

Simultaneous density contrast and binocular integration

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Most research on texture density has utilized textures rendered as two-dimensional (2D) planar surfaces, consistent with the conventional definition of density as the number of texture elements per unit area. How the brain represents texture density information in the three-dimensional (3D) world is not yet clear. Here we tested whether binocular information affects density processing using simultaneous density contrast (SDC), in which the perceived density of a texture region is changed by a surround of different density. We considered the effect on SDC of two types of binocular information: the stereoscopic depth relationships and the interocular relationships between the center and surround textures. Observers compared the perceived density of two random dot patterns, one with a surround (test stimulus) and one without (match), using a 2AFC staircase procedure. In Experiment 1 we manipulated the stereo-depth of the surround plane systematically from near to far, relative to the center plane. SDC was reduced when the difference in stereo-depth between test center and surround increased. In Experiment 2 we spread the surround dots randomly across a stereo-depth volume from small to large volume sizes, and found that SDC was slightly reduced with volume size. The decrease of SDC in both experiments was observed with dense surrounds only, but not with sparse surrounds. In the last experiment we presented center and surround in the same depth plane but dichoptically, monoptically, and binocularly. A strong interocular transfer of SDC was found in the dichoptic condition. Together these results show that texture density processing is sensitive to binocularity.

routinely perceive is texture density (henceforth, “density”). Most studies of density encoding are performed under 2D conditions, since density is conventionally defined as the number of elements per unit visual area (Anobile, Cicchini, & Burr, 2016; Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2001; Durgin & Hammer, 2001; Sun, Baker, & Kingdom, 2016; Tibber, Greenwood, & Dakin, 2012). There is evidence that density information is coded via multiple channels selective to different ranges of density (Sun et al., 2016; Sun, Kingdom, & Baker, 2017), in a manner that is separable from the processing of spatial frequency and luminance contrast (Durgin, 2001; Durgin & Hammer, 2001; Sun et al., 2016).

Some studies suggest that density information is represented at a 2D retinotopic level through planar filters of high and low spatial frequencies (Bell, Manson, Edwards, & Meso, 2015; Dakin et al., 2011). A similar model that computes contrast energy has also been proposed for numerosity estimation (Morgan, Raphael, Tibber, & Dakin, 2014). In support of this idea, density is biased by area, with larger patches perceived as denser (Dakin et al., 2011; Raphael, Dillenburger, & Morgan, 2013; Raphael & Morgan, 2016; Tibber et al., 2012), but not biased by stereo-depth volume (Bell et al., 2015). If density perception is implicitly involved in size scaling, one should expect density biases in both 2D (area) and 3D (stereo-depth volume) size scaling. However, a bias only in 2D has been interpreted as supporting the idea that density is only represented in 2D (Bell et al., 2015). Note that the size scaling mentioned here is a change in the space within which the texture elements are distributed, not including changes in the size of elements and inter-dot distance, since these might also be affected after adapting to a different sized disk (Zimmermann & Fink, 2016). While an exclusively 2D representation of

Introduction

A variety of textures are encountered in everyday object surfaces and scenes, and a salient attribute we

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density might seem odd, given that our visual environment is 3D, a 2D representation might be an efficient basis for the rapid estimation of the numbers of objects in 3D clusters. On the other hand, there is evidence that density estimation takes into account stereo-depth information. For example in surfaces defined by stereo-disparity, observers perceive more elements when they are assigned to multiple depth surfaces rather than to a single surface, and perceive farther surfaces as having more elements than nearer ones (Aida, Kusano, & Shimono, 2013; Aida, Kusano, Shimono, & Tam, 2015; Schütz, 2012). These studies, however, measured numerosity not density, two attributes that may be processed by different mechanisms (Anobile, Cicchini, & Burr, 2014; Anobile et al., 2016; Anobile, Turi, Cicchini, & Burr, 2015; Burr & Ross, 2008). Note that the high numerosity conditions in these studies may fall into the density regime as well (Aida et al., 2015; Burr & Ross, 2008). Also one should note that other studies have suggested a common basis for coding density and numerosity (Dakin et al., 2011; Morgan et al., 2014; Raphael & Morgan, 2016; Sun et al., 2016; Sun et al., 2017; Tibber et al., 2012). Therefore, it remains unclear whether depth can affect density perception directly.

Evidence from the converse situation (i.e. the influence of density on depth) may provide some hints. Several studies have shown that the perception of random element, transparent surfaces defined by either stereo-depth or motion parallax is impaired at high element densities (Akerstrom & Todd, 1988; Buckthought & Wu, 2017; Gepshtein & Cooperman, 1998; Tsirlin, Allison, & Wilcox, 2008). One explanation of this finding is that increasing density will increase the “correspondence problem” (Tsirlin et al., 2008). Tsirlin, Allison, and Wilcox (2012) found that a larger between-plane depth was required to segregate two transparent planes when the nearer plane was the sparser of the two, perhaps because the larger between-dot spaces were more likely to be assigned to the farther surface. In addition, the gradient of texture density is an important cue for depth (Gibson, 1950) but only when the gradient of texture element size changes with it. Texture density gradients alone do not give a percept of depth variations (Durgin, 1995; Stevens, 1981).

There is also evidence of a non-depth-based binocular involvement in density perception through studies of interocular transfer of density adaptation. Monocular density adaptation can transfer to the unadapted eye, up to 75% of the effect of same eye adaptation (Durgin, 2001; Durgin & Proffitt, 1996). This indicates that, unlike luminance contrast adaptation and simultaneous contrast (Chubb, Sperling, & Solomon, 1989; Durgin, 2001; Durgin & Proffitt, 1996), which do not show interocular transfer, density encoding is primarily a binocular process.

