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Texture contrast aftereffects are monocular; texture density aftereffects are binocular

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Abstract

Two experiments examined interocular transfer for simple and dynamic aftereffects of density and contrast. Simple aftereffects of texture contrast were shown to be primarily monocular. Texture density aftereffects were shown to be primarily binocular. Similarly, dynamic aftereffects to repeated changes in contrast were found to be completely monocular; those to repeated changes in density were found to be entirely binocular. Since contrast and density aftereffects differ in their sensitivity to eye-of-origin, they likely depend on different neural loci, and are not manifestations of the same underlying adaptation. Consistent with this conclusion, it is proposed that, whereas contrast normalization (and perhaps contrast aftereffects) may be localized to simple cells in V1, density coding and normalization require computations only available in complex cells and beyond. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Adaptation; Aftereffects; Contrast; Density; Texture

1. Introduction

The visual system is highly susceptible to adaptation, and visual aftereffects are a convenient way of non-invasively examining the primitive codes of vision. In this paper, aftereffects of texture contrast and aftereffects of texture density are studied and compared. One goal of this paper is to draw an analogy between texture density and texture contrast, while at the same time pointing out a very salient dis-analogy: suprathreshold contrast aftereffects seem to be monocular, whereas those of density are binocular.

Superthreshhold contrast aftereffects have been investigated previously (Blakemore, Muncey, & Ridley, 1971; Blakemore, Muncey, & Ridley, 1973) in the context of studying orientation and spatial frequency selectivity in vision, but there have been only limited investigations of the interocular transfer of this suprathreshold effect (e.g. Snowden & Hammett, 1996) and almost no investigation of non-periodic stimuli. Although threshold elevation aftereffects are known to show substantial interocular transfer (e.g. Bjørklund & Magnussen, 1981), there is mounting evidence that suprathreshold contrast aftereffects are produced by different mechanisms (Snowden & Hammett, 1992, 1996; Ross & Speed, 1996). Chubb, Sperling, and Solomon (1989) showed that perceived texture contrast was subject to simultaneous contrast effects reflecting lateral interactions. This latter phenomenon has been related to contrast normalization in V1 (e.g. Geisler & Albrecht, 1992; Heeger, 1992, 1994). Chubb et al. reported that these simultaneous effects could not be generated interocularly, thus seeming to involve a monocular site.

Another suprathreshold aftereffect under recent investigation is the texture density aftereffect. Durgin (Durgin, 1995; Durgin & Proffitt, 1991, 1996) has demonstrated that adaptation to differentially dense textures produces an aftereffect of perceived texture density. Although there had been previous reports of texture ‘density’ aftereffects (e.g. Anstis, 1974; see also MacKay, 1973, for a simultaneous contrast version), these studies had employed texture scaling to alter density. As a result, texture density was confounded with spatial frequency changes in the textures. In

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Anstis' (1974) paper, this led to the conclusion that texture density aftereffects were nothing other than spatial frequency shift aftereffects. Durgin and Huk (1997) have since shown this interpretation to be incorrect. If it is not a spatial frequency shift, what, then, is the basis for texture density aftereffects?

The present paper will consider (and reject) an alternative explanation of density aftereffects — that they are simply a reflection of contrast energy adaptation. Although dense textures contain more contrast energy than sparse texture composed of the same elements, increasing the contrast of a texture will not make it appear substantially denser. Moreover, although there are demonstrable interactions between brightness and density (Mulligan & MacLeod, 1988; Cornelissen & Kooijman, 1994), these dimensions are not normally confusable. Thus, density and contrast appear to be separable perceptual dimensions. However, it remains to be shown that adaptation to these dimensions produces different aftereffects.

Following up Durgin and Hammer's (2001) findings of similarities between dynamic texture density aftereffects and dynamic contrast aftereffects, I sought to investigate the relationship between density and contrast adaptations further. The analogy goes as follows. Whereas contrast can be thought of as the standard deviation of luminance (cf. Moulden, Kingdom, & Gatley, 1990), density is effectively equivalent to the kurtosis of luminance distribution, which is equivalent to computing the standard deviation of contrast itself. Clearly, a wiring scheme that computes contrast from luminance patterns can be iterated to compute density from contrast patterns. Empirical support for the relative lateness of the computation of density will be offered in this paper by documenting that aftereffects of texture density are predominantly binocular (show substantial interocular transfer) whereas texture contrast aftereffects that follow upon adapting to textures of different luminance contrasts are predominantly monocular (do not show substantial interocular transfer).

Two experimental studies will be presented in which patterns of interocular transfer are examined. First, I will consider simple aftereffects of texture contrast and texture density in Experiment 1, and next, I will examine dynamic aftereffects (Durgin & Hammer, 2001) of texture contrast and texture density in Experiment 2. In particular, it will be shown that adaptation to differences in texture contrast produces predominantly monocular aftereffects of apparent contrast. Adaptation to differences in texture density, however, produces predominantly binocular density aftereffects (perceived as differences in texture spacing). Moreover, a similar monocular/binocular dissociation of texture contrast and texture density will be demonstrated for dynamic aftereffects of density and of contrast. Finally, a similar comparison will be made for the simultaneous contrast effects of texture density and texture contrast. Together, these findings suggest that very similar patterns of normalizing computations (over time as well as space) may occur for texture contrast and texture density, but that they probably occur at different neural loci.

2. Experiment 1: aftereffects of texture contrast and of texture density

The purposes of Experiment 1 are twofold. First, texture contrast aftereffects and texture density aftereffects will be tested for interocular transfer. In addition, the experiment will test for psychophysical interaction between texture contrast adaptation and texture density adaptation.

Interocular studies of texture density adaptation have been reported previously, showing a high degree of transfer (roughly 75% — Durgin & Proffitt, 1996). These findings will be replicated here for direct comparison to the texture contrast aftereffects. Moreover, assessments of apparent-contrast aftereffects following density adaptation and density aftereffects following contrast adaptation will be examined in order to determine the extent, if any, of interaction between these two texture properties.

