

Surface continuity and discontinuity bias the perception of stereoscopic depth

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Binocular disparity signals can provide high acuity information about the positions of points, surfaces, and objects in three-dimensional space. For some stimulus configurations, however, perceived depth is known to be affected by surface organization. Here we examine the effects of surface continuity and discontinuity on such surface organization biases. Participants were presented with a series of random dot surfaces, each with a cumulative Gaussian form in depth. Surfaces varied in the steepness of disparity gradients, via manipulation of the standard deviation of the Gaussian, and/or the presence of differing forms of surface discontinuity. By varying the relative disparity between surface edges, we measured the points of subjective equality, where surfaces of differing steepness and/or discontinuity were perceptually indistinguishable. We compare our results to a model that considers sensitivity to different frequencies of disparity modulation. Across a series of experiments, the observed patterns of change in points of subjective equality suggest that perceived depth is determined by the integration of measures of relative disparity, with a bias toward sharp changes in disparity. Such disparities increase perceived depth when they are in the same direction as the overall disparity. Conversely, perceived depth is reduced by the presence of sharp disparity changes that oppose the sign of the overall depth change.

& Freeman, 1991; Fleet, Wagner, & Heeger, 1996; Goncalves & Welchman, 2017; Nienborg, Bridge, Parker, & Cumming, 2004; Ohzawa, DeAngelis, & Freeman, 1990; Prince, Cumming, & Parker, 2002; Qian & Zhu, 1997; Read & Cumming, 2007). This conception of a point-by-point disparity map matches current approaches for the initial stages of disparity estimation in computer vision (e.g., Hirschmüller, 2008), and is supported by results from several psychophysical studies, which show that proposed mechanisms for dense disparity estimation are sufficient to account for performance in a range of tasks (Allenmark & Read, 2010, 2011; Banks, Gepshtein, & Landy, 2004; Filippini & Banks, 2009; Goutcher & Hibbard, 2014). Several other avenues of research suggest, however, that while dense disparity maps may be an important initial processing step, they cannot account for multiple aspects of our perception of the three-dimensional (3-D) structure of our environment.

Recently, researchers have shown that the perception of quantitative depth in binocular stimuli depends upon surrounding disparity information, with the presence of continuous gradations in disparity resulting in a reduction in perceived depth (Cammack & Harris, 2016; Deas & Wilcox, 2014, 2015; Hornsey, Hibbard, & Scarfe, 2016). These recent findings are consistent with much earlier results, which showed that disparity discrimination thresholds are increased for pairs of vertical lines when intervening horizontal lines create a closed figure (McKee, 1983; Mitchison & Westheimer, 1984). Similarly, such thresholds are reduced for random-dot stereograms (RDSs) of curved surfaces containing gaps between surface segments (Vreven, McKee, & Verghese, 2002). Deas and Wilcox (2014, 2015) suggested that these reductions in perceived depth were due to the effects of Gestalt grouping

Introduction

An extensive body of physiological and computational work suggests that the perception of depth from binocular disparity is derived from a dense map of disparity measurements, encoded in retinal coordinates at the early stages of visual cortex (DeAngelis, Ohzawa,

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principles of similarity and good continuation. While these papers provided compelling evidence of the effects of grouping rules on depth perception, they did not provide a mechanism through which such rules might influence quantitative estimates of depth.

One potential mechanism was proposed by Cammack and Harris (2016), who suggested that reductions in perceived depth might be a consequence of spatial averaging procedures operating to improve the signal-to-noise ratio of absolute (i.e., retinal coordinate) disparity estimates. To account for reductions in perceived depth, Cammack and Harris (2016) measured the size of the spatial window over which such averaging would operate. These were found to be very large (around 90% of the size of their stimulus), although their modeling does not provide a mechanism, or a computational reason, for deciding the area over which any averaging should occur. While an intriguing possibility, the absence of a mechanism through which to determine the area for averaging means that Cammack and Harris's (2016) results provide no means to predict when we should find reductions in perceived depth in novel stimuli.

An alternative possibility is that biases in the perceived depth of continuous surfaces are due to disparity measurement mechanisms operating at the level of relative disparities. One such mechanism was proposed by Tyler (1975, 2013; Tyler & Kontsevich, 2001), who adopted the terminology *hypercyclopean* to describe cells selective for specific frequencies of disparity modulation, analogous to frequency-tuned cells in the luminance domain. These hypercyclopean channels have been used to account for cyclopean-level tilt and size aftereffects (Tyler, 1975) as well as anisotropies in stereoacuity for disparity corrugations (Bradshaw & Rogers, 1999; Hibbard, 2005; Serrano-Pedraza & Read, 2010; Tyler & Kontsevich, 2001).

To provide new insight into possible mechanisms governing surface-related reductions in perceived depth, this paper examines the interaction between factors of surface continuity (Cammack & Harris, 2016; Deas & Wilcox, 2014, 2015), considered in terms of the steepness of disparity variation across a stimulus, and surface discontinuity. Previous research on surface discontinuities has shown contradictory effects. In some cases, the presence of discontinuous edges can enhance perceived depth compared to continuous disparity changes (Cammack & Harris, 2016; Deas & Wilcox, 2014, 2015), and can improve slant discrimination thresholds (Wardle & Gillam, 2016). Conversely, some discontinuous surface arrangements lead to reductions in perceived depth, as in the depth variant of the Craik-O'Brien-Cornsweet illusion (Anstis, Howard, & Rogers, 1978; Rogers & Graham, 1983). Here, we examine the effects of combined surface steepness and surface discontinuity manipulations on perceived depth.

Together, these experiments provide a test of both disparity averaging and good continuation accounts of perceived depth biases. We further test the results of these experiments against a model of hypercyclopean-level processing. Our results suggest that, while neither averaging nor good continuation explanations can account for the range of observed effects, the smoothing effect of hypercyclopean filtering plays a critical role in determining perceived depth for continuous surfaces. The effects of surface discontinuities suggest, however, that understanding perceived depth depends upon the encoding and integration of relative disparities by any hypercyclopean-like mechanism, rather than their capacity to smooth estimates of absolute disparity.

General methods

Six experiments were conducted to examine the roles of surface steepness and surface discontinuity parameters in biasing the perception of depth. In each, participants were presented with an RDS, depicting a surface or set of surfaces with binocular disparity-defined depth. Each RDS was presented as part of a two-interval forced-choice (2IFC) design, where participants were asked to select the interval containing the greater depth difference between the far-left and far-right edges of the stimulus (referred to here as the *edge-to-edge* depth).

Participants

Data was collected for five participants in each experiment, with the exception of Experiments 2 and 6, where there were four participants. All participants had normal or corrected-to-normal vision, and were experienced psychophysical observers, including authors RG and EC. Each participant was screened for functional stereoscopic vision using the Random Dot 2 Stereo Acuity Test (Vision Assessment Corp., Elk Grove Village, IL), with each demonstrating stereoacuity of at least 60 arcsecs on this test. All gave written, informed consent for their participation, with ethical approval granted by a local University of Stirling ethics board, in accordance with the guidelines of the British Psychological Society and the Declaration of Helsinki. Author RG participated in all six experiments, with author EC participating in Experiments 1 and 3 through 6. One participant participated in Experiments 1 through 5, another in Experiments 1 through 4 and another in Experiments 1, 2, and 6. The remaining participants took part in only one experi-

ment each, resulting in data collection for a total of 10 participants across the six experiments.

Stimuli

The base stimulus for each experiment was a random dot surface, with disparity defined by the error function, adjusted to conform to a cumulative Gaussian profile, scaled between ± 1 (Equation 1).

$$\delta = d \left[\operatorname{erf} \left(\frac{x}{s/\sqrt{2}} \right) / n \right] + r \quad (1)$$

For each stimulus, the disparity δ of each dot depended upon its x coordinate, together with a scaling factor d to vary overall change in disparity, and a steepness factor s , which altered the standard deviation of the cumulative Gaussian function. A normalization parameter n divided the scaled function by the absolute maximum of the function prior to disparity scaling. This ensured that the edge-to-edge depth of the final surface was always defined by the scaling parameter only, irrespective of the standard deviation of the function. To ensure that participants could not simply respond to the absolute disparity of surface end points, the disparity of the whole surface was shifted in depth by a random value r on a trial-by-trial basis, where r was selected between limits of ± 2 arcmin. As a further guard against this possibility, the direction of the change in disparity was randomized for each stimulus, such that either the left or right side of the surface could be the section nearer the observer.

Stimulus elements were white circular dots of diameter 7.7 arcmin. Stimuli covered an area of $4.7^\circ \times 4.7^\circ$, with the exception of those in Experiments 2 and 6, where lateral displacements and changes to stimulus size altered the horizontal extent for some conditions. Dot density was kept constant for all stimuli, at a value of 13.5 dots per degree squared. All stimuli were displayed against a mid-gray background for a period of 2 s, preceded by the 500-ms presentation of a central white fixation cross and a pair of white flanking lines. Both flanking lines, and constituent elements of the cross-measured 16.5 arcmin in length. Flanking lines were presented 16.5 arcmin above and below the area where the stimulus appeared. The fixation cross was not visible during stimulus presentation, leaving only the flanking lines as a fixation aid and cue to the depth of the screen plane. This minimal fixation aid ensured that participants could not make judgments using relative disparity information between the stimulus edges and any surrounding fixation stimulus (e.g., Wardle & Gillam, 2016).

