, literature on the neural mechanisms underlying these effects is scarce. Relative disparity is encoded in a number of areas beyond V1 including both dorsal and ventral streams (Parker, 2007). However, neurons sensitive to one configuration of relative disparity are not necessarily sensitive to another (Parker, 2007). Cells in V2 have been identified which respond to disparity-defined edges in random-dot stereograms, (von der Heydt, Zhou, & Friedman, 2000) and some of these cells are selective for the direction of the depth step. In this case the disparity-defined edges have a constant value and do not involve slant, but it is possible that the processes responsible for detecting a depth step between two surfaces are also recruited for detecting relative disparity gradients. Similarly, there are cells in V5 that respond to the relative disparity of two transparent surfaces at different depths (Krug & Parker, 2011). However, no study to our knowledge has examined neural sensitivity to relative disparity gradients. The general view concerning the role of disparity discontinuities is summarized by Orban et al. (2006): "Sudden changes in absolute disparity give rise to discontinuities that, like discontinuities in motion or texture, can be used as a cue for segmentation and extraction of 2D shape. Smooth changes in absolute disparity provide information about the 3D shape of objects and the 3D layout of the environment" (p. 467). Indeed, cells tuned to the orientation and curvature of stereoscopic surfaces in macaque inferotemporal cortex and the caudal intraparietal (CIP) regions have been reported (summarized by Orban et al., 2006). However, in physiological studies of surfaces with higher order disparities such as slant, stimuli are sometimes presented with extra details forming backgrounds or apertures. This means that there may be unacknowledged disparity discontinuities (e.g., gradients and monocular regions) at the surface edges, possibly influencing the responses of cells, which are assumed to be responding to higher order absolute disparities.

Physiological and neuroimaging studies of slant and tilt have typically used single surfaces—and usually with stereoscopic slant around a horizontal axis. Recently, Ban and Welchman (2015) reported sensitivity to disparity gradients for stereoscopic slant about a horizontal axis in area V3A, an area associated with disparity processing in both human and macaque (Tsao et al., 2003). They found that the similarity of the fMRI BOLD response in area V3A to different slant stimuli was moderated as a function of slant—similar angles of slant produced similar patterns of BOLD activation, independently of whether other low-level stimulus features of the slanted surface (i.e., the mean disparity or the spatial extent of the surface) were fixed or varied. However, because the stimuli were random-dot stereograms depicting stereo slanted surfaces with a random-dot frontal plane background, it is not possible to determine whether absolute or relative disparity gradients (or even the presence of monocular regions) were responsible for the BOLD response that varied with slant. Additionally, as behavioral results suggest that the perception of stereoscopic slant around horizontal and vertical axes is fundamentally different, we hesitate to assume that the underlying neurophysiological mechanisms are the same in both cases. Future work is required to clarify the neurophysiological basis for the observed behavioral differences.

Keywords: stereoscopic slant, disparity gradients, relative disparity, depth matching, slant anisotropy

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Commercial relationships: none.
Corresponding author: Susan G. Wardle.
Email: susan.wardle@mq.edu.au.
Address: Department of Cognitive Science, Macquarie University, NSW, Sydney, Australia.

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