2.1. Methods

2.1.1. Participants

Forty students at Swarthmore College who were naïve to the purpose of the experiment were each paid \$5 for their participation.

2.1.2. Design

There were four (between-subject) experimental conditions representing the four possible inter- and intra-dimensional adaptation test pairs. Specifically, observers were adapted to differences in either texture density or texture contrast, and then were tested for either relative density perception or relative contrast perception. Note that some observers were adapted to density and tested for density aftereffects, and some were adapted to density and tested for aftereffects of perceived apparent contrast. Similarly, some of those adapted to differences in texture contrast were tested for aftereffects of perceived contrast, and some were tested for density aftereffects. All participants were adapted monocularly and tested for interocular transfer of the relevant aftereffect.

Because greater interest was attached to quantifying interocular transfer within each adapted dimension, 12 participants were assigned to each of conditions in which the tested dimension was the same as the adapted

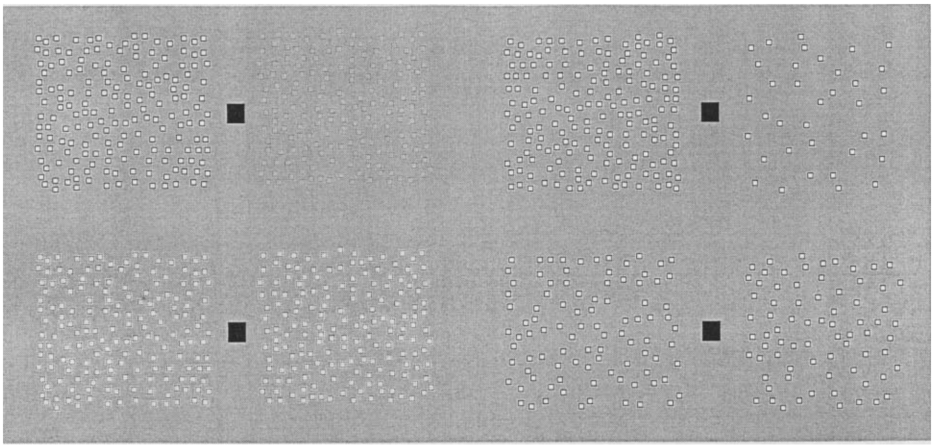

Fig. 1. Schematic illustrations above can be used to observe aftereffects of contrast (left) and of texture density (right). These reproductions of balanced-dot textures are not actually balanced in the illustration, nor are appropriate contrasts reproduced here. None the less, 20–30 s of adaptation to the upper left pair (using the black square as a fixation mark), will produce a noticeable difference in contrast in the lower two textures. Similarly adaptation to the upper right pair will produce a noticeable difference in perceived density of the lower right pair.

dimension, while only eight were assigned to cross-dimensional conditions. All adaptation and testing were surreptitiously monocular. The adapting stimuli were always presented to the same eye. The test stimuli were also monocular, but each eye was assessed for all observers.

2.1.3. Apparatus

All textures were viewed on a CRT (ViewSonic 17, 75 Hz, 37 pixels/cm) through a stereo-viewer built with first surface mirrors. Displays were controlled by Macintosh Quadra 610. The optical distance to the CRT was 48 cm.

2.1.4. Stimuli

Textures were composed by the random scatter of luminance-balanced dots (Carlson, Moeller, & Anderson, 1984; Gilden, Bertenthal, & Othman, 1990; Durgin & Proffitt, 1996). The mean texture luminance was 16.3 cd/m^2. The dots themselves consisted of a bright 2×2 pixel square surrounded by a dark square annulus one pixel wide. The peak spatial frequency of the textures thus composed was 9.8 cpd (spatial frequency is essentially independent of texture density for a random scatter[1]). Texture density was manipulated by varying the number of dots randomly scattered in the textured region while keeping the contrast of each individual element fixed ($\sim$100%). Texture contrast was manipulated by varying the contrast of the individual dots, while keeping dot density and average luminance fixed. Fig. 1 shows schematic illustrations of representative balanced-dot textures configured so as to demonstrate the two aftereffects.

Some discussion of the definition of contrast used here is required, since the stimuli employed are neither like gratings nor like random dot grayscale images (cf. Moulden et al., 1990). The theoretical values[2] of the pixels of a maximum-contrast balanced dot against a background of luminance, L, would be 0 for the annulus, and 4L for each of the central pixels. (The luminance ratio is 4 to 1 because there are 3 non-contributing annular pixels for each central pixel.) This theoretical maximum contrast dot was assigned the contrast value of 100. Contrast is lowered by reducing the luminance of the center of the dot while (of necessity) raising the luminance of the annular pixels (of which there are twelve for each dot). For example, if each pixel in the center were 3L, the annular pixels would have needed to be L/3, for the average luminance to remain L. In the limit, a contrast of 0 is reached when the center (and the annulus) reaches L. Accordingly, the computation of contrast in this paper reflects a linear scale in which a value of L for the central pixels is considered 0%, and a value of 4L for the central pixels is considered 100%. If the central luminance is called C, and the average luminance is L, then contrast equals $100 \times (C - L)/3$.

In fact, luminance balance was determined in advance for different values of C, at a constant value of L

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[1] Mathematically, the power spectrum of a random scatter of a texture should be the spectrum of an individual element multiplied by noise. Consistent with this, FFT power spectra of textures differing only in density have the same appearance as one another.

[2] These values are only 'theoretical' because of the unavoidable distortions produced by raster monitors: pixel luminance values are not truly independent of neighboring pixels to the left. The dots used in these experiments were composed of three theoretical luminance values — that for the center, that for the annulus and that for the background. The calibration of the center and annulus of the dots of various contrasts was achieved by empirical measurement of screen luminance with and without dots present. Thus, we can be certain that the dots had the correct average luminance, but the exact luminance structure was probably distorted somewhat by the raster process.

by adjusting the luminance of the annulus and measuring average luminance across the texture with a photometer. The actual luminance profile would have departed somewhat from these theoretical values[2], but this contrast scale would remain a sensible one for this purpose. Note that the textures employed here are balanced in photometric luminance, but are probably unbalanced by front-end non-linearities in the visual system. Although this would introduce luminance artifacts, such artifacts are probably of limited concern because of the high spatial frequencies employed. That is, the remaining incidental differences in effective luminance are probably less visually powerful than the intended differences in contrast and in density.