Experiments 1 and 2 varied the steepness of surfaces, with either keeping stimulus width constant (Experiment 1), or scaling width in line with surface steepness

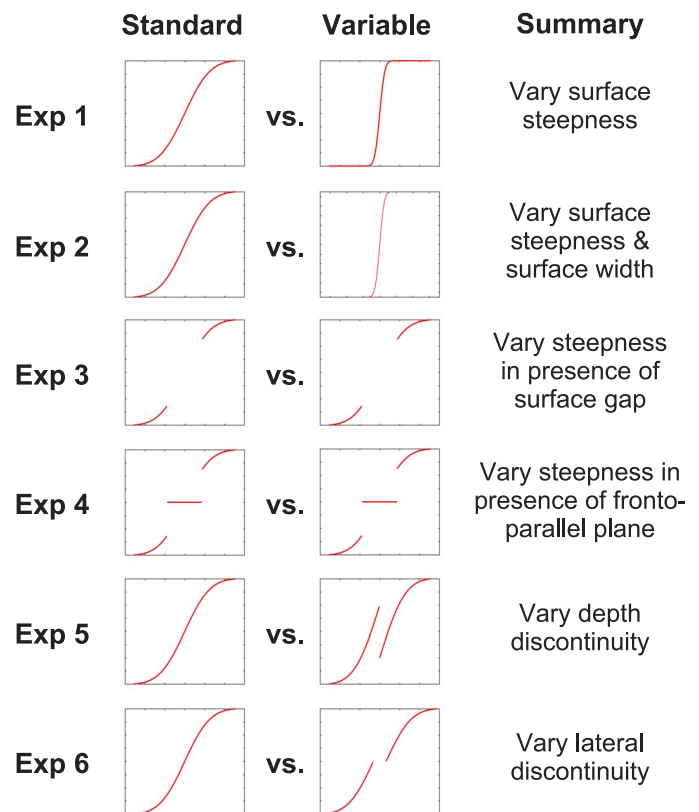


Figure 1. Summary of stimulus manipulations and comparisons used across all experiments.

(Experiment 2). Experiments 3 and 4 examined the impact of central stimulus regions either by removing them (Experiment 3) or by replacing the central region with a frontoparallel surface (Experiment 4). Finally, Experiments 5 and 6 examined the role of surface depth discontinuities (Experiment 5) and lateral discontinuities (Experiment 6). These manipulations are summarized in Figure 1, and described in detail in sections below.

Design and procedure

Stimuli for all experiments were programmed using Matlab (Mathworks, Inc.), in conjunction with the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). Stimulus presentation was controlled using a MacPro computer coupled with a 49×31 cm Apple Cinema HD display with a resolution of $1,920 \times 1,200$ pixels and a refresh rate of 60 Hz. At the 76.4-cm viewing distance, each pixel measured 1.1 arcmin. The display was calibrated to a linear grayscale using a Spyder2Pro calibration device (DataColor, Dietlikon, Switzerland), resulting in a luminance range of 0.18 cdm^{-2} to 45.7 cdm^{-2} . The presentation of images containing binocular disparity

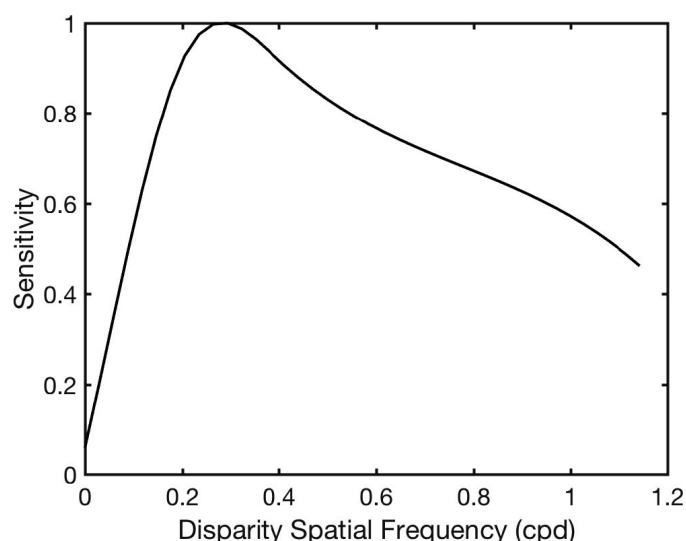


Figure 2. Disparity frequency sensitivity function, derived from estimates in Serrano-Pedraza and Read (2010).

was enabled through the use of a four-mirror modified Wheatstone stereoscope, with head movements restricted using a Headspot chinrest (UHCO, Houston, TX). All experiments were conducted in a darkened laboratory.

In each experiment, participants completed a 2IFC task to determine which interval contained the stimulus with the larger edge-to-edge depth difference. Edge-to-edge disparity was systematically varied in each experiment using a method of constant stimuli to allow for the recovery of psychometric functions defining the proportion of times the standard stimuli was judged as having greater depth. The point of subjective equality (PSE) was measured for each function. A minimum of 20 repeated trials were collected for each participant on each stimulus condition over multiple sessions, with each experimental session containing the randomized presentation of five repeated trials of each stimulus condition. Responses were made via a key press on a standard computer keyboard. Each key press initiated the presentation of the next trial.

Modeling perceived depth

To provide a model of perceived depth in our tasks, we convolved 1D versions of the disparity profile for each stimulus with a weighted set of hypercyclopean filters, describing a disparity frequency sensitivity function (Figure 2). The form of this sensitivity function followed existing psychophysical estimates, covering a range of 0.05 to 1.2 cpd, with a peak at 0.3 cpd (Serrano-Pedraza & Read, 2010). This disparity sensitivity function was defined for all spatial frequencies in this range by using piecewise cubic spline

interpolation of the data provided for horizontal disparity variation by Serrano-Pedraza and Read (2010) in their figure 6.

This convolution process was performed by taking the Fourier transform of the disparity profile of each stimulus, multiplying this by the disparity tuning function, and then taking the inverse Fourier transform. The perceived depth of each stimulus was taken as the difference between maximum and minimum responses at surface edges. For Experiments 3 and 6, there was a gap in the stimulus over which disparity was not defined. In these cases, the gap was filled using linear interpolation. To allow for trial-by-trial variation in response, perceived depth estimates were corrupted by a random additive noise term of ± 1 arcmin for each stimulus. Simulations show the results of 400 repeated trials of each experimental condition. Model results are shown alongside human psychophysical data as filled yellow circles throughout the paper.

Experiments 1 and 2: Manipulation of surface steepness

Experiments 1 and 2 examined the effects of manipulations of surface steepness on perceived depth. Results from both Deas and Wilcox (2014, 2015), and Cammack and Harris (2016) suggest that perceived depth should decrease as surface steepness is reduced. In Experiment 1, we test this hypothesis while keeping stimulus width constant. In Experiment 2, stimulus width was varied as a function of surface steepness (i.e., surfaces were constant in terms of the displayed number of standard deviations from the mean).

Stimuli

In Experiment 1 surface steepness was varied by manipulating s , the standard deviation of the cumulative Gaussian function. Standard deviations of 11, 55, and 110 arcmin were used to define RDS stimuli in the variable intervals, with the standard stimulus fixed at a standard deviation of 55 arcmin, and an edge-to-edge disparity of 11 arcmin. For the variable intervals, edge-to-edge disparity ranged from 0.9 to 16.7 arcmin for the 11 arcmin SD , from 2.2 to 28.6 arcmin for the 55 arcmin SD , and 4.4 to 44 arcmin for the 110 arcmin SD . Edge-to-edge disparity levels were sampled uniformly across the range for each standard deviation. Examples of the stimuli for Experiment 1 are shown in Figure 3.

Stimuli for Experiment 2 followed the same structure as Experiment 1, except that stimulus width varied with surface steepness, such that each surface covered a