Based on all the above evidence, we consider here the possibility that density coding is not entirely independent of stereopsis and binocular processing. We have tested whether density information is simply represented at a 2D retinotopic level, as has been suggested (Bell et al., 2015; Dakin et al., 2011), or whether there are binocular effects on density computation as other evidence implies (e.g., the effect of depth on numerosity, the influence of density on depth, and interocular transfer of density adaptation). We have examined this issue using simultaneous density contrast, or SDC, the phenomenon in which the perceived density of a texture region is altered by a surround of different density (Sun et al., 2016). Our previous study revealed that SDC is bidirectional; that is, sparser surrounds increase perceived density and denser surrounds decrease it (Sun et al., 2016). The use of SDC allows us to manipulate surround properties (e.g., stereo-disparity) independently from those of the center, so that the measurement of density perception in the center is not confounded with other variables. In this study we investigated binocular integration of texture density processing with SDC in three experiments. In each experiment, three density levels of the surround elements were used: zero, sparse, and dense. In the first experiment we tested whether SDC is attenuated when the center and surround are in different stereo-depth planes. In the second experiment we dispersed the surround dots across a stereo-depth volume, and investigated how perceived density of the center was affected by the volume depth. In the last experiment we examined interocular transfer with SDC, by presenting test center and surround in different eyes.

General methods

Subjects

Three naïve volunteers (BC, SJ, and AB) participated in Experiment 1. BC and another two naïve volunteers (KY and SP) participated in Experiment 2. Still another three naïve volunteers (CA, AF, and LK) participated in Experiment 3. Two of the authors (HCS and FK) participated in all the experiments. All had normal or corrected-to-normal vision and stereoacuity.

Apparatus

Participants viewed the stimuli binocularly via a custom-built, eight-mirror Wheatstone stereoscope with a viewing distance along the light path of 100 cm. Stimuli were presented on a Sony Trinitron GDM-F520 CRT monitor (20 in., 1,600 × 31,200 pixels, 85 Hz) generated

using custom MATLAB (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, Pelli, & Broussard, 2007; Pelli, 1997). Screen luminance was measured with an Optikon universal photometer (Optikon Corp. Ltd., Ontario, Canada), and linearized using Mcalibrator2 (Ban & Yamamoto, 2013).

Stimuli

Stimuli consisted of quasi-randomly placed, non-overlapping uniform discs, termed *dots*, as described in our previous studies (Sun et al., 2016; Sun et al., 2017). Half of the dots were black (7 cd/m^2) and half white (115 cd/m^2), each with a diameter of 0.05° , and placed on a mid-gray background of 61 cd/m^2 . Each dot pattern was presented in a circular center-surround arrangement with a fixation cross (0.26°) in the center (Figure 1). The diameters of the center and surround areas were 2.2° and 7.9° .

A match stimulus and a test stimulus were presented successively in each trial. The match covered the center area only, while the test contained textures covering both center and surround areas. The match stimulus was selected from 95 logarithmically spaced density levels ($0.53\text{--}100 \text{ dots/deg}^2$) based on a staircase procedure for each trial. For the test stimulus, the center density was fixed to 12.9 dots/deg^2 (49 dots). There were three values of surround density: 0, 2.15, and 38.7 dots/deg^2 , termed no-surround baseline (see Figure 1C right for example), sparse surround (center density $\times 1/6$, see Figure 1C left), and dense surround (center density $\times 3$, see Figure 1A & B), respectively. These surround densities were selected to induce strong SDC based on our previous study (Sun et al., 2016).

The stereo disparities of test center and match stimuli were kept at the fixation plane (i.e., a stereo disparity of zero). The disparity of the test surround varied across experiments and conditions with positive (nearer than fixation) or negative (farther) disparities. In Experiment 1, all the surround dots were at the same depth plane with disparities of 24, 12, 6, 3, 1.5, 0, -1.5 , -3 , -6 , -12 , or -24 minutes (Figure 1A) in each condition. In Experiment 2, surround dots were randomly distributed across a range of disparities of 0, ± 1.5 , ± 3 , ± 6 , or ± 12 minutes (Figure 1B) in each condition. This made the surround dots appear to be spread throughout a 3D volume with small to large stereo-depths. Overlapped dots were reassigned to other randomized locations until all the dots in the surround were neither overlapping with one another nor overlapped with center dots after assigning their disparities. In Experiment 3 all the surround dots were at disparity 0 with test center and surround presented in both eyes (binocular), same eye (monoptic), or different eyes (dichoptic, see Figure 1C).

Procedure

Observers viewed two stimuli in sequence in each trial and pressed buttons on a numeric keypad to indicate which stimulus, the first or the second, appeared to have the denser center region. The match stimulus was always presented first and the test stimulus second (i.e., asymmetrical match procedure. See Discussion for more detail) to avoid potential adaptation effects from the surround in the first interval (Sun et al., 2016). The match and test stimuli were each presented for 650 ms, separated by a 600-ms interstimulus interval (ISI). Observers had unlimited time to make a response, without feedback, and they were instructed to fixate throughout the experiment to avoid misalignment of the retinal images of the center areas between the test stimulus and the match.

Each participant completed 150 trials (six independent staircases, each 25 trials) for each condition in each experiment, gathered across several sessions. For each staircase, the density level of the test stimulus was specified by the experimental condition and was fixed throughout a block. The density level of the match stimulus in each trial was adjusted using a 1-up, 1-down staircase procedure for acquiring a point of subjective equality (PSE) in an appearance judgment (Kingdom & Prins, 2016). In the first trial, match density was randomly chosen in the range bracketing 11 to 15 levels above or below the physical density of the test. The match density change (jump size) for the subsequent 12 match trials was gradually reduced from 13 to 2 levels, and then remained constant for the remaining trials for convergence. During each block there were three or four randomly interleaved staircases of different conditions such that conditions on successive trials were unpredictable. This procedure also helps prevent observers from exerting specific response biases toward each trial/condition (see Discussion).