Textured regions were 10 deg high × 9 deg wide and were presented monocularly 1 deg to the left and right of a binocular fixation mark. The other eye image was matching gray, apart from the fixation mark. Because of the band-pass content of these stimuli, no binocular rivalry was experienced (cf. Durgin, 1992; Liu, Tyler, & Schor, 1992), and observers were, in general, unaware that the texture presentations were actually monocular.

2.1.5. Adaptation

Adaptation consisted of 180 initial flashes (200 ms duration; separated by an ISI of 800 ms) of texture pairs in which the region to one side of fixation always contained a dense (6 dot/deg^2), high-contrast ($\sim 100\%$) texture, and the other contained either a dense, low-contrast ($\sim 25\%$) texture (Contrast Adaptation Condition) or a sparse (1 dot/deg^2), high-contrast texture (Density Adaptation Condition). New textures were generated for each flash. It is worthy of note that differences in density do produce differences in global contrast energy when local element contrast is held constant.

2.1.6. Measurement

Following adaptation, participants made forced-choice judgments, according to their assigned condition, about which of two simultaneously presented test textures was either denser (Density Assessment) or brighter (Contrast Assessment). Points of subjective equality (PSE) were measured by four interleaved staircases that started at objective equality (cf. Durgin, 1995). Each staircase was terminated at the eighth turn, and the final six turns were averaged to estimate the PSE. Two PSEs were established for each eye for either perceived density or perceived contrast. For density aftereffect assessments, the fixed densities in the adapted region were 2 and 3 dots/deg^2 presented in the adapted region (100% contrast). For contrast aftereffect assessment, the standard contrasts used were 50 and 67% (6 dots/deg^2 in density). The entire procedure took less than 30 min.

Each measurement trial was preceded by three readaptation texture pairs presented to the originally adapted eye in order to maintain the strength of adaptation. The test trial therefore appeared as a fourth flash in the sequence presented on each trial. The test-flash durations were 200 ms, the same as for adaptation. No further trial was presented until the observer indicated that one or the other of the two textures was greater in value (denser or brighter) along the dimension to be assessed.

Because the fixed-value stimulus for each staircase was always placed in the dense or high-contrast adapted field, and the variable region (unbeknownst to the observer) was in the field corresponding to the sparse or low-contrast adapting texture, aftereffects in each dimension should be expressed by a reduction in the value of the variable field at PSE, and thus as a positive difference between the standard value and the value of the variable field at the PSE.

It should be noted that all deviations are expressed here in terms of the relative perception of density or contrast between two regions when one of the to-be-compared regions has been adapted to a high value and the other to a low value of the intended dimension. Thus, separate computations for the effect of the low-value adapting stimulus and the high-value adapting stimulus are not available. Indeed, adapting to low density, low contrast or even low luminance will always produce a decrement relative to no density, no contrast or no luminance. Thus, unlike spatial frequency, which (even ignoring orientation) permits independent variation in amplitude and frequency, these other kinds of dimensions are probably better understood as scalar values (Durgin & Proffitt, 1996; Durgin & Huk, 1997).

2.1.7. Analysis

PSEs for density were converted to differences between the logarithms of the numbers of dots presented in each field (natural log of the standard minus the natural log of the variable field at PSE). Prior research has shown that density aftereffects can be approximated as a constant ratio of the standard density, which is conveniently expressed for statistical purposes as a difference of logarithms (cf. Durgin, 1996).

PSEs for apparent-contrast aftereffects were treated as simple arithmetic differences between the contrast of the standard and its subjectively matching contrast. This was because arithmetic differences at PSE were consistent for the high-contrast and low-contrast standard values, whereas the use of logarithmic differences produced statistical interactions that appeared to be an artifact of the log transformation. (As a precaution, however, statistics were computed both ways for contrast, to ensure that the use of arithmetic differences did not affect any of the theoretically important statistical differences. It did not. Only contrast statistics based on arithmetic differences will be presented below for the apparent-contrast aftereffects.)

2.2. Results and discussion

2.2.1. Aftereffects of apparent contrast

PSEs for Contrast were shifted in all adaptation conditions, as illustrated in Fig. 2. A 2 × 2 repeated-measures ANOVA was conducted on the contrast differences at PSE, with a between-subjects factor of Adapting Dimension (Adapt Density or Adapt Contrast) and a within-subject factor of Eye Tested (Adapted Eye or Unadapted Eye). Consistent with the existence of a monocular aftereffect of apparent contrast, there was a reliable interaction of Adapting Dimension and Eye Tested [$F(1,18) = 11.1$, $P < 0.01$]. In the adapted eye, the aftereffect of adapting to a difference in contrast (15.6 contrast units) was much stronger than that of adapting to a difference in density (9.6 contrast units) [$t(18) = 3.53$, $P < 0.01$]. In the other eye, however, apparent contrast following contrast adaptation (6.1 contrast units) did not differ from that following density adaptation (5.3 contrast units) [$t(18) = 0.307$, $P > 0.1$]. Thus, the apparent-contrast aftereffects found here appear to represent both a strongly monocular process that is specific to the registration of (and adaptation to) texture contrast and a weaker, rather binocular, process that is equally sensitive to differences in local contrast energy and to density differences.

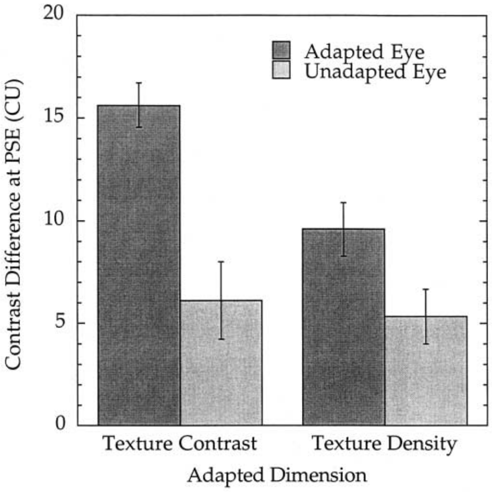

Fig. 2. Texture contrast aftereffects in Experiment 1. Average differences in objective contrast at the point of subjective equality are plotted as a function of eye and adapted dimension. Error bars represent standard errors of the mean.