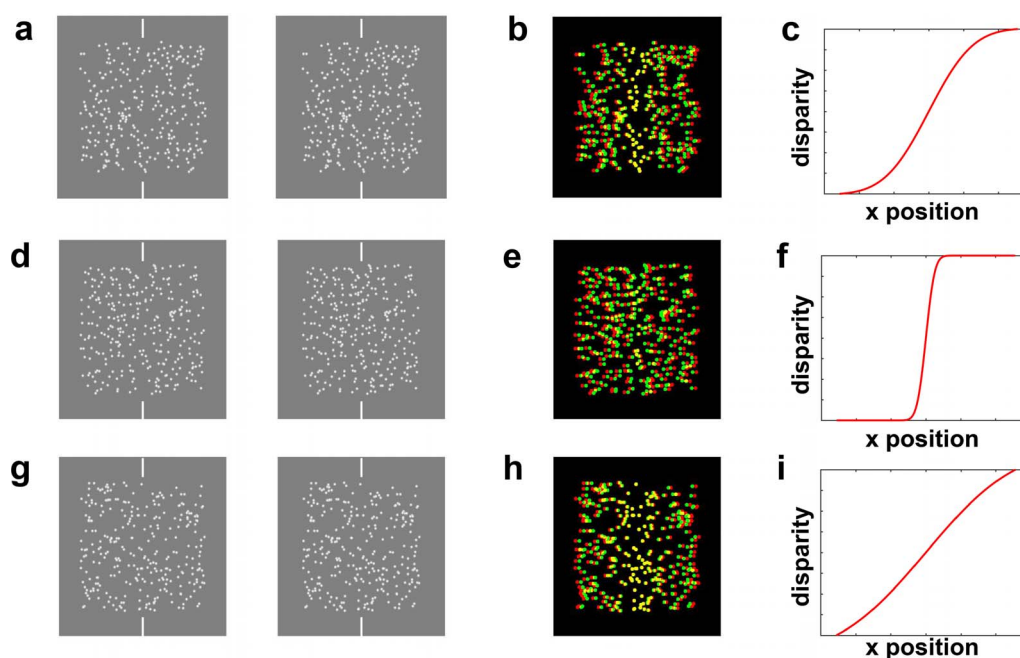


Figure 3. Examples of the stimuli used in Experiment 1. (a–c) Stimulus containing the change in disparity for the standard surface, of standard deviation 55 arcmin. (d–f) Stimulus showing a steeper change in disparity, through the use of a smaller surface standard deviation of 11 arcmin. (g–i) Stimulus containing a more gradual change in disparity, through the use of a larger (110 arcmin) surface standard deviation. All examples are shown as a free-fusion pair, red–green anaglyph and as a 1-D illustration.

distance of ± 3.3 SDs from the center of the screen. Stimulus widths were thus 1.2° , 6° , and 12° in 11, 55, and 110 arcmin conditions, respectively. All other stimulus parameters, including dot density and vertical extent, we identical to those used in Experiment 1. Example stimuli for Experiment 2 are shown in Figure 4.

By examining conditions where stimulus width is constant alongside conditions where it varies with surface standard deviation, we may determine whether surface steepness effects depend upon stimulus edge regions. In cases where width is kept constant, changes in surface steepness alter the extent of near-frontopar-

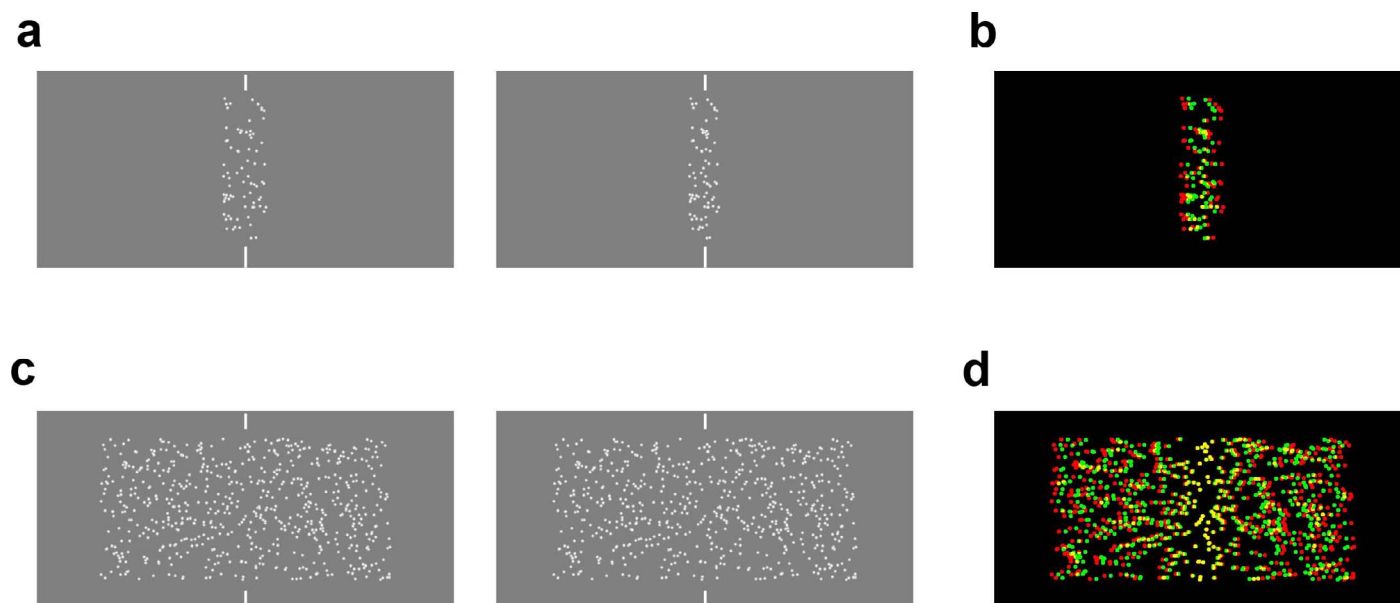


Figure 4. Examples of the stimuli used in Experiment 2. (a–b) Stimulus with a steeper change in disparity, defined by a function with standard deviation 11 arcmin. (c–d) Stimulus showing a more gradual change in disparity, through the use of a larger 110 arcmin surface SD. All stimuli cover a range of ± 3.3 SDs. Other than changes in width, surface layout is identical to Experiment 1.

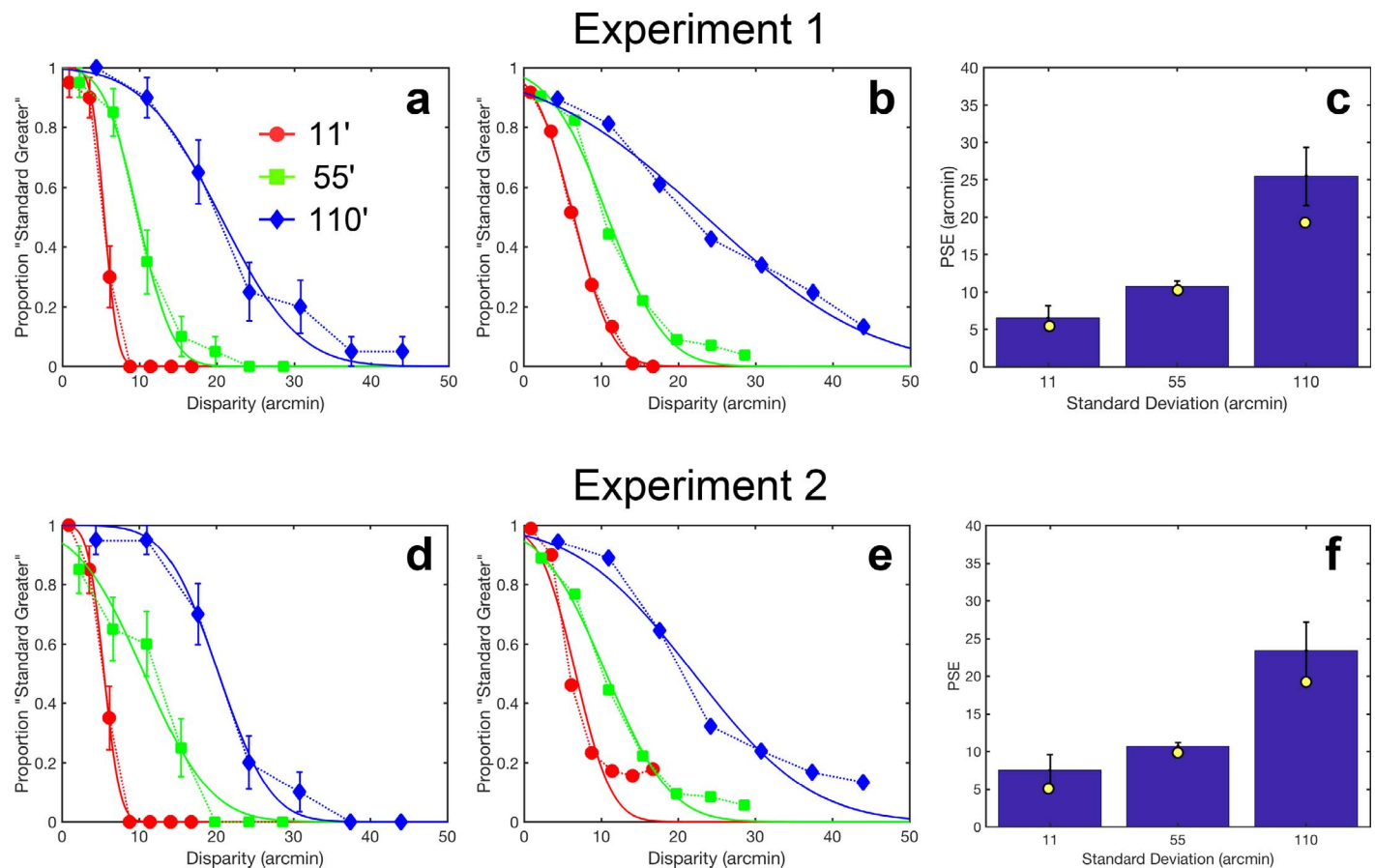


Figure 5. Results of Experiments 1 (a–c) and 2 (d–f). Psychometric functions plot proportion “standard greater” responses against edge-to-edge disparity for each surface standard deviation and are shown for example participants (a, d: error bars show binomial standard errors) as well as averaged across all five participants in each experiment (b, e). PSEs for each surface standard deviation are shown for each experiment (c, f), averaged across all five participants. Error bars show the standard error on the mean. There is a clear increase in PSE with decreasing surface steepness. Filled yellow circles show the predictions of the hypercyclopean filtering model.

allel areas at stimulus edges. Such areas may be critically important for disparity measurement (Allenmark & Read, 2010, 2011; Banks et al., 2004), resulting in improved disparity estimates for sharp disparity changes and impaired estimates for more gradual changes.