Data analysis

Individual and group data analysis was the same as in (Sun et al., 2016). Trial responses in each condition were first summed across the six staircases. Since the match and test density levels were logarithmically spaced, they were log-transformed before fitting a logistic psychometric function (PF) to the responses according to a maximum likelihood criterion, using routines from the Palamedes Toolbox (Prins & Kingdom, 2009). PSEs were estimated from the fits, and all statistical tests were performed using these log-scale values. They were then transformed back to linear-scale values for plotting in graphs.

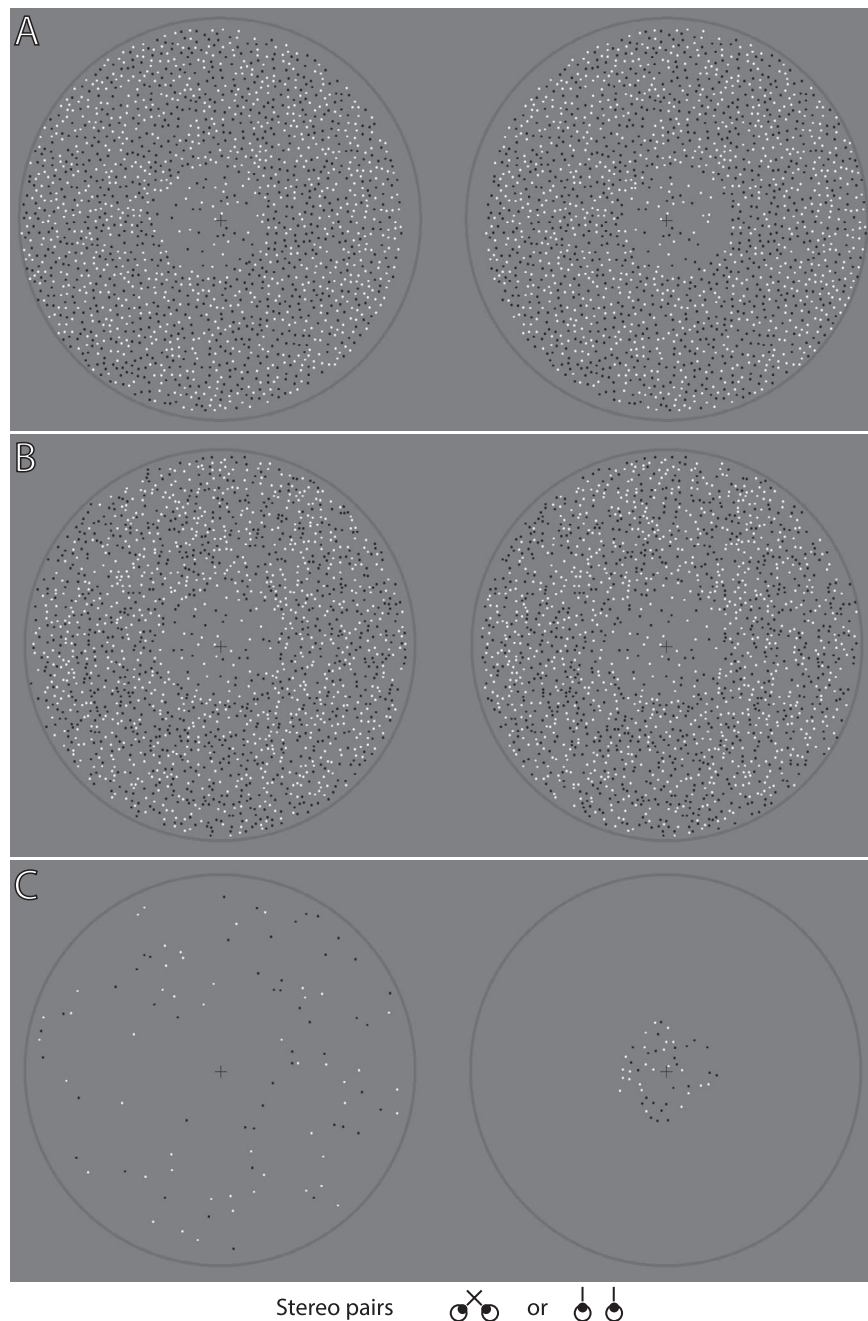


Figure 1. Examples of stimuli (stereo pairs) used in Experiment 1 (A), Experiment 2 (B) and Experiment 3 (C). In (A) all the surround dots reside in the same plane, which appears nearer (farther) than the fixation and center area with crossed (or parallel) free-fusion. In (B) surround dots were randomly distributed across the range of stereo-depth volume with the center plane in the middle of the depth (cross fusion or parallel fusion). (C) is an example of stimuli used in Experiment 3, in which center dots and surround dots were all at the fixation plane but presented in different eyes (dichoptic condition). (A) and (B) show stimuli in dense-surround conditions, while in (C), a sparse surround is shown.

Standard errors for PSEs were estimated by a bootstrap analysis (Efron & Tibshirani, 1994) in Palamedes, based on 400 resamplings from the collected data per psychometric function (Kingdom & Prins, 2016). Group data were calculated by taking geometric means and geometric standard errors across all the observers in each condition of an experiment.

Experiment 1

In the first experiment, we aimed to test whether and how perceived density of the test center changes when the surround dots were in different stereo-depth planes. If density representation is at a 2D retinotopic level as

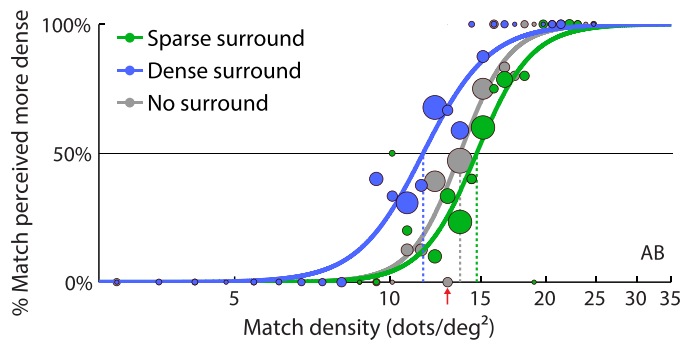


Figure 2. Psychometric functions for naïve observer AB in Experiment 1, for the stereo disparity 0 condition. Each graph plots the proportion of times the match stimulus appears denser than the test, as a function of match density. Test center density is 12.9 dots/deg² (red arrow) and relative surround densities are $\times 0$ (no surround, gray line, and circles), $\times 1/6$ (sparse surround, green line, and circles) and $\times 3$ (dense surround, blue line, and circles). Continuous lines are best fitting logistic functions to the filled circles, whose diameters correspond to the number of trials tested with that value of match density, as determined by the staircase procedure. The PSEs are the match density values at which the vertical dashed lines, corresponding to the 50% horizontal line, meet the abscissae.