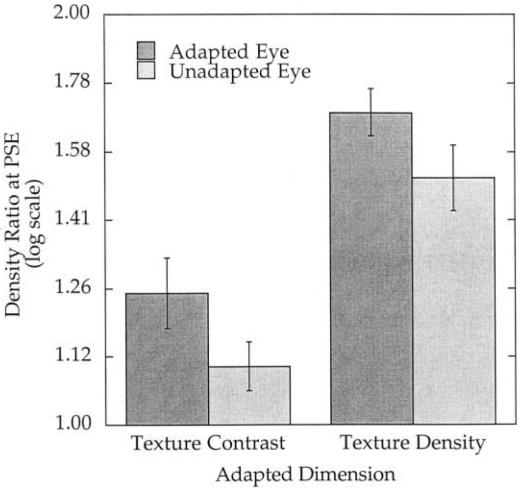

Fig. 3. Texture density aftereffects in Experiment 1. Average ratio differences in objective density at the point of subjective equality are plotted as a function of eye and adapted dimension. Error bars represent standard errors of the mean.

2.2.2. Aftereffects of perceived density

A similar analysis was performed on the log differences in density at PSE. As illustrated in Fig. 3, however, a rather different pattern of results emerged. Density aftereffects in the adapted eye (0.375 log units of density — LUD — corresponding to a ratio of 1.45) were greater than those in the unadapted eye [0.258 LUD or ln(1.29)], [$F(1,18) = 17.7$, $P < 0.01$]. Moreover, these aftereffects were greater following density adaptation [0.472 LUD or ln(1.60)] than following contrast adaptation [0.172 LUD or ln(1.19)], [$F(1,18) = 21.9$, $P < 0.01$]. However, of principal importance, there was no reliable interaction between these two factors in the repeated measures ANOVA, [$F(1,18) < 1$, $P > 0.1$]. Thus, for example, the difference in density aftereffect strength between the density adaptation condition and the contrast adaptation condition does not differ in the adapted eye [0.304 LUD or ln(1.36)] from the unadapted eye [0.318 LUD or ln(1.37)], [$t(18) = 0.25$, $P > 0.1$]. From this, it appears that the density aftereffect may depend on a single process that is largely binocular and is highly specific to a texture density rather than simply to local contrast energy.

2.2.3. Conclusions

Monocular adaptation to differences in texture contrast produces a primarily monocular aftereffect of apparent contrast. The binocular component of this apparent-contrast aftereffect is equally well produced by adaptation to differences in texture density, which, as was noted above, do produce differences in global contrast energy. Thus, the local contrast process appears to be monocular, and the more global contrast process appears to be more binocular. This interpretation is supported by the finding that the *interocular* aftereffect of apparent-contrast was the same following density adaptation and contrast adaptation, because both increases in density and increases in local contrast represent increases in total contrast energy.

Conversely, monocular adaptation to differences in texture density produces a primarily binocular aftereffect of perceived texture density. Durgin and Proffitt (1996) reported 75% interocular transfer for texture density using similar textures. The present data are consistent with a transfer rate of a similar magnitude (69% overall; 79% if only the density adaptation condition is considered). This aftereffect is quite specific to density, rather than contrast energy. The amount of monocular density aftereffect that followed texture contrast adaptation was only 42% of that following density adaptation. Moreover, the interocular density aftereffect from texture contrast adaptation was only 24% of that produced by density adaptation.

3. Experiment 2: dynamic aftereffects of texture contrast and texture density

Durgin and Hammer (1994, 2001) have demonstrated a pair of related aftereffects involving texture contrast and texture density. These aftereffects were to changes in density or contrast. Specifically, Durgin and Hammer showed that if an adaptation stimulus consisted of two textures presented in the same location, one after the other, then observers who became adapted to the change itself would show a negative aftereffect to the direction of change. For example, if the adapting stimulus always consisted of a dense texture followed by a sparse texture (e.g. 200 ms dense texture, 200 ms ISI, 200 ms sparse texture), then later judgements of sequentially presented texture pairs would be oppositely distorted. If the same density was presented in the first and second flash, the second texture would seem denser. Durgin and Hammer (1994) demonstrated that a similar aftereffect of sequential apparent contrast was found if the adapting textures differed in local contrast, rather than density, and that neither of these effects could be attributed to simple motion signals. However, much as we saw in Experiment 1 of this paper, Durgin and Hammer (1994) found little or no cross-adaptation between texture density and texture contrast. Adapting to changes in texture contrast did not produce aftereffects of sequential density, and adapting to changes in texture density produced only a small amount of aftereffect of sequential apparent contrast.

Anstis (1967) has shown that adaptation to steadily changing luminance produces a negative aftereffect of luminance change. If the adapting luminance was steadily increasing, then a steady luminance would appear to be gradually dimming. Anstis found that this dynamic aftereffect of lightness did not show interocular transfer. The present study was designed to test for interocular transfer of dynamic aftereffects of contrast and density.

3.1. Method

3.1.1. Participants

Five students at Swarthmore College who were naïve to the purpose of the experiment were paid $5 for each of four experimental sessions. All could perceive cyclopean figures in simple random dot stereograms. Four were adapted via their preferred eye (assessed by incidentally asking the observer to close one eye and counting the one that remained open 'preferred'). The fifth, CJH, completed only the two contrast sessions and was adapted via her non-preferred eye.