Results and discussion

Experiments 1 and 2 examined the effects of surface steepness manipulations on perceived depth. Data for each surface standard deviation were fitted to a decreasing cumulative Gaussian, with the 0.5 threshold—the PSE—extracted. These functions, together with the PSEs, are shown in Figure 5a through c, averaged across all five participants. PSEs were calculated based on 1,000 bootstrapped fits for each participant.

As is evident from these graphs, increasing the standard deviation of the surface increased the PSE.

Thus, for stimuli with the same edge-to-edge disparity, steeper changes in disparity, as in the 11 arcmin *SD* condition, were reliably judged as having greater depth than the standard interval. In the same way, stimuli in the 110 arcmin *SD* condition were reliably judged as having less depth than the standard. Average PSEs were 6.5, 10.8, and 25.4 arcmin for, respectively, the 11, 55, and 110 arcmin conditions. The effects of these manipulations of surface steepness were statistically significant on a repeated-measures ANOVA, $F(2, 8) = 17.74$, $p = 0.0011$. Pairwise comparisons, using related-samples t tests with Holm-Bonferroni corrections (Holm, 1979), showed significant differences between all surface standard deviations, $t(4) = 2.38$, 4.42, and 4.26, $p = 0.038$, 0.0057, and 0.0065 on a one-tailed test, for differences between 55 and 11 arcmin, 110 and 11 arcmin, and 110 and 55 arcmin conditions, respectively. Similar effects were seen in Experiment 2 (Figure 5d through f), where a repeated-measures ANOVA also showed a significant effect of surface standard deviation.

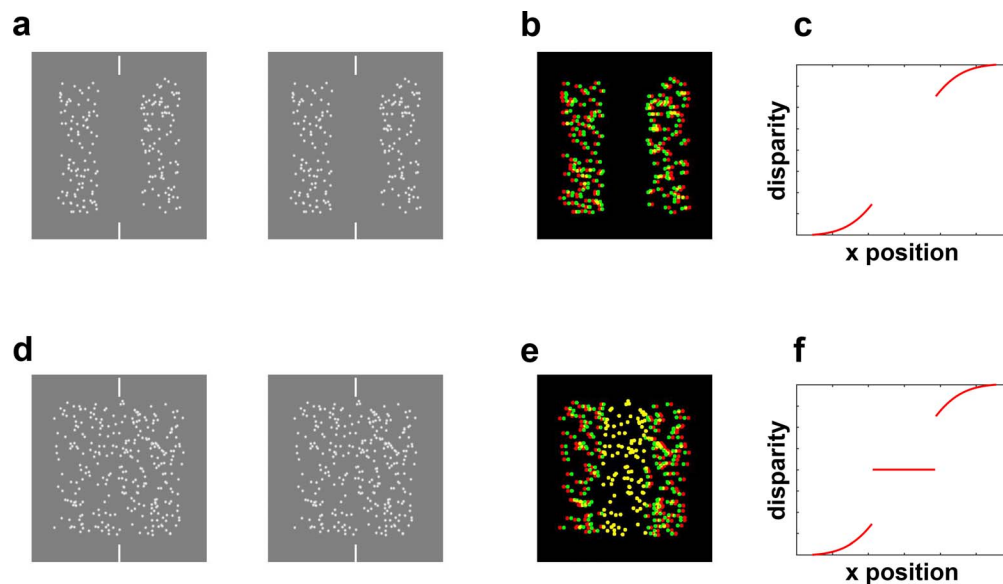


Figure 6. Examples of the stimuli used in Experiments 3 and 4. (a–c) Free-fusion pair, red–green anaglyph and 1-D illustration of a stimulus containing a gap between surface edges, as used in Experiments 3. (d–f) Free-fusion pair, red–green anaglyph, and 1-D illustration of a stimulus where the central portion has a frontoparallel profile in depth, as used in Experiment 4.

tion, $F(2, 6) = 22.58$, $p = 0.0016$. Pairwise comparisons, using related-samples t tests with Holm-Bonferroni corrections showed significant effects for the difference between 11 and 110 arcmin, and 55 and 110 arcmin conditions, $t(3) = 8.74$, $p = 0.0016$, $t_3 = 3.66$, $p = 0.0176$ on one-tailed tests, although not between 11 and 55 arcmin conditions, $t(3) = 1.73$, $p = 0.0913$.

These experiments confirm the findings of both Deas and Wilcox (2014, 2015) and Cammack and Harris (2016), showing that more gradual changes in disparity are perceived as having less depth than sharper changes. By manipulating surface steepness while either holding surface width constant, or allowing it to vary as a function of steepness, we have shown that these changes in perceived depth cannot be attributed to either the lateral edge-to-edge distance, or the extent of near-frontoparallel regions in the stimulus. Instead, surface steepness must directly contribute to perceived depth, with central areas of the stimulus impacting upon edge-to-edge disparity measurements.

While these effects of steepness are consistent with both disparity averaging and good continuation accounts of perceived depth, they are also well-accounted for by our model of hypercyclopean processing. PSEs for the model are 5.5, 10, and 18.8 arcmin in both Experiments 1 and 2, for 11, 55, and 110 arcmin conditions, respectively. These PSEs provide a close quantitative match to human performance. The observed effects of surface steepness manipulations are therefore consistent with the action of putative hypercyclopean channels in smoothing out lower frequency disparity modulations, with

perceived depth determined by higher frequency modulations.

Experiments 3 and 4: Effects of changes to central stimulus regions

While the manipulation of surface steepness in Experiments 1 and 2 confirmed earlier findings (Cammack & Harris, 2016; Deas & Wilcox, 2014), they did not allow us to distinguish between disparity averaging, hypercyclopean and good continuation accounts of perceived depth biases. Experiments 3 and 4 addressed this issue. In these experiments, we examined the contribution of the central stimulus region by measuring the consequences of its omission (Experiment 3), or its replacement with a task-irrelevant frontoparallel plane (Experiment 4).

Stimuli

Stimuli for Experiment 3 were identical to those in Experiment 1, except that the central portion of each was removed. Stimulus dots with x coordinates within 48 arcmin of the center of the stimulus were removed from each image prior to the addition of disparity (i.e., dots were removed from both left and right images leaving no unmatched dots). An example stimulus is shown in Figure 6a and b, and schematically in Figure 6c.

As in Experiment 1, the standard interval contained a RDS with a standard deviation of 55 arcmin, and an edge-to-edge disparity of 11 arcmin. Note, however, that the central portion of the stimulus was also removed for the standard interval. Variable intervals contained stimuli with standard deviations of 11 arcmin or 110 arcmin only, covering an edge-to-edge disparity range of 0.9 to 16.7 arcmin and 4.4 to 44 arcmin, respectively, across seven uniformly sampled levels.

Experiment 4 examined the effects of manipulations of surface steepness for stimuli containing intervening surface discontinuities. Stimuli for Experiment 4 were RDS surfaces similar to those in Experiments 1 and 3, with the exception that the central portion of the stimulus removed in Experiment 3 was replaced, for both standard and variable intervals, with a frontoparallel plane, whose depth was defined by the random depth shift parameter r . As in Experiment 3, this central portion included all dots with x coordinates within 48 arcmin of the stimulus center. The presence of this frontoparallel central region created depth discontinuities between the outer and inner portions of each stimulus surface. An example stimulus is shown in Figure 6d and e and schematically in Figure 6f. Surface standard deviations and edge-to-edge disparities were identical to those used in Experiment 3.

Results and discussion

Results for Experiment 3, where stimuli contained a central gap, followed a similar pattern to those in Experiments 1 and 2. Once again larger standard deviation stimuli were judged as having less depth than equivalent stimuli with a steeper disparity change. Psychometric functions for these conditions are plotted in Figure 7a for an example participant, and in Figure 7b averaged over participants. Average PSEs, shown in Figure 7c, were 6.6 and 31.1 arcmin for, respectively, 11 and 110 arcmin standard deviation conditions. The difference between PSEs was significant on a related samples t -test, $t(4) = 5.34$, $p = 0.003$ on a one-tailed test.

