Contrasting the processes of texture segmentation and discrimination with static and phase-reversing stimuli

L.J. Norman *, C.A. Heywood, R.W. Kentridge

Department of Psychology, University of Durham, Durham DH1 3LE, United Kingdom

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ABSTRACT

Regions of visual texture can be automatically segregated from one another when they abut but also discriminated from one another if they are separated in space or time. A difference in *mean orientation* between two textures serves to facilitate their segmentation, whereas a difference in *orientation variance* does not. The present study further supports this notion, by replicating the findings of Wolfson and Landy (1998) in showing that judgments (odd-one-out) made for textures that differ in mean orientation were more accurate (and more rapid) when the textures were abutting than when separated, whereas judgments of variance were made no more accurately for abutting relative to separated textures. Interestingly, however, responses were overall faster for textures differing in variance when they were separated compared to when they were abutting. This is perhaps due to the clear separation boundary, which serves to delineate the regions on which to perform some regional estimation of orientation variance. A second experiment highlights the phase-insensitivity of texture segmentation, in that locating a texture edge (defined by a difference in mean orientation) in high frequency orientation-reversing stimuli can be performed at much higher frequencies than the discrimination of the same regions but with the texture contour masked. Textures that differed in variance did not exhibit this effect. A final experiment demonstrates that the phase-insensitive perception of texture borders improves with eccentric viewing relative to the fovea, whereas perception of the texture regions does not. Together, these experiments show dissociations between edge- and region-based texture analysis mechanisms and suggest a fast, sign-invariant contour extraction system mediating texture segmentation, which may be closely linked to the magnocellular subdivision of visual processing.

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1. Introduction

Natural scenes contain contours, which separate figures from their ground or represent discontinuities in object surfaces. These are typically associated with spatial gradients in chromaticity or luminance, although contours can also be perceived as a result of spatial changes in texture in the absence of such cues. This occurs very noticeably when two abutting textures differ in the mean orientation of their textural elements (see Bergen, 1991; Nothdurft, 1991; Thielscher & Neumann, 2003). Although the strength of the border's perception is dependent on the orientation noise within the stimuli (Motoyoshi & Nishida, 2001), generally the greater the contrast, the more compelling the border (Nothdurft, 1991).

This process of contour localisation allows effortless texture segmentation to occur. The rapidity of this process is highlighted in a number of psychophysical and neurophysiological findings. Motoyoshi (1999) showed that when a uniform texture was presented briefly and followed by a smaller mask, the textured area

within the mask would be suppressed and the overall perception would be that of a uniform texture with a 'hole' in the centre. Importantly, however, if the texture contained an orientation discontinuity within the area of the mask, this region survived the mask's effect. Additionally, Lamme, Rodriguez-Rodriguez, and Spekreijse (1999) found single-cell evidence in the awake macaque of a response enhancement at the location of an orientation contrast that occurred prior to any location within the regions of the textures themselves. The largest response latencies were recorded for regions farthest away from the contours. Similar findings were recorded by Romani et al. (1999) using visual evoked potentials, which, together, corroborate with Motoyoshi (1999) in suggesting the workings of a texture analysis mechanism that prioritises locations of contrast relative to regions of uniform texture.

This process of edge-based texture perception is thought to be achieved first through the application of first order orientation-specific filters in the visual system, whose outputs are then transformed through a second stage non-linearity. A final stage of linear filtering is then conducted on this output with larger receptive fields than those of the first, and is sensitive to the location of any spatial gradient in the orientation-defined texture (see Bergen,

* Corresponding author. Fax: +44 (0) 191 3343241.
E-mail address: liam.norman@dur.ac.uk (L.J. Norman).

1991, for a detailed review of such a model). The output of the filtering is such that a peak response is created at the location of contrast. In other words, the process of segmentation based on orientation contrast, and potentially texture segmentation more generally, is *edge-based* (Wolfson & Landy, 1998).

The term *segmentation* is often reserved for the description of the processes of edge-based mechanisms, whereas the term *discrimination* is most often applied to instances in which an observer is able to discern two textures despite the absence of an informative boundary (Landy & Graham, 