3.1.2. Textures

As in Experiment 1, textures were composed of luminance-balanced dots (Carlson et al., 1984; Durgin & Proffitt, 1991, 1996). The mean luminance was 16.3 cd/m. The peak spatial frequency was 9.8 cpd viewed at the optical distance of 48 cm. Textures were 9.4 × 9.4 degrees and were presented monocularly within a larger gray region of 10.3 × 10.3 degrees that was binocularly specified. The high-contrast border between the gray region and the black background supported binocular fusion. No binocular rivalry was experienced (cf. Durgin, 1992). Changes in density and contrast do not produce changes in spatial frequency (except in amplitude) or texture luminance for balanced-dot textures.

3.1.3. Design

There were four adaptation conditions representing two directions of change (Increase or Decease) and two different adapting dimensions (Texture Contrast or Texture Density). Following an initial period of adaptation, staircase techniques analogous to those of Experiment 1, were used to measure the point of subjective equality for sequentially displayed textures. Those adapted to contrast differences were tested for apparent contrast; those adapted to density were tested for density matches. All observers performed all conditions, except one, who only completed the two contrast-adaptation sessions.

3.1.4. Adaptation

Initial adaptation consisted of 180 initial dual flashes of textures presented monocularly. Each dual flash had a cycle of 200 ms first texture on, 200 ms off (homogenous gray) and then 200 ms second texture on, with an inter-dual-flash delay of 1000 ms. All textures were newly generated on each trial. A Density-increase (DI) adaptation stimulus consisted of a sparse (100 dot, or ~ 1.1 dot/deg^2), high-contrast texture ($\sim 100\%$) followed by dense (400 dot, or ~ 4.5 dot/deg^2), high-contrast texture. A Density-decrease (DD) adaptation stimulus consisted of a dense, high-contrast texture followed by sparse, high-contrast texture. A Contrast-increase (CI) adaptation stimulus consisted of a dense,

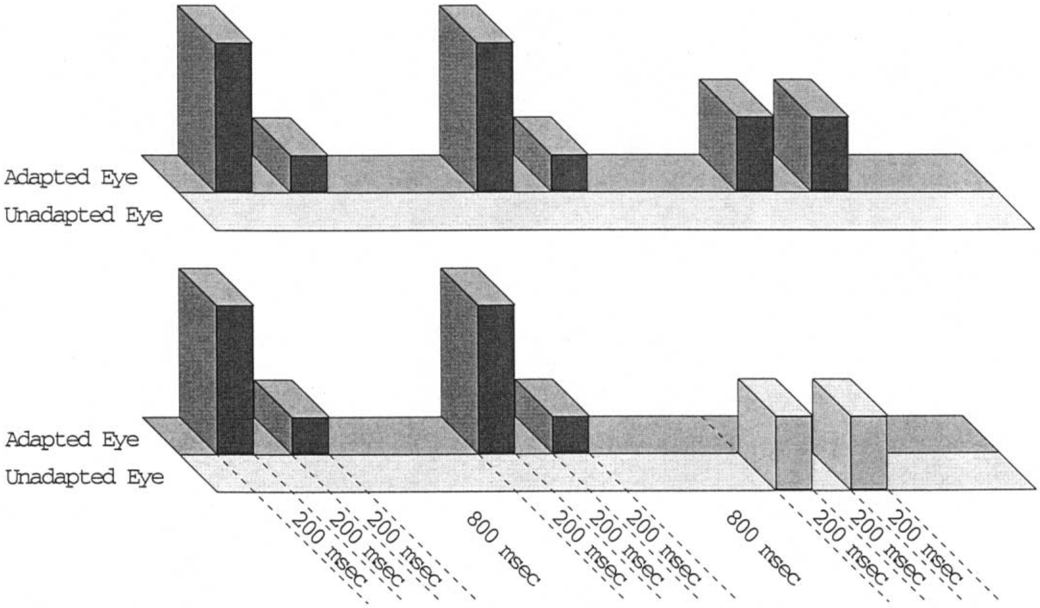

Fig. 4. Schematic illustration of the timing of events to each eye for test trials of Experiment 2. Here are depicted an intraocular trial (top) and an interocular trial (bottom) of a 'decrease' condition. Height of bar represents value along tested dimension (density or contrast). The thickness of the bar, left to right, represents time. Each trial consists of two pairs of adapting textures presented in sequence, with pairs separated by 800 ms, and a final test pair for comparison. The value of the final test texture varied according to the interleaved staircases.

low-contrast (25%) texture followed by dense, high-contrast (100%) texture. A Contrast-decrease (CD) stimulus consisted of a dense, high-contrast texture followed by dense, low-contrast texture.

3.1.5. Measurement

A staircase technique, analogous to that of Experiment 1 was employed to measure the effects of adaptation. Each measurement trial involved a decision about the relative density or apparent contrast of two textures presented sequentially. Cross-adaptation was not measured in this experiment (but cf. Durgin & Hammer, 2001), so only relative density judgments were made following density adaptation, and only relative apparent contrast judgments were made following contrast adaptation.

To maximize aftereffect strength, each test trial included two further monocular adaptation stimuli pairs, followed by the monocular presentation of the test stimulus to either the adapted eye or the other eye. Thus, a measurement trial consisted of two pairs of adapting textures and a third pair of sequentially presented test textures. The temporal profile of events is shown in Fig. 4. Observers were unaware of the eye of presentation (some remained unaware that presentation was monocular).

The values of the test textures were determined by eight staircases that were quasi-randomly interleaved. Four of these staircases involved measurements in the adapted eye and four in the other eye. For each eye, two separate staircases measured the aftereffect at each of two standard values. In measuring the dynamic contrast aftereffect, the standard contrast values used were 50 and 67% (see Experiment 1 for the definition of contrast units; density was maintained at 400 dots). In measuring the dynamic density aftereffect, the standard density values were 200 and 300 dots (contrast was maintained at $\sim 100\%$). All staircases commenced at objective equality and, for all staircases, it was the second-presented texture whose value varied according to the judgments of the participant. Thus, if an observer in a density adaptation session indicated that the first texture had seemed denser, then the value of the second texture would be increased in density on the next trial sampled from that staircase. If the observer judged the second to be denser, then the second would be decreased in density on the next trial sampled from that staircase.