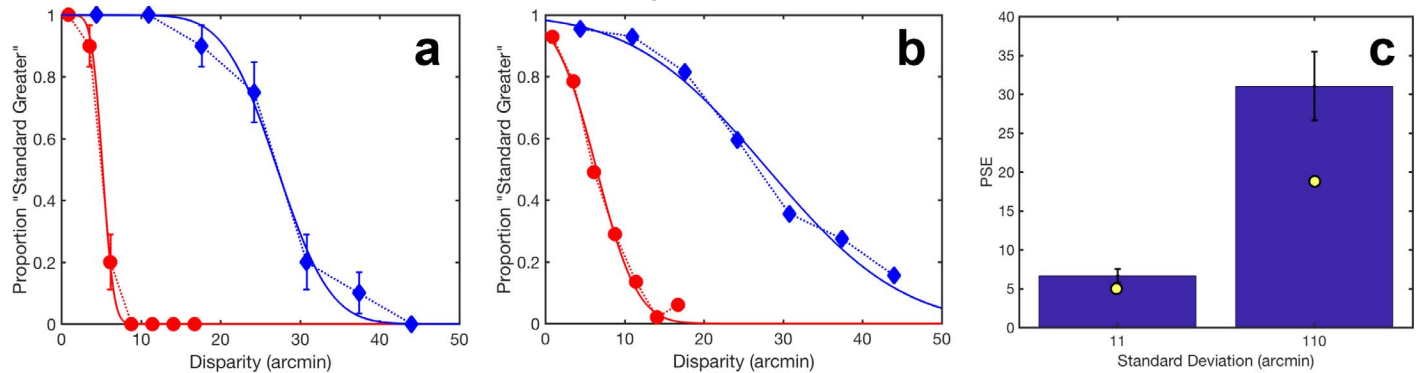
The effects of manipulating surface steepness were also evident in the results of Experiment 4 (Figure 7d through f), in which the gap was replaced by a frontoparallel plane. Here, average PSEs were 9.1 and 18 arcmin, for 11 and 110 arcmin SD conditions, respectively. The difference between PSEs was significant on a related samples t -test, $t(4) = 5.3$, $p = 0.003$ on a one-tailed test. Note that the effects of surface smoothness manipulations appear to differ in magnitude between these experiments. To examine this effect, we compared PSEs for 11 and 110 arcmin SD

conditions between Experiments 3 and 4. A repeated-measures ANOVA, with experiment as a between-participants variable, showed an expected main effect of standard deviation, $F(1, 8) = 46.74$, $p = 0.0001$, and a significant interaction, $F(1, 8) = 10.174$, $p = 0.0128$. Pairwise comparisons were conducted via Holm-Bonferroni corrected t tests (related samples for within-participants effects and two sample for between-participants effects). These tests show expected significant effects of standard deviation manipulations in each experiment, supporting the analysis above, $t(4) = 5.34$ and 5.29 , $p = 0.0030$ and 0.0031 on a one-tailed test for the difference between 11 and 110 arcmin conditions, and significant differences between Experiments 3 and 4 for both the 11 arcmin, $t(8) = 2.69$, $p = 0.028$, and 110 arcmin, $t(8) = 2.80$, $p = 0.023$, conditions. The reduction in perceived depth for surfaces with larger standard deviations were greater when there was a gap in the stimulus, than when this gap was filled with a frontoparallel plane.

The observed changes between these experiments are difficult to reconcile with either disparity averaging (Cammack & Harris, 2016) or good continuation (Deas & Wilcox, 2014, 2015) accounts of perceived depth. If good continuation processes underpinned the surface steepness effects found in Experiments 1 through 4, one would expect a reduction in bias for both Experiments 3 and 4, since the inclusion of the surface gap and the frontoparallel region both serve to weaken surface continuity. Our results instead show that the effects of surface steepness manipulations persist, despite changes to the central structure of the stimulus. Instead, a reduction in bias was only observed with the addition of depth discontinuities in Experiment 4. This is contrary to Deas and Wilcox (2015), where a reduction in the number of dots describing a line in depth increased perceived depth (see also Vreven et al., 2002). This suggests that absence of the central stimulus region in Experiment 3 (present in the manipulations used by both Deas & Wilcox, 2015, and Vreven et al., 2002) may be critical for maintenance of biases in perceived depth.

Our findings also pose difficulties for the disparity averaging account proposed by Cammack and Harris (2016). These authors suggested that surface smoothness biases arise due to averaging processes occurring as part of local binocular disparity estimation. Such disparity estimation processes operate in an absolute co-ordinate frame, encoding retinal offsets, not relative depth. For averaging of absolute disparities to account for the surface smoothness effects found in Experiments 1 through 3 would, however, require any averaging process to operate over a smaller area in Experiment 4 than in Experiment 3 (i.e., bias in perceived depth is smaller in Experiment 4, than in Experiment 3).

Experiment 3



Experiment 4

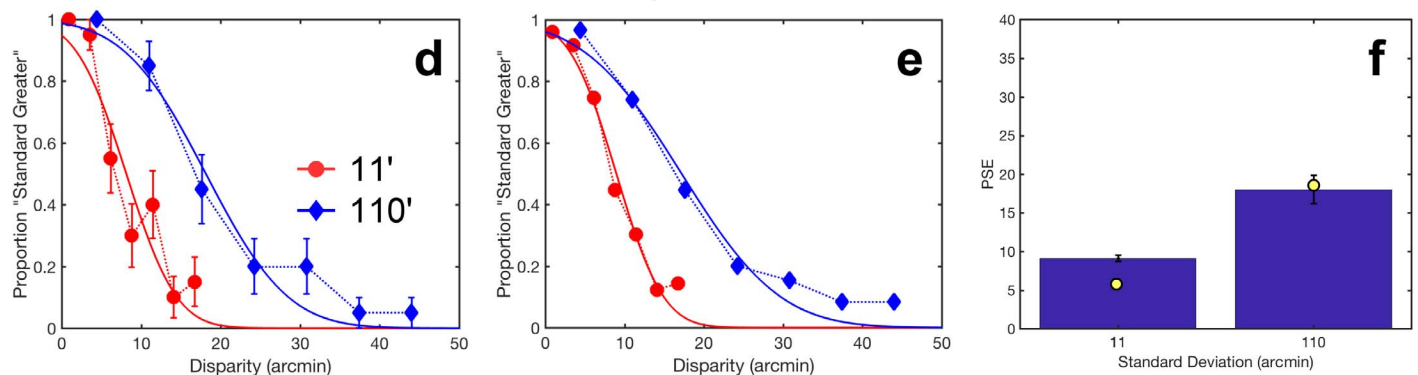


Figure 7. Results of Experiments 3 (a–c) and 4 (d–f). Psychometric functions plot the proportion “standard greater” responses against edge-to-edge disparity for each surface standard deviation for example participants (a, d: error bars show binomial standard errors) and averaged across all five participants (b, e). PSEs are plotted for each surface standard deviation, for each experiment (c, f), averaged across all five participants. Error bars show standard errors on the mean. Filled yellow circles show the predictions of the hypercyclopean filtering model.

To better understand this point, let us consider the principles under which any averaging process must function. For any monotonic function, such as the modified scaled cumulative Gaussian surfaces used in Experiments 1 through 4, estimated depth varies inversely with the area over which disparity measurements are averaged. Increasing the area for disparity averaging will necessarily reduce estimated depth. Surfaces with more gradual depth changes will show the greatest reduction, as disparity varies more over local areas. The consistency in biases across Experiments 1 through 3 thus requires comparable averaging areas. The reduced bias in Experiment 4 can only be accounted for, however, by a smaller averaging area, despite the increase in measurable disparities for stimuli in this experiment. For absolute disparity averaging to account for our findings, more stimulus information (at smaller disparities) must somehow translate to less averaging. Without a means for determining, a priori, the area over which averaging should occur, such

processes cannot match the patterns of results observed in Experiments 1 through 4.

The hypercyclopean model similarly does little to predict the observed changes in performance. For the 110 arcmin condition in Experiment 3, hypercyclopean responses significantly underestimate the bias in perceived depth, $t(4) = 2.846$, $p = 0.047$ on a two-tailed related-samples test. While human and model performance are very similar in Experiment 4, this simply serves to mask the fact that the manipulations across Experiments 1 through 4 have no effect on observed biases in the hypercyclopean model's estimates of perceived depth. PSEs were 5.4 and 18.8 arcmin for 11 and 110 arcmin conditions in Experiment 3, and 5.5 and 18.8 arcmin for equivalent conditions in Experiment 4, effectively unchanged from PSEs for Experiments 1 and 2. The observed changes in human performance between these experiments would not, therefore, appear to be attributable to the smoothing effects of hypercyclopean filtering on absolute disparity estimates. Other

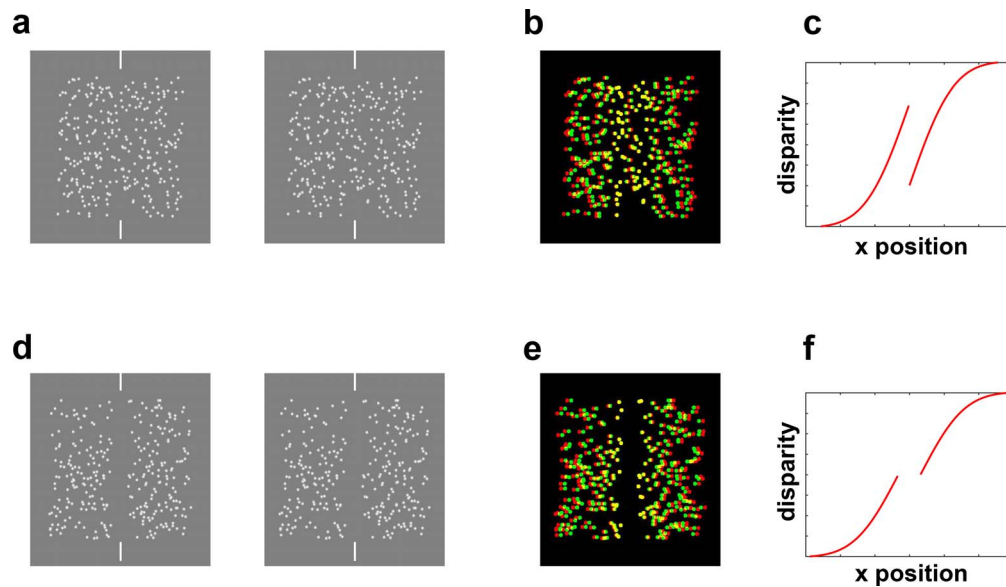


Figure 8. Examples of the stimuli used in Experiments 5 and 6. (a–c) Free-fusion pair, red–green anaglyph and 1-D illustration of a stimulus containing a depth discontinuity, as used in Experiments 5. (d–f) Free-fusion pair, red–green anaglyph, and 1-D illustration of a stimulus containing a lateral discontinuity, as used in Experiment 6.

factors, such as surface interpolation processes and the presence of surface discontinuities, may instead play a critical role in determining perceived depth. We consider the role of such discontinuities in Experiments 5 and 6, below.