previous studies suggested (Bell et al., 2015; Dakin et al., 2011), this manipulation should not affect perceived SDC since the 2D projections of the surrounds are all the same across depth levels. On the other hand, systematic changes of perceived SDC with surround depth might suggest that stereopsis is taken into account in density processing.

Two surround densities (sparse and dense) were tested at 11 plane depth levels (24, 12, 6, 3, 1.5, 0, −1.5, −3, −6, −12, or −24 minutes) together with a no-surround condition; therefore, in total there were $2 \times 11 + 1 = 23$ conditions. For naïve observers AB and SJ, only 7 of the 11 plane depth levels (24, 6, 1.5, 0, −1.5, −6, or −24 minutes) were tested, giving $2 \times 7 + 1 = 15$ conditions in total for them. Group data was calculated based on the 15 conditions across the four observers.

Example psychometric functions (PFs) for naïve observer AB are shown in Figure 2, for the three experimental conditions: zero-disparity sparse surround (green), dense surround (blue), and no-surround baseline (gray). Test center density is 12.9 dots/deg² as indicated by the red arrow. Each filled circle shows the percentage of trials the match density appeared denser than the test, as a function of the match density. The diameters of the circles correspond to the relative number of trials at that value of match density. Most of the trials tend to be concentrated around the PSE as expected from the staircase procedure. Continuous lines are best-fitting logistic functions to the filled circles, and the PSEs are shown as the vertical dashed

lines where the fitted functions meet the 50% horizontal line. Consistent with our previous findings (Sun et al., 2016), the sparser surround PF (green) is shifted to the right of, and the denser surround PF (blue) shifted to the left of the no-surround PF (gray), indicating the bidirectionality of SDC for this observer.

The PSEs for the five observers and their group average are shown in Figure 3. The graphs plot PSEs as a function of the surround disparities for sparse surround (green), dense surround (blue), and no-surround baseline (gray). PSEs above (below) the gray baselines imply an enhancement (decline) in perceived density compared to the no-surround conditions. Importantly, the pattern of the data is generally consistent across observers: for dense surrounds there is a small decline near very small disparities, indicating a stronger SDC, (i.e., a decline in perceived density). However, for sparse surrounds the PSEs seem not to change with the surround disparity.

To assess how the surround disparities and densities affected the perceived density of the test center, we ran a 2 (surround density: sparse or dense) $\times$ 7 (surround plane depth: 24, 6, 1.5, 0, −1.5, 6, or 24 minutes in stereo disparity) repeated-measures ANOVA for the five observers. This analysis indicated a significant main effect of surround density, $F(1, 4) = 20.75$, $p < 0.05$, with a higher perceived density for sparse than for dense surrounds, consistent with our previous results (Sun et al., 2016). Importantly, the analysis also indicates a significant main effect of surround plane depth, $F(6, 24) = 10.82$, $p < 0.001$, and an interaction between surround density and surround plane depth, $F(6, 24) = 2.8$, $p < 0.05$. Therefore, surround depth does appear to influence the perceived density of the center, and in a different way for denser compared to sparser surrounds.

To further examine the results, we averaged the PSEs of the three small plane depth conditions (disparity 1.5, 0, and −1.5) and the four large plane depth conditions (disparity 24, 6, −6, and 24) for each observer. We then ran paired-samples t tests of small versus large depth conditions for sparse- and dense-surround conditions. The results show significantly lower PSEs (i.e., larger SDC) in the small depth conditions for dense surrounds ($t_4 = 7.34$, $p < 0.01$, two-tailed). However, for the sparse surround, no significant difference was found ($t_4 = 1.62$, $p = 0.18$, two-tailed). The normalized PSE shifts, $(\text{PSE} - \text{baseline PSE}) \div \text{baseline PSE} \times 100\%$, for small versus large depth in dense surrounds were −35.3% versus −12.4% (22.9% difference) on average, while the PSE shifts for sparse surround were 13.8% versus 16.7% (only a 2.9% difference). Taken together, these results indicate that SDC is reduced for dense-surround patterns when the surround is in a different depth plane from the center.