The expected pattern of results is that adaptation to increases in density (or contrast) would be manifest as a higher value of density (or contrast) in the second test texture at the point of subjective equality (PSE). Adaptation to decreases, however, should be manifest as a lowered value of the adapted property in the second texture at PSE. As in Experiment 1, all staircases terminated after eight 'turns' in the staircase, and the mean value of the final six turns was used to estimate the PSE. Aftereffect scores were collapsed across duplicate staircases and standard values by averaging either arithmetic differences in contrast at PSE or logarithmic differences in density at PSE, consistent with Experiment 1.

3.2. Results and discussion

The PSE values for density and for contrast were independently subjected to a repeated-measures ANOVAs, with Direction of Adaptation (Increase or Decrease) and Eye of Test (Adapted or Other) as within-observer variables. As in Experiment 1, our principle interest is in characterizing patterns of interocular transfer for each property, but this time for dynamic aftereffects of contrast and density.

3.2.1. Dynamic aftereffects of apparent contrast

The mean PSE contrast deviation values are shown in Fig. 5. Because the second-appearing texture was always the one adjusted via the staircase, a raised physical contrast at PSE is expected following adaptation to a contrast increase, whereas a lowered physical contrast at PSE is predicted following adaptation to a contrast decrease. Consistent with the predicted monocularity of the dynamic contrast aftereffect, the repeated measures ANOVA showed that Direction of Adaptation produced different effects, depending on the Eye Tested, [$F(1,4) = 14.8$, $P < 0.05$]. This statistical interaction required that separate analyses be carried out for each eye. Indeed, the predicted patterns of deviations from objective equality held true for the Adapted Eye: the contrast deviation at PSE was higher following CI adaptation ($+3.2$ contrast units) than following CD adaptation (-3.4 contrast units), [$t(4) = 5.39$, $P < 0.01$]. For the stimuli presented via the other eye, however, there were no reliable differences between the PSE deviations in the CI condition (-0.96 contrast units) and the PSE deviations in the CD condition (-0.32 contrast units), [$t(4) = 0.404$, $P > 0.10$]. Indeed, the deviations are tiny and in the wrong direction. Overall, then, it would appear that dynamic contrast aftereffects are exclusively monocular, just as was Anstis' (1967) dynamic luminance aftereffect. This is, of course, roughly consistent with the predominant monocularity of the simple contrast aftereffects reported in Experiment 1.

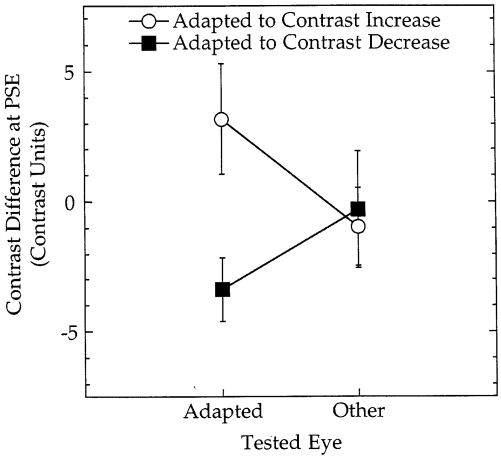

Fig. 5. Deviations at the points of subjective (sequential) equality are shown following dynamic contrast adaptation to increases and to decreases in contrast as a function of tested eye (Experiment 2). Average data for five observers are shown. Error bars depict standard errors of the means.

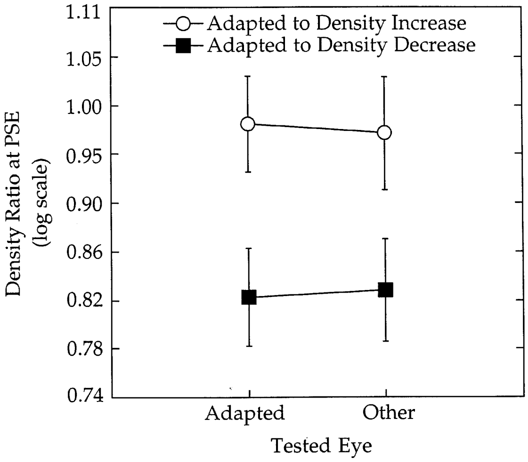

Fig. 6. Ratios of deviations at the points of subjective (sequential) equality are shown following dynamic density adaptation to increases and to decreases in contrast as a function of tested eye (Experiment 2). Average data for four observers are shown. Error bars depict standard errors of the means.

3.2.2. Dynamic aftereffects of perceived density

The geometric mean PSE density deviation ratios are shown in Fig. 6 (based on logarithmic differences). Consistent with the predicted binocularity of the dynamic density aftereffect, there was only a marginal statistical interaction between Tested Eye and Direction of Adaptation in the repeated-measures ANOVA, [$F(1,3) = 6.64$, $P = 0.082$]. In fact, as is evident from Fig. 6, for both eyes, the PSEs were reliably higher in the DI condition [-0.024 LUD or ln(0.98)] than the DD condition [-0.194 LUD or ln(0.82)], [$F(1,3) = 50.4$, $P < 0.01$]. Overall, then, it would appear that dynamic density aftereffects are predominantly binocular. This is consistent with the predominant binocularity of the density aftereffects found in Experiment 1.

It is unclear why dynamic density PSEs appear to be shifted downward. However, Durgin and Hammer (2001) observed the same phenomenon.