Experiments 5 and 6: Effects of surface discontinuity

The results of Experiment 4 suggest that surface discontinuities may play an important role in determining perceived depth. In that experiment, the addition of surface discontinuities reduced the impact of manipulations of surface standard deviation. It is unclear, however, whether this was due to a direct effect of discontinuity on perceived depth, or the impact of discontinuities on surface steepness effects. Here, we further addressed the role of surface discontinuities, examining the effects of both depth discontinuities (Experiment 5) and lateral discontinuities (Experiment 6) on perceived depth.

Stimuli

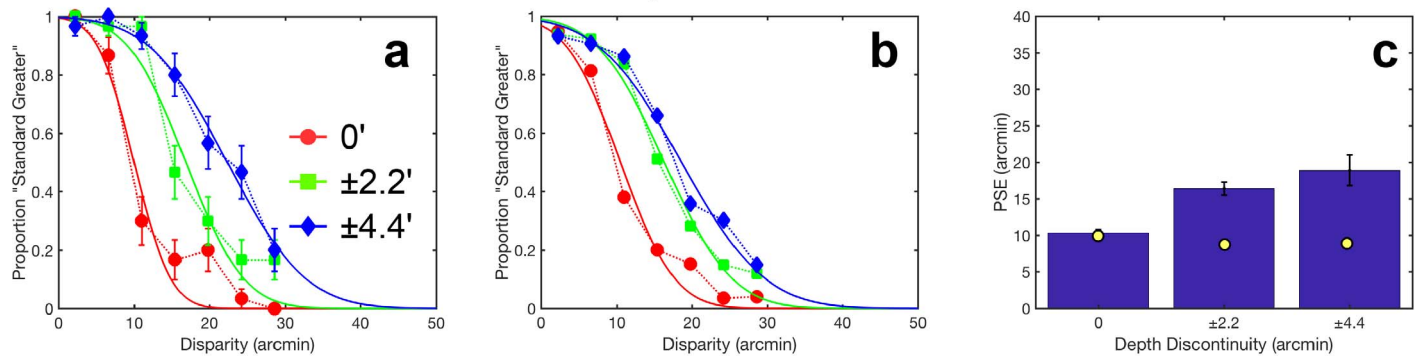
To examine surface discontinuity effects on perceived depth, participants in Experiment 5 were presented with stimuli containing a single depth discontinuity at the centre of each RDS. Unlike Experiments 1 through 4, there were no manipulations

of surface steepness. Instead, all stimuli in Experiment 5 were scaled cumulative Gaussian curves in depth, with a fixed standard deviation of 55 arcmin. Edge-to-edge disparity ranged from 2.2 to 28.6 arcmin in the variable interval, with the standard interval again having an edge-to-edge disparity of 11 arcmin.

Depth discontinuities were added to this basic stimulus by shifting left and right halves in opposite directions in depth. The near half of the stimulus was shifted away from the observer in depth, while the far half was brought forward. Discontinuity sizes were 0, ± 2.2 , and ± 4.4 arcmin, with the standard interval containing no discontinuity. Note that, in Experiment 5, the calculation of edge-to-edge disparities was adjusted to take depth discontinuities into account. Thus, rather than scaling by the edge-to-edge disparity d , as in Equation 1, surfaces were scaled by a value of d , plus the relevant discontinuity size, resulting in a stimulus with edge-to-edge disparity of $2d$ (equivalent to the edge-to-edge disparity for stimuli in Experiments 1 through 4) once the depth discontinuity was introduced. An example stimulus is shown in Figure 8a and b and schematically in Figure 8c.

In Experiment 6, participants were presented with stimuli containing discontinuities produced by opposing lateral shifts of each half of the RDS surface. As with Experiment 5, stimuli in Experiment 6 were always of $SD = 55$ arcmin, with the standard interval having an edge-to-edge disparity of 11 arcmin. Edge-to-edge disparity ranged from 2.2 to 28.6 arcmin in the variable interval, across seven uniformly sampled levels. Lateral shifts were of size 0, ± 17.6 , and ± 35.2 arcmin for the variable intervals, and were added by shifting left and

Experiment 5



Experiment 6

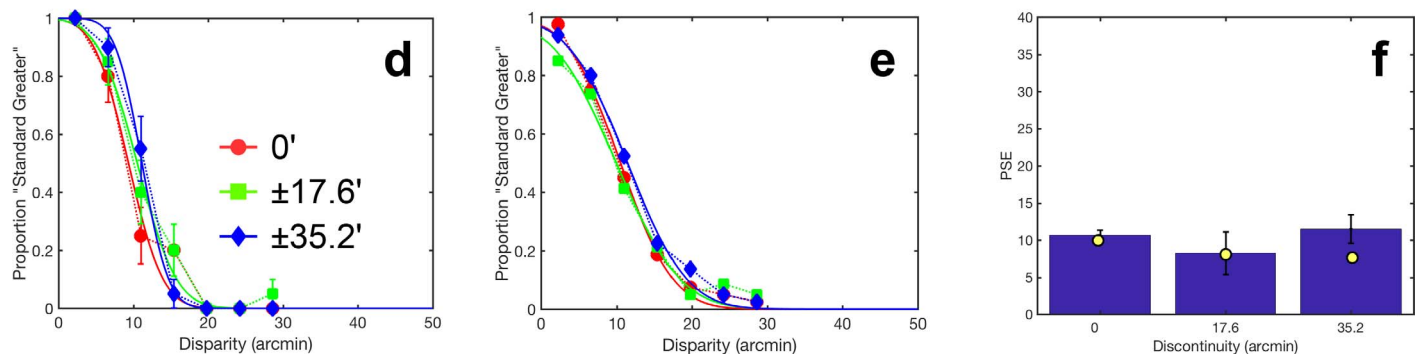


Figure 9. Results of Experiments 5 (a–c) and 6 (d–f). Fitted psychometric functions plot the proportion of “standard greater” responses against edge-to-edge disparity for each depth discontinuity in Experiment 5, and lateral discontinuity in Experiment 6. Fitted functions show the results for example participants (a, d: error bars show binomial standard errors) and averaged across participants (b, e). PSEs are shown for each depth discontinuity in Experiment 5 (c) and lateral discontinuity in Experiment 6 (f), averaged across participants. Error bars show the standard error on the mean. Filled yellow circles show the predictions of the hypercyclopean filtering model.

right stimulus halves in opposite directions. This increased the horizontal extent of stimuli to 5.3° and 5.9° for, respectively, ± 17.6 and ± 35.2 arcmin shifts. The standard interval contained no lateral shifts. An example stimulus is shown in Figure 8d and e, and schematically in Figure 8f.

Results and discussion

Data for each discontinuity size in Experiment 5 were fit to a decreasing cumulative Gaussian curve, as in Experiments 1 through 4, with PSEs recovered based on 1,000 bootstrapped fits. Fitted curves and associated PSEs are plotted in Figure 9a through c. The presence of a depth discontinuity increased the value of the PSE, relative to a continuous surface. Thus, for two surfaces with equivalent edge-to-edge disparities, a discontinuous surface was judged as having less depth than a continuous surface. PSEs for ± 2.2 and ± 4.4 arcmin

discontinuities were 16.4 and 18.9 arcmin, respectively, compared to a PSE of 10.3 arcmin for continuous surfaces. Differences between continuous and discontinuous surface PSEs were significant on a repeated-measures ANOVA, $F(2, 8) = 16.77$, $p = 0.0014$. Pairwise comparisons, conducted via related samples t tests with Holm-Bonferroni corrections, indicated significant differences between the continuous condition and each discontinuity size, but not between discontinuities, $t(4) = 7.06, 4.14$ and 1.82 , $p = 0.0021, 0.0144$, and 0.1424 on a two-tailed test for differences between 0 and ± 2.2 , 0 and ± 4.4 , and ± 2.2 and ± 4.4 arcmin conditions, respectively). Unlike depth discontinuity manipulations, however, the addition of lateral surface discontinuities in Experiment 6 had no effect on PSEs (Figure 9d through f). Average PSEs across all participants were 10.70, 8.26, and 11.47 arcmin for 0, ± 17.6 , and ± 35.2 arcmin lateral discontinuities, with no statistically significant differences on a repeated-measures ANOVA, $F(2, 6) = 1.17$, $p = 0.37$.