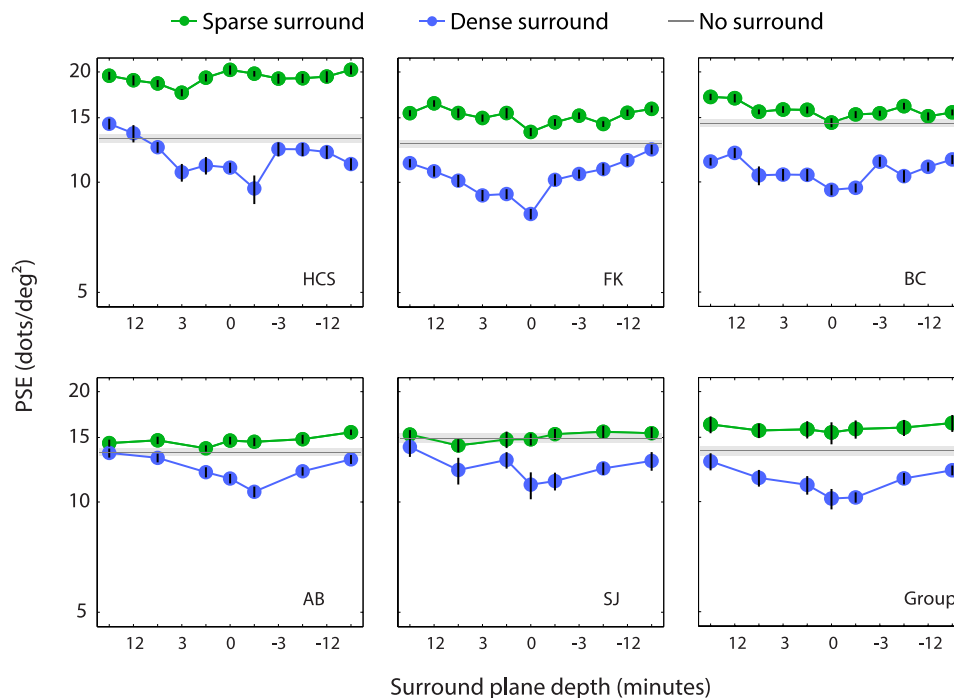


Figure 3. Individual and group PSE results of Experiment 1. Graphs show PSE data as a function of surround depth from near planes (positive disparities) to far planes (negative disparities). Disparity 0 is also fixation depth and test center depth. Green, blue, and gray lines represent sparse surround, dense surround, and no-surround conditions, respectively. Error bars (for no-surround conditions the light gray areas) are bootstrap-estimated standard errors. For the group data, the geometric mean PSEs and geometric standard errors calculated across the four observers are shown.

Experiment 2

In the second study, we spread the surround dots throughout a stereo-depth volume, and tested whether the perceived SDC changed with the volume depth. If perceived density is not biased by volume as a previous study suggested (Bell et al., 2015), this manipulation should not affect perceived SDC since the perceived densities of surrounds are unchanged across volume depth. On the other hand, if 3D size scaling is taken into account when estimating density, perceived SDC should reduce with volume depth.

Two surround densities (sparse and dense) were tested with five volume depths, each with dots randomly distributed across the disparity ranges of 0, ± 1.5 , ± 3 , ± 6 , or ± 12 minutes, plus a no-surround condition. Therefore, in total there were $2 \times 5 + 1 = 11$ conditions.

The PSEs for the five observers and their group average are shown in Figure 4. The graphs plot PSEs as a function of the surround volume depth for sparse surround (green), dense surround (blue), and no-surround baseline (gray). Importantly, the data are consistent across observers and experiments: for dense surrounds there is a strong SDC at a depth volume of 0, which gradually declines as volume depth increases. However, for sparse surrounds the PSEs do not appear

to change with volume depth. We observed similar findings in Experiment 1.

We ran a 2 (surround density: sparse or dense) $\times$ 5 (surround volume depth 0, ± 1.5 , ± 3 , ± 6 , or ± 12 minutes) repeated-measures ANOVA for the five observers. Again there was a significant main effect of surround density, $F(1, 4) = 77.96$, $p < 0.001$, showing higher perceived density for sparse than dense surrounds as in Experiment 1. There was also a significant main effect of surround volume depth, $F(4, 16) = 8.10$, $p < 0.001$, indicating that SDC varied with surround volume depth. We averaged the PSEs of the two small volume conditions (surround volume depths 0 and ± 1.5) and the three large volume conditions (surround volume depths ± 3 , ± 6 , and ± 12) for each observer, and ran paired-samples t tests of small versus large volume conditions for sparse and dense surrounds. The results show a significant lower PSE in the small volume conditions for dense surrounds ($t_4 = -4.36$, $p < 0.05$, two-tailed) but no significant difference for sparse surrounds ($t_4 = -1.75$, $p = 0.16$, two-tailed). The normalized PSE shifts for small versus large volumes in dense surrounds were -42.4% versus -36.7% (5.7% difference, on average). For sparse surrounds, the normalized PSE shifts were 8.4% versus 11.7% (3.3% difference). These results suggest only a moderate effect of surround volume depth on

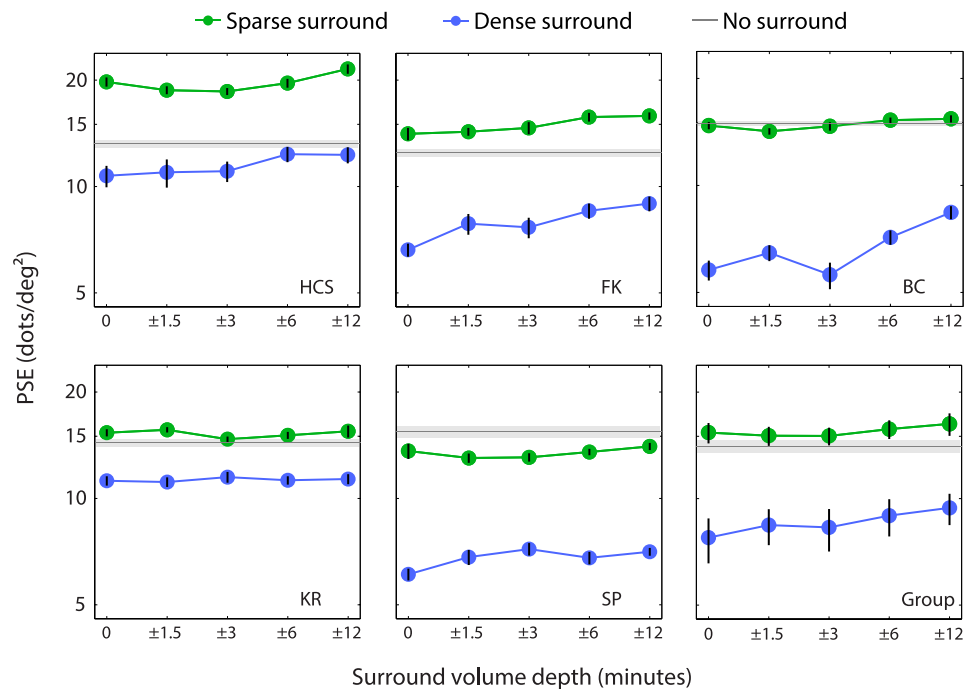


Figure 4. Individual and group PSE results of Experiment 2. Graphs show PSE data as a function of surround dots spread throughout a stereo-depth volume of varying extent in volume. Disparity 0 indicates that all the surround dots lie in the same depth plane as the fixation and test center. Green, blue, and gray lines represent sparse surround, dense surround and no-surround conditions, respectively. Individual error bars and group data were calculated in the same way as in Experiment 1.

perceived SDC: perceived SDC is slightly reduced when the surround volume is increased, for dense-surround conditions. Further comparison between the results of Experiment 1 and 2 are addressed in the Discussion section.