4. General discussion

Overall, there are striking and important analogies between adaptations of texture density and of texture contrast. Both visual properties show simple aftereffects and dynamic aftereffects. However, the patterns of interocular transfer of these aftereffects are consistent with the involvement of two separate systems. Contrast

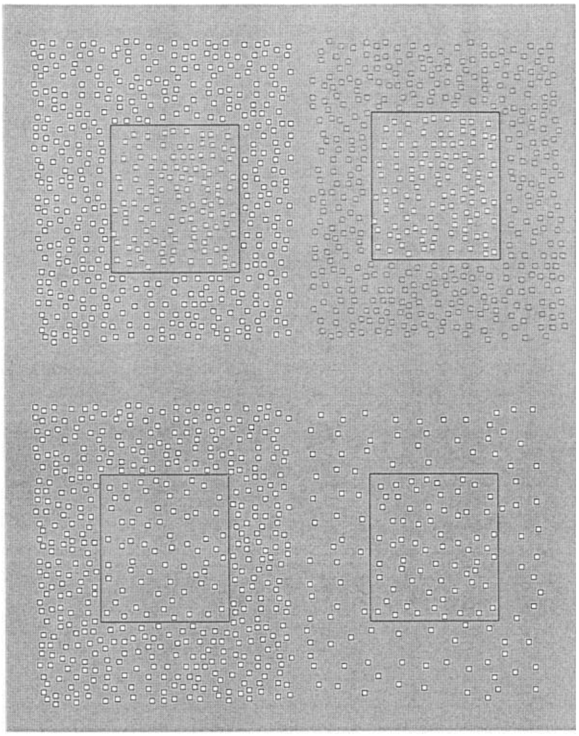

Fig. 7. Illustrations of simultaneous contrast of texture contrast (Chubb et al., 1989) and of texture density (Durgin & Proffitt, 1991). Although the inner textures in the top panels are of equal contrast, the one on the left may appear to be somewhat lower in contrast than that on the right because of the differences in contrast of the surrounding textures. Similarly, the two inner textures in the lower figure are physically identical, but the one on the left appears less dense because it is surrounded by a relatively dense texture. If the centers and surrounds of such figures are combined dichoptically, no effect is observed for texture contrast, but simultaneous contrast of texture density persists. Note that reproduced textures do not, unfortunately, maintain appropriate luminance balance or contrast values.

normalization (simultaneous contrast of contrast) is likely the result of interactions among monocular simple cells (e.g. Heeger, 1992), and it is not unreasonable to imagine that similar cells may be involved in successive contrast effects of contrast, as well as dynamic contrast adaptation. However, the substrate for density adaptation is clearly predominantly binocular. I will argue below that texture density normalization may involve lateral interactions at a second stage of processing which is quite analogous to contrast processing — except that it operates on a rectified signal.

4.1. *Simultaneous effects of texture contrast and texture density*

Before proceeding, however, let us consider one further observation. Chubb et al. (1989) reported that the lateral interactions that produced simultaneous contrast of texture contrast were monocular. Dichoptic combination of the center texture in one eye and the inducing surround in the other eye produced no contrast illusion. This same finding can be observed using balanced-dot textures with varied contrast such as I have employed throughout this paper, as illustrated in Fig. 7. What about simultaneous contrast of texture density? Durgin and Proffitt (1991) reported a 15% simultaneous contrast illusion of texture density using balanced-dot textures. Although I have not completed a formal study, I have observed with several naïve observers that presenting the inducing textures to one eye and the center textures to the other does produce a dichoptic simultaneous contrast illusion of texture density.

4.2. *Toward a model for texture density encoding*

In addition to the evidence of the present paper, there are two other kinds of experimental evidence that should help constrain the development of a model of density encoding. Durgin (1996) has demonstrated that texture density is also susceptible to aftereffects contingent on surrounding color. This McCollough-like effect is consistent with a peripheral locus of density encoding (see Humphrey, 1998, for a comprehensive review). Moreover, Durgin and Huk (1997), have shown that texture density aftereffects are relatively blind to orientation and spatial frequency, suggesting that density may be computed, or in parallel with spatial-frequency analyses, pooling across orientations and scales. Durgin and Cole (1997) have found that density aftereffects, like many other kinds of early adaptation, can occur, with little disruption, under conditions of binocular suppression of the adapting texture. These findings suggest an 'early' locus of adaptation, like V1, while also demanding that the locus be composed of cells that are primarily binocular.

I have developed a preliminary model of density encoding that is based on models of contrast normalization in V1 (e.g. Heeger, 1992, 1994; see also Albrecht & Geisler, 1991; Geisler & Albrecht, 1992). Barlow (1978) argued that texture density was the simplest statistic of a texture, but it is not quite so easy to compute that statistic when the elements composing the texture are not known in advance. A working model of texture density must be able to compute roughly the same output density for equally dense texture composed of a variety of texture elements independent of their contrast, for example. When divisive normalization is applied to complex cells, this amounts to encoding the variance of the outputs of simple cells. Exploration of this model is beyond the scope of this paper. However, I have observed that such a computation produces equivalent output for textures that have the same density of texture elements, no matter what the individual elements are. That is, this kind of model tracks density independent of luminance, contrast, and (with some restrictions) element size or structure.

The computations required to encode density are no more complex than what might be encoded at the level of a complex cell. This sketch of a model and the interocular-transfer data primarily serve to rule out certain loci for density adaptation. Apart from differential sensitivity to eye-of-origin, contrast and density seem quite similar (e.g. both are scalar dimensions subject to simple and dynamic aftereffects, as well as simultaneous contrast, etc.). It therefore seems reasonable to suppose that texture density might be encoded at a fairly early stage.

4.3. Suprathreshold contrast aftereffects

Blakemore et al. (1973) argued that suprathreshold contrast reduction was a manifestation of the same underlying process of adaptation that results in tilt aftereffects, spatial-frequency-specific threshold elevation, and, by extension, spatial-frequency shift aftereffects. Klein, Stromeyer, and Ganz (1974) argued that suprathreshold spatial frequency shift aftereffects were different than contrast elevation, and a number of more recent studies have challenged the view that suprathreshold aftereffects of perceived contrast are similar in etiology to threshold elevation. For example, the spatial frequency and orientation tuning of suprathreshold contrast aftereffects is quite different from that of threshold elevation (Snowden & Hammett, 1992, 1996). Snowden and Hammett (1996) also failed to find interocular transfer of contrast aftereffects.