The changes in perceived depth in Experiment 5 are line with the depth Cornsweet illusion first reported by Anstis et al. (1978). Importantly, our results show that this depth Cornsweet effect does not just occur when edge-to-edge disparity is close to zero. Instead, we found that the presence of a depth discontinuity reduced perceived depth for much larger disparities. Several of our participants did, however, report an illusory reversal of depth, consistent with a depth Cornsweet illusion, for some stimuli in this experiment. The shift in PSEs observed in Experiment 5 suggests that depth Cornsweet effects will be evident for stimuli with edge-to-edge disparities of less than around 7 arcmin. This is substantially larger than the effect reported by Anstis et al. (1978), which was around 2 arcmin for the most comparable viewing distance.

The direction of bias observed in Experiment 5 is difficult to reconcile with Deas and Wilcox's (2014, 2015) good continuation effects, where the presence of surface discontinuities should increase, rather than decrease, perceived depth. For the same reason, good continuation cannot explain why increases in perceived depth are not found for the lateral discontinuities used in Experiment 6. A disparity averaging account also struggles with these discrepancies. In Experiment 6, an averaging account would predict that increases in lateral separation result in less averaging, increasing perceived depth. Similarly, our hypercyclopean model also failed to predict the observed change in perceived depth. PSEs for this model showed a very slight decrease with increasing discontinuity size for both Experiment 5 (10, 9.2, and 8.4 arcmin for 0, ± 2.2 , and ± 4.4 arcmin discontinuities) and Experiment 6 (19, 8.1, and 7.1 arcmin for 0, ± 17.6 , and ± 35.2 arcmin discontinuities). Observed decreases in perceived depth would not, therefore, appear to be attributable to the action of these channels.

What factors might, then, drive the reduction in perceived depth observed in Experiment 5? One possibility might be that the sharp depth discontinuities at the centre of the stimulus violate the disparity gradient limit (Burt & Julesz, 1980; McKee & Verghese, 2002), and thus produce regions of diplopia, reducing depth sensitivity with these areas. Analysis of the local gradients in the stimulus suggests, however, that violations of the gradient limit are more a property of the functions underlying each RDS, rather than dot patterns that define them. While maximum gradients in Experiment 5 fall around a value of 1, similar maximum gradient values are also found in Experiment 4. In that case, however, discontinuities are associated with an increase in perceived depth. Diplopia does not, therefore, seem able to explain both of these effects. Instead, we would seek to explain changes in perceived depth in both Experiment 4 and 5, and the absence of effects in Experiment 6, through consideration of the

disparity gradients within these stimuli, rather than any diplopia that might potentially arise. Discontinuities with disparity gradients in the same direction as the overall change in disparity appear to add to perceived depth, while disparity gradients of opposing sign reduce it. The lateral discontinuities added in Experiment 6 have no effect as the gradients they introduce are equal to zero. We discuss these ideas in detail, below.

General discussion

The experiments reported in this paper examined the combined effects of surface steepness and surface discontinuity manipulations on perceived depth from binocular disparity. The results of these experiments provide new insight into earlier findings showing that more gradual changes in disparity are perceived as having less depth than stimuli containing steep disparity changes (Cammack & Harris, 2016; Deas & Wilcox, 2014, 2015; McKee, 1983; Mitchison & Westheimer, 1984). In Experiments 1 through 4, changing PSEs indicated a reduction in perceived depth with increasing surface steepness. In Experiments 5 and 6, manipulations of surface discontinuity also led to reductions in perceived depth, but only if the discontinuity was in depth. While this set of findings is consistent with earlier results (Anstis et al., 1978; Rogers & Graham, 1983), they appear contrary to the effects of manipulating surface steepness. These results show that previously established surface-level effects on stereoacuity (Anstis et al., 1978; McKee, 1983; Mitchison & Westheimer, 1984; Rogers & Graham, 1983; Wardle & Gillam, 2016) extend to discrimination judgements for suprathreshold depth.

The observed pattern of results across experiments cannot be accounted for by existing good continuation (Deas & Wilcox, 2014, 2015) and disparity averaging (Cammack & Harris, 2016) accounts, which predict contrary effects for stimuli containing surface discontinuities (Experiments 4 through 6), or surface gaps (Experiment 3). Similarly, while a model of hypercyclopean processing indicates that sensitivity to different disparity frequencies can account for basic effects of surface steepness manipulations (Experiments 1 and 2), it fails to predict changes in these effects, or the effects of surface discontinuities. This suggests that, while the role of hypercyclopean processing in smoothing absolute disparity estimates is important, effects of surface steepness and surface discontinuity manipulations depend critically on mechanisms measuring the relative disparity at surface discontinuities. Such relative disparity processing has previously been implicated in stereoacuity judgements relative to reference planes (Glennerster & McKee, 1999, 2004) and in the resolution

of binocular correspondence (Goutcher & Hibbard, 2010; Mitchison & McKee, 1987). While hypercyclopean-level detectors are conceptually suited to the encoding of relative disparities, our current modelling cannot be interpreted in these terms.

Perceived depth from relative disparities

Unlike disparity averaging and good continuation accounts, an interpretation of our observed biases in terms of relative disparity content reveals a consistent pattern of results. Effects of surface standard deviation manipulations suggest that perceived edge-to-edge depth is driven primarily by sharp local changes in relative disparity—that is, by large disparity gradients. The impact of these large gradients seems particularly important for discontinuous surfaces, where observed biases cannot be accounted for by the smoothing effects of hypercyclopean processing. Instead, perceived depth seems to conform to a rule where sharp changes in disparity increase perceived depth when they have the same sign as the overall change in disparity, and decrease perceived depth when they are of opposite sign. This rule would also appear to be consistent with the findings of Deas and Wilcox (2015), where additive disparity noise leads to an increase in perceived depth, dependent on the magnitude of the noise. The noise in Deas and Wilcox's (2015) experiments systematically increased the range of disparity gradients within a stimulus, as a function of the size of the noise. While the average gradient of the noise would be zero, leading to no additional biasing of perceived depth, the increased range of disparity gradients would, under the rule proposed here, lead to a general increase in perceived depth.

Relative disparity effects of these kinds could be implemented by considering the responses of hypercyclopean units, modelled after relative disparity selective cells in cortex. Neurons selective for relative disparity are found in multiple visual areas (cf. Parker, 2007), including V2 (Bredfeldt & Cumming, 2006; Thomas, Cumming, & Parker, 2002) and V4 (Fang et al., 2018; Umeda, Tanabe, & Fujita, 2007). Such neurons could be used to encode disparity differences at multiple scales, following the disparity frequency sensitivity approach applied here (Hibbard, 2005; Serrano-Pedraza & Read, 2010; Tyler, 1975, 2013; Tyler & Kontsevich, 2001). Critically, however, our results suggest that perceived depth requires the integration of relative disparity measurements across the stimulus, perhaps following the association field approach used for contour perception (Field, Hayes, & Hess, 1993; Hess & Field, 1995). Such an approach may also help to explain apparent grouping effects (e.g., Deas & Wilcox, 2014), which cannot be accounted for solely in terms of disparity measurements.

Roles for averaging and grouping processes?

Above, we have argued against a general disparity averaging or good continuation-based account of biases in perceived depth, in favor of an explanation based on the integration of relative disparity estimates across the stimulus, with hypercyclopean channels as a potential basis for such encoding. Such an argument does not, however, rule out possible roles for both averaging and good-continuation processes in the perception of disparity-defined depth. Deas and Wilcox (2014, 2015) demonstrate grouping-based effects that fall outside of the scope of manipulations presented here. Deas and Wilcox (2014), for example, used similarity-based grouping to show effects on perceived depth, which suggests that grouping may still play a role in determining the stimulus elements used for measuring relative depth. Similarly, the manipulation of element number in Deas and Wilcox (2015) cannot be accounted for by a change in local disparity gradients, given the linear disparity change of their stimulus. An explanation of these effects would require further elaboration of any relative disparity-based account.

As with grouping principles, our results also do not rule out possible roles for averaging processes acting on absolute disparities, such as those proposed by Cammack and Harris (2016). While averaging alone is not sufficient to account for our findings, it may still play a role in biasing depth estimates. Our findings suggest, however, that such averaging must be contingent on relative disparity stimulus content, take into account the smoothing effects of hypercyclopean processing and consider areas of surface discontinuity. Similar proposals have been made previously, with the suggestion that the detection of surface discontinuities can provide coarse disparity measurements to be used as the basis for more precise estimates (Gillam & Borsting, 1988; Wilcox & Lakra, 2007). Discontinuity detection could thus delimit any averaging processes, helping improve signal-to-noise ratios as suggested by Cammack and Harris (2016). Such averaging could, however, operate on disparity estimates encoded in either absolute or relative coordinate domains.