Experiment 3

In addition to a dichoptic density aftereffect, Durgin (2001) also observed a dichoptic SDC, though this was not explored in a systematic manner. Here we formally measure the interocular transfer effect of SDC and compare it with monoptic and binocular SDC. If density encoding occurs before binocular integration (i.e., at a monocular level), there should be no SDC when test center and test surround are presented dichoptically. However, if density is encoded subsequent to binocular integration, interocular transfer effect of SDC should be observed.

To this end, we presented test center and test surround in the same eye or in different eyes, with sparse or dense surrounds, plus a no-surround baseline. Match stimuli were always presented in the same way as the test center. To control for eye dominance and investigate its potential influence on the interocular transfer of SDC, we tested all these conditions for dominant and nondominant eyes separately. There

were [2 (sparse or dense surrounds) $\times$ 2 (same eye or different eyes) + 1 (no-surround baseline)] $\times$ 2 (dominant or nondominant eye) = 10 conditions. For comparison we also tested sparse surround, dense surround, and no-surround conditions for both eyes. In total there were 13 conditions.

The PSEs for the 13 conditions were measured for each condition on the five observers. Since there was no major difference in perceived density observed between dominant and nondominant eyes under each condition (no-surround baseline: $t_4 = 1.10$, $p = 0.34$; sparse-surround same eye: $t_4 = 1.57$, $p = 0.19$; dense-surround same eye: $t_4 = 0.46$, $p = 0.67$; sparse-surround different eye: $t_4 = 1.77$, $p = 0.15$; dense-surround different eye: $t_4 = 1.45$, $p = 0.22$, all paired-samples, two-tailed), we therefore combined the trials across dominant and nondominant eye conditions, fitted the resultant psychometric functions and calculated their PSEs.

The PSEs for the five observers and their group average are shown in Figure 5. The graphs plot PSEs as a function of the three center-surround presentation types: both eyes (circles), same eye (triangles), and different eyes (squares), for sparse surround (green), dense surround (blue), and no-surround baseline (gray). The no-surround baseline is combined across three baseline conditions (both eyes, dominant eye, and nondominant eye) as they are not significantly different from one another according to a 1-way repeated-measures ANOVA, $F(2, 8) = 2.14$, $p = 0.18$.

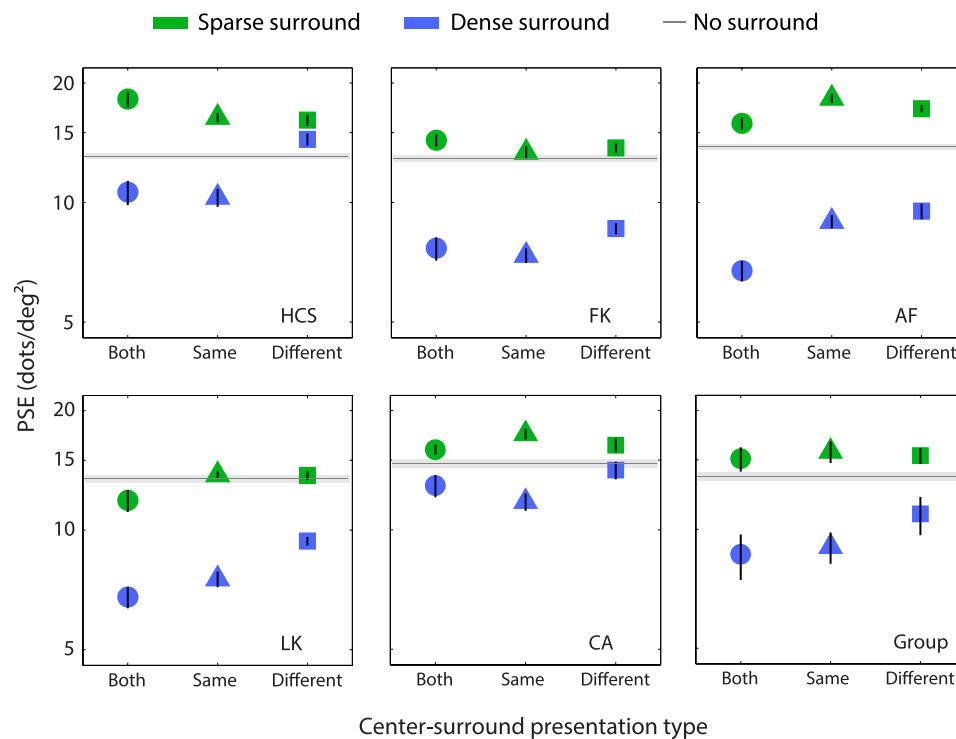


Figure 5. Individual and group PSE results of Experiment 3. Graphs show PSE data as a function of the three center-surround presentation types: both eyes (circles), same eye (triangles), and different eyes (squares). Green, blue, and gray lines represent sparse surround, dense surround, and no-surround conditions, respectively. Individual error bars and the group data were calculated in the same way as in the previous experiments.

We ran a 2 (surround density: sparse or dense) $\times$ 3 (center-surround presentation type: both eyes, same eye, or different eyes) repeated-measures ANOVA. The ANOVA again indicated a significant main effect of surround density, $F(1, 4) = 47.14$, $p < 0.01$, consistent with the previous experiments. The main effect of presentation type, $F(2, 8) = 3.68$, $p = 0.07$, was not significant; however, the interaction between surround density and presentation type was, $F(2, 8) = 5.55$, $p < 0.05$, meaning that center-surround presentation type affected perceived density in different ways for sparse and dense surrounds. We therefore calculated the PSE difference between the sparse and dense-surrounds separately for the three presentation types. A 1-way repeated-measures ANOVA showed a significant effect of presentation type for dense surrounds, $F(2, 8) = 9.77$, $p < 0.01$, but not for sparse surrounds, $F(2, 8) = 0.49$, $p = 0.63$. Tukey's honest significant difference (HSD) post hoc test showed significantly larger SDC differences for both eyes versus different eyes ($p < 0.05$). The SDC difference for both eyes versus same eye and same eyes versus different eyes are not significantly different. Since the monoptic SDC is significantly stronger than the dichoptic SDC, it indicates that there is monocular processing of density at some level. To test how much SDC is transferable between eyes, we defined interocular transfer rate (ITR) of SDC as:

$$1 - \frac{|\text{same eye PSE} - \text{different eye PSE}|}{\text{same eye PSE}} \times 100\%$$

The ITR for the sparse surround is on average 96.8% across the four observers, and for the dense surround, 88.5%. These high ITRs of SDC along with high ITR (75%) observed in the density aftereffect (Durgin, 2001) suggest that density processing is primarily binocular.

Discussion

In three experiments we investigated for the first time binocular effects on texture density processing using simultaneous density contrast, or SDC. We found weaker SDC when the center and surround planes were separated in stereo-depth. SDC was also slightly reduced when the surround dots were distributed across a stereo-depth volume. These findings are consistent with previous findings that the effects of surrounding textures are lessened when presented in different stereoscopic depth planes (Harris & Morgan, 1993). Interestingly, these small but significant binocular effects found here were only for dense but not for sparse surrounds—possible reasons for this are discussed below. Finally, we found strong interocular

transfer of SDC, in line with the interocular transfer observed in density adaptation (Durgin, 2001; Durgin & Proffitt, 1996), and strengthening the idea that density encoding is primarily binocular. In summary, we consistently found evidence that density perception is affected by binocular information across the three experiments. Thus stereo-depth information is taken into account when estimating density, in line with studies on numerosity (Aida et al., 2013; Aida et al., 2015; Schütz, 2012). Along with the findings that density affects depth perception and depth-plane segmentation (Akerstrom & Todd, 1988; Buckthorpe & Wu, 2017; Gepshtein & Cooperman, 1998; Tsirlin et al., 2008; Tsirlin et al., 2012), density and depth processes appear to have a mutual influence.

Our findings appear to conflict with studies showing that density information is represented in a 2D retinotopic manner (Bell et al., 2015; Dakin et al., 2011). Note, however, that the test center and dense surround used here, 12.9 and 38.7 dots/deg², were much denser than the 5.2 dots/deg² density used by Bell et al. (2015). When the surround is sparser (2.15 dots/deg²), the result is largely consistent with Bell et al. (2015). Thus, density representation might not be 3D at low densities.

Sparse versus dense surrounds

Why then the absence of the influence of surround depth on SDC with sparse surrounds? Possibly a sparse surround contains weak depth information because the number of dots is small. Or perhaps stereo-depth only affects high-density not low-density channels. The latter is not supported by previous studies showing an influence of stereo-depth on low numerosity judgments, but these studies of course deal with numerosity and not density (Aida et al., 2013; Aida et al., 2015; Schütz, 2012). Another possibility is that the sparse surround activated the numerosity system while the center activated the density system, and that the SDC is reduced between these systems. Here the sparse surround density is 2.15 dots/deg², which is close to the numerosity regime (less than 2.3 dots/deg² for central vision) found by Anobile et al. (2015). However, note that this density-numerosity boundary shifts to lower values dramatically with increasing eccentricity (e.g., 1 dot/deg² for 5° in eccentricity and 0.5 dots/deg² for 15°, according to Anobile et al., 2015). Therefore, the sparse surround in this study should be mostly within the density regime, since it was presented at eccentricities of 2.2° to 7.9°. In that case, the small SDC found in our sparse-surround condition is unlikely due to the center and surround activating different systems.

However, even if the sparse surround here is activating a numerosity mechanism, because of the

spontaneity and dominance of number perception (Cicchini, Anobile, & Burr, 2016), it is unlikely to be the cause of the low SDC found here. According to our earlier SDC study (Sun et al., 2016), strong SDCs were observed even when sparse surrounds were within the numerosity regime while centers were not (center density 6.4 or 12.8 dots/deg², and surrounds 1/6 or 1/36 of them). Based on this evidence, density and numerosity coding might share a common mechanism (Dakin et al., 2011; Morgan et al., 2014; Raphael et al., 2013; Raphael & Morgan, 2016; Sun et al., 2016; Tibber et al., 2012). The low SDC for sparse surrounds found in this study might be due to other factors (e.g., smaller size of dots, center area, and surround area, and a longer stimulus duration) that we did differently than our earlier SDC study to accommodate stereoscopic presentation. However, we cannot rule out the possibility that there might be some unknown interactions between binocular information and the numerosity-surround-density-center SDC. In addition, unlike density perception, numerosity perception was not found to be affected by area (i.e., no 2D size scaling; Anobile et al., 2016; Dakin et al., 2011). It is therefore probably the case that numerosity would not exhibit a volume bias (i.e., no 3D size scaling). That might explain why SDC is insensitive to sparse-surround volumes.

The difference in interocular transfer between sparse and dense surrounds is a different situation. Sparse surrounds showed higher interocular transfer than dense surrounds. The reason for this result is not clear. One possibility is that SDC for sparse surrounds is much smaller than for dense surrounds in general. As a result, any difference at low densities would become difficult to observe (i.e., because of a “floor effect”).

Stereo-depth planes versus volumes

The effect on SDC of spreading the dots in the surround into a stereo volume was not large: a 5.7% reduction in SDC for the dense surround and 3.3% reduction in SDC for the sparse surround. As such, the results with the volume condition should not be considered a serious challenge to the results of Bell et al. (2015), who measured perceived density as a function of volume depth and found no effect of volume depth.

However, it is worth considering whether the modest effect of volume depth on SDC is commensurate with the other results of the study. To compare SDC between the depth plane and depth volume experiments (Experiments 1 and 2), we selected observers who completed both experiments (BC, HCS, and FK) and calculated the percentage PSE shifts from the depth 0 baseline using the formula $(\text{PSE} - \text{depth 0 PSE})/(\text{depth 0 PSE})$.

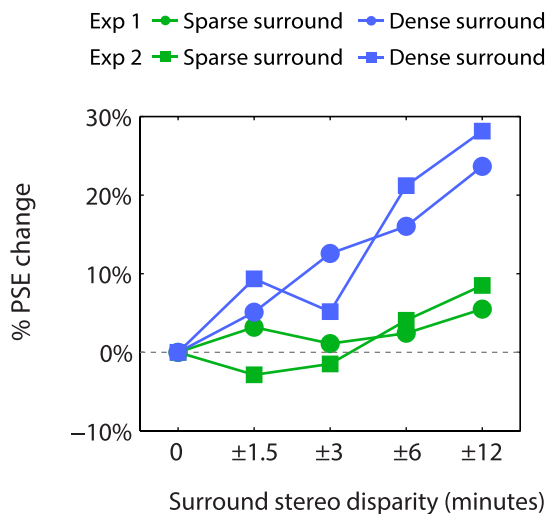


Figure 6. Normalized PSEs of Experiment 1 (circles) and Experiment 2 (squares) plotted as a function of stereo disparity of the surround. Percentage PSE changes were normalized to the depth 0 condition, $(PSE - \text{depth } 0 \text{ PSE}) / \text{depth } 0 \text{ PSE}$, averaged across the three observers. The normalized PSEs were calculated separately for sparse-surround (green lines) and dense-surround (blue lines) conditions.

0 PSE). The normalized PSEs for the depth plane experiment were averaged separately for dense and sparse surrounds to match the maximum stereo disparity in the volume conditions which have both positive and negative disparities in Experiment 2 (e.g., 12 and -12 conditions in Experiment 1 were averaged to match the ± 12 condition in Experiment 2). The normalized PSEs are highly similar between the two experiments as shown in Figure 6, especially for dense-surround conditions (correlation $r = 0.83$). This result suggests that the maximum disparity of the surround was the principal determinant of how much SDC was affected. In sparse-surround conditions the correlation between the two experiments is lower ($r = 0.71$), which is not surprising since in this case disparity shows little effect on SDC in both cases.

Individual differences in bidirectionality

SDC for most of our observers was bidirectional, in that perceived density of a central region was increased by sparse surrounds and decreased by dense surrounds, as found in our previous study (Sun et al., 2016). However, the shifts in perceived density from the sparser surround reported here (12.2%, 9.6%, and 16.5% on average for the depth 0 condition in Experiments 1, 2, and 3) were less than in Sun et al. (2016; 25% on average, with almost the same test density 12.9 dots/deg² and surround density, $\times 1/6$). Moreover, unidirectionality was observed in some of

the observers (SJ in Experiment 1, SP and BC in Experiment 2, LK in Experiment 3) in conditions where there were no stereo-depth or interocular differences. However, the stimulus parameters differed in several ways from our previous study in order to accommodate stereoscopic presentation (e.g., smaller size of dots, center area, and surround area, and a longer stimulus duration for binocular fusion). These changes might reduce the strength of the bidirectionality in SDC. It is possible that the bidirectionality of observers with only small degrees of intrinsic bidirectionality would be harder to reveal using stimulus parameters optimized for stereopsis rather than for SDC. The important point is that the patterns of binocular effects on SDC were consistent across observers regardless of their directionality, which is consistent with our main conclusion.

Other potential factors

Could an illusory size effect cause the effect of stereo disparity on SDC? When the surround plane is near, the center would appear relatively far in depth, even though at a disparity of 0, making the perceived size of the center area bigger and therefore lower perceived density. If that is the case, the predicted perceived density of the center should gradually increase when surround depth was varied from near to far. However, this tendency is not seen in any of our observers under either sparse- or dense-surround conditions. Instead, we observed a rather symmetric pattern between near and far conditions (Figure 3), suggesting an effect of stereo-depth per se rather than an illusory size effect.

Is it possible that the binocular effect on SDC is due to observers' response biases (Morgan, Dillenburger, Raphael, and Solomon (2012)? Although we presented the match before the test in every trial (to avoid potential adaptation effects), it is unlikely that observers could ignore the test before making a response. This is because we mixed three to four interleaved staircases from different conditions in each block, so that the test (both the surround and the appearance of the center) was changing trial by trial. Response bias would be difficult to exert on this basis since observers would need to identify the condition of the test stimulus first, then bias their response based on it for that trial. This would be extremely challenging and unlikely, given that the differences between conditions were often subtle (e.g., different stereo-depth planes or volumes), not to mention that observers would need to apply slightly different biases across conditions in rapid succession. We applied the same "asymmetrical match" procedure for all the conditions, and the patterns of binocular

effect on SDC are generally consistent across observers, which cannot simply be explained by response bias.

Conclusion

We have revealed the influence of binocular information on texture density processing. Strong SDC was observed when the surround texture was at a similar stereo-depth as the center, with a gradual decline in SDC as the difference in depth between center and surround increased. We also found that density induction from the surround texture is transferable between eyes. This evidence challenges the previous view of a solely 2D representation of texture density.

Keywords: texture, texture density, binocular disparity, three-dimensional, interocular transfer

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