Suprathreshold contrast effects may only represent the adaptation of monocular channels, whereas threshold elevation and spatial-frequency shift aftereffects show substantial interocular transfer (Blakemore, Nachmias, & Sutton, 1970; Meyer, 1974; Bjørklund & Magnussen, 1981). Ross and Speed (1996) have contested Snowden and Hammett's (1992) conclusions, and suggest that the observers may have confounded apparent brightness with apparent contrast. However, it is unclear exactly what the significance of this criticism is and whether a similar criticism could make sense for balanced-dot textures. At higher contrast, the individual elements in a balanced-dot texture seem to (and do!) have brighter centers, but the luminance values of the annuli are also darker. That is what perceived contrast means. Ross and Speed claim to have obtained different results than Snowden and Hammett (1992) by ignoring how dark the bars were in their gratings and to have judged true contrast (they did not examine interocular transfer). It is not self-evident what were they judging, but their ability to make such a distinction may be related to differences between sinusoidal stimuli and non-periodic stimuli. In the present experiments we have employed naïve observers who made judgments based on what they saw in non-periodic stimuli. Their judgments were presumably based upon the apparent brightness of the dots, but that is as it should be.

Note that interpreting suprathreshold contrast aftereffects mechanistically may not take sufficient account of the functional role of contrast adaptation in the scaling of lightness perception (e.g. Gilchrist, Kossyfidis, Bonato, Agostini, Cataliotti, Li, Spehar, Annan, & Economou, 1999). The apparent broad tuning of contrast normalization and adaptation may be related to the functional role of perceived contrast scaling. Although the monocularity of these effects may be of some anatomical importance in understanding how contrast gets scaled, it may also reflect a functional advantage to scaling the front-end inputs of each eye independently.

4.4. First-order and second-order aftereffects

Laming (1986, 1991) has pointed out that reason that the threshold for the detection of increments is much higher than that for gratings is that increments represent a powerful stimulus only for the 'first analytic stage' — which he identifies with simple cells. This is consistent with studies of dichoptic masking (Legge, 1979), suggesting that this first analytic stage is monocular. Add to this the finding by Fiorentini, Sireteanu and Spinelli (1976) that threshold elevation effects for gratings are predominantly binocular, whereas those to simple lines are predominantly monocular, and a consistent picture starts to emerge that suggests that threshold elevation effects are not exclusively the domain of first order units. Since threshold elevation is generally found to be about 66% binocular, the effect may, in fact, be due to the adaptation of first-order and second-order units.

The strong bias to suppose that aftereffects of perceived contrast are directly related to threshold elevation effects is not fully motivated — certainly not for contrast aftereffects for non-periodic stimuli. In fact, the opposite view is well motivated by the clear monocularity of both simultaneous versions (Chubb et al., 1989) and successive versions (Snowden & Hammett, 1996; Experiment 1, this paper) of contrast-contrast.

It might be argued that the monocular contrast aftereffects measured here are actually retinal luminance aftereffects, rather than cortical contrast aftereffects, and Georgeson (1991) has made some interesting arguments about afterimages as combinations of cortical contrast and retinal luminance effects. However, his arguments apply only to steadily fixated stable patterns, and seem still to require that cortical contrast aftereffects are monocular (so as not to turn up in the contralateral eye). The textures adapted to here were newly randomized scatters on each presentation, which argues against an afterimage interpretation (though not against a retinal interpretation). None the less, it is possible that the center-surround character of these elements has contrast-adapted appropriate cells in LGN.

Whitaker, McGraw, and Levi (1997) have studied aftereffects of perceived position using luminance-defined stimuli as well as contrast-defined stimuli. Their conclusion is that only the contrast-defined location aftereffects show interocular transfer of these position aftereffects. It would seem equally appropriate to argue that *perceived* contrast is defined by luminance differences (e.g. the variance or standard deviation of luminance), whereas second-order properties like density are defined by *variations* in local contrast energy across space. That is, perceived location is a property that can be computed upon luminance or contrast (e.g. a centroid — cf. Whitaker et al., 1997), whereas perceived contrast itself is a property computed upon variations in luminance. Thus, consistent with the findings of Legge (1979) and Fiorentini et al. (1976), as well as the views of Laming (1986, 1991), Whitaker et al. (1997)(cf. McGraw, Levi, & Whitaker, 1999) may be interpreted as further evidence that first-order computations may be primarily monocular, whereas second-order computations are primarily binocular. Perceived contrast is apparently a first-order property.

4.5. What has been dissociated from what?

One goal of the present paper was to show that density aftereffects were not simply aftereffects of contrast energy. This was accomplished by manipulating contrast energy independently of density. However, a secondary outcome of these studies is support that aftereffects of perceived contrast are not equivalent to contrast threshold elevation effects (Snowden & Hammett, 1996), because they are monocular. Threshold elevation effects are predominantly binocular. Thus, the present data may not bear directly on the question of whether threshold elevation is itself responsible for density aftereffects.

None the less, Durgin and Huk (1997) did dissociate spatial frequency and density adaptation, and showed that the tuning for density adaptation is rather broad (though not flat). In so far as tuning for threshold elevation is not broad (monocularly or binocularly — Bjørklund & Magnussen, 1981), density adaptation and threshold elevation clearly differ.

The broadband character of texture density adaptation (Durgin & Huk, 1997) may be regarded as analogous to the apparently broadband character of contrast adaptation (Snowden & Hammett, 1996). Certainly, the common susceptibility to dynamic adaptation suggests there may be important analogies between perceived contrast and perceived texture density. Texture density may reflect texture energy (a second-order property), rather than contrast energy, but the two processes seem highly analogous otherwise.

Further work needs to be done, but the results presented here suggest that separate effects on first-order and second-order contrast processing may underlie these two kinds of suprathreshold gain control in early vision.

4.6. Conclusions

The evidence from the experimental studies reported here suggests that texture density encoding is a primarily binocular process, whereas perceived-contrast encoding is primarily monocular. Comparisons between these dimensions have been reported for successive contrast (simple adaptation) as well as for dynamic adaptations to biased sequences (see, also, Durgin & Hammer, 2001). I have also discussed simultaneous contrast effects of these dimensions. Although density and contrast may interact, density aftereffects are clearly not reducible to texture contrast or luminance adaptation. It seems likely that texture density is initially encoded as what might be called second-order contrast (the variability of the luminance-variability or texture energy), computed at a binocular stage following monocular processes of contrast normalization in space and time.

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