Conclusions

This paper examined how manipulations of both the steepness of changes in disparity and the presence of surface discontinuities affected perceived depth. Our results show that, while an increase of surface steepness leads to a decrease in perceived depth, the effects of surface discontinuity manipulations depend critically on discontinuity structure. These results are not consistent with existing accounts of continuity-related biases in perceived depth, which focus on grouping

processes or disparity averaging, and are not predicted by the smoothing effects of hypercyclopean channels. Instead, our results are consistent with processes that integrate relative disparity measurements across the stimulus. Such processes are biased toward steeper changes in disparity with such changes reducing perceived depth when their sign opposes the overall change in depth across the stimulus, and enhancing perceived depth when they are of the same sign. Future research should seek to further constrain the principles governing the encoding and integration of relative disparities in the perception of stereoscopic depth in order to allow for a full computational account of these processes.

Keywords: *depth perception, depth discontinuities, stereopsis, relative disparity, disparity sensitivity*

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References

- Allenmark, F., & Read, J. C. A. (2010). Detectability of sine-versus square-wave disparity gratings: A challenge for current models of depth perception. *Journal of Vision*, 10(8):17, 1–16, <https://doi.org/10.1167/10.8.17>. [PubMed] [Article]
- Allenmark, F., & Read, J. C. A. (2011). Spatial stereoresolution for depth corrugations may be set in primary visual cortex. *PLoS Computational Biology*, 7(8), e1002142, <https://doi.org/10.1371/journal.pcbi.1002142>.
- Anstis, S. M., Howard, I. P., & Rogers, B. (1978). A Craik-O'Brien-Cornsweet illusion for visual depth. *Vision Research*, 18(2), 213–217.
- Banks, M. S., Gepshtein, S., & Landy, M. S. (2004). Why is spatial stereoresolution so low? *Journal of Neuroscience*, 24(9), 2077–2089.
- Bradshaw, M. F., & Rogers, B. J. (1999). Sensitivity to horizontal and vertical corrugations defined by binocular disparity. *Vision Research*, 39(18), 3049–3056.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Bredfeldt, C. E., & Cumming, B. G. (2006). A simple account of cyclopean edge responses in macaque V2. *Journal of Neuroscience*, 26(29), 7581–7596.
- Burt, P., & Julesz, B. (1980, May 9). A disparity gradient limit for binocular fusion. *Science*, 208, 615–617.
- Cammack, P., & Harris, J. M. (2016). Depth perception in disparity-defined objects: Finding the balance between averaging and segregation. *Philosophical Transactions of the Royal Society of London: B*, 371(1697), 20150258.
- DeAngelis, G. C., Ohzawa, I., & Freeman, R. D. (1991, July 11). Depth is encoded in the visual cortex by a specialized receptive field structure. *Nature*, 352(6331), 156–159.
- Deas, L. M., & Wilcox, L. M. (2014). Gestalt grouping via closure degrades suprathreshold depth percepts. *Journal of Vision*, 14(9):14, 1–13, <https://doi.org/10.1167/14.9.14>. [PubMed] [Article]
- Deas, L. M., & Wilcox, L. M. (2015). Perceptual grouping via binocular disparity: The impact of stereoscopic good continuation. *Journal of Vision*, 15(11):11, 1–13, <https://doi.org/10.1167/15.11.11>. [PubMed] [Article]
- Fang, Y., Chen, M., Xu, H., Li, P., Han, C., Hu, J., . . . Lu, H. D. (2018). An orientation map for disparity-defined edges in area V4. *Cerebral Cortex*, <https://doi.org/10.1093/cercor/bhx348>.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local “association field.” *Vision Research*, 33, 173–193.
- Filippini, H. R., & Banks, M. S. (2009). Limits of stereopsis explained by local cross-correlation. *Journal of Vision*, 9(1):8, 1–18, <https://doi.org/10.1167/9.1.8>. [PubMed] [Article]
- Fleet, D. J., Wagner, H., & Heeger, D. J. (1996). Neural encoding of binocular disparity: Energy models, position shifts and phase shifts. *Vision Research*, 36(12), 1839–1857.
- Gillam, B., & Borsting, E. (1988). The role of monocular regions in stereoscopic displays. *Perception*, 17(5), 603–608.
- Glennerster, A., & McKee, S. P. (1999). Bias and sensitivity of stereo judgements in the presence of a slanted reference plane. *Vision Research*, 39, 3057–3069.
- Glennerster, A., & McKee, S. P. (2004). Sensitivity to depth relief on slanted surfaces. *Journal of Vision*, 4(5):3, 378–387, <https://doi.org/10.1167/4.5.3>. [PubMed] [Article]
- Goncalves, N. R., & Welchman, A. E. (2017). “What

- not” detectors help the brain see in depth. *Current Biology*, 27(10), 1403–1412.
- Goutcher, R., & Hibbard, P. B. (2010). Evidence for relative disparity matching in the perception of an ambiguous stereogram. *Journal of Vision*, 10(12): 35, 1–16, <https://doi.org/10.1167/10.12.35>. [PubMed] [Article]
- Goutcher, R., & Hibbard, P. B. (2014). Mechanisms for similarity matching in disparity measurement. *Frontiers in Psychology*, 4, 1014.
- Hess, R. F., & Field, D. J. (1995). Contour integration across depth. *Vision Research*, 35(12), 1699–1711.
- Hibbard, P. B. (2005). The orientation bandwidth of cyclopean channels. *Vision Research*, 45(21), 2780–2785.
- Hirschmüller, H. (2008). Stereo processing by semi-global matching and mutual information. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 30(2), 328–341.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6(2), 65–70.
- Hornsey, R. L., Hibbard, P. B., & Scarfe, P. (2016). Binocular depth judgments on smoothly curved surfaces. *PLoS One*, 11(11), e0165932, <https://doi.org/10.1371/journal.pone.0165932>.
- Kleiner, M., Brainard, D., & Pelli, D. (2007). What’s new in Psychtoolbox-3. *Perception*, 36S, 14.
- McKee, S. P. (1983). The spatial requirements for fine stereoacuity. *Vision Research*, 23(2), 191–198.
- McKee, S. P., & Verghese, P. (2002). Stereo transparency and the disparity gradient limit. *Vision Research*, 42, 1963–1977.
- Mitchison, G. J., & McKee, S. P. (1987). The resolution of ambiguous stereoscopic matches by interpolation. *Vision Research*, 27(2), 285–294.
- Mitchison, G. J., & Westheimer, G. (1984). The perception of depth in simple figures. *Vision Research*, 24(9), 1063–1073.
- Nienborg, H., Bridge, H., Parker, A. J., & Cumming, B. G. (2004). Receptive field size in V1 neurons limits acuity for perceiving disparity modulation. *Journal of Neuroscience*, 24(9), 2065–2076.
- Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1990, August 31). Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors. *Science*, 249(4972), 1037–1041.
- Parker, A. J. (2007). Binocular depth perception and the cerebral cortex. *Nature Reviews Neuroscience*, 8, 379–391.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Prince, S. J. D., Cumming, B. G., & Parker, A. J. (2002). Range and mechanism of encoding of horizontal disparity in macaque V1. *Journal of Neurophysiology*, 87(1), 209–221.
- Qian, N., & Zhu, Y. (1997). Physiological computation of binocular disparity. *Vision Research*, 37(13), 1811–1827.
- Read, J. C. A., & Cumming, B. G. (2007). Sensors for impossible stimuli may solve the stereo correspondence problem. *Nature Neuroscience*, 10(10), 1322–1328.
- Rogers, B. J., & Graham, M. E. (1983, September 30). Anisotropies in the perception of three-dimensional surfaces. *Science*, 221(4618), 1409–1411.
- Serrano-Pedraza, I. & Read, J. C. A. (2010). Multiple channels for horizontal, but only one for vertical corrugations? A new look at stereo anisotropy. *Journal of Vision*, 10(12):10, 1–11, <https://doi.org/10.1167/10.12.10>. [PubMed] [Article]
- Thomas, O. M., Cumming, B. G., & Parker, A. J. (2002). A specialization for relative disparity in V2. *Nature Neuroscience*, 5(5), 472–478.
- Tyler, C. W. (1975). Stereoscopic tilt and size aftereffects. *Perception*, 4, 187–192.
- Tyler, C. W. (2013). Shape processing as inherently three-dimensional. In S. J. Dickinson & Z. Pizlo (Eds.), *Shape perception in human and computer vision* (pp. 357–372). London, United Kingdom: Springer-Verlag.
- Tyler, C. W., & Kontsevich, L. L. (2001). Stereo-processing of cyclopean depth images: Horizontally elongated summation fields. *Vision Research*, 41, 2235–2243.
- Umeda, K., Tanabe, S., & Fujita, I. (2007). Representation of stereoscopic depth based on relative disparity in macaque area V4. *Journal of Neurophysiology*, 98, 241–252.
- Vreven, D., McKee, S. P., & Verghese, P. (2002). Contour completion through depth interferes with stereoacuity. *Vision Research*, 42, 2153–2162.
- Wardle, S. G., & Gillam, B. J. (2016). Gradients of relative disparity underlie the perceived slant of stereoscopic surfaces. *Journal of Vision*, 16(5):16, 1–13, <https://doi.org/10.1167/16.5.16>. [PubMed] [Article]
- Wilcox, L. M., & Lakra, D. C. (2007). Depth from binocular half-occlusions in stereoscopic images of natural scenes. *Perception*, 36(6), 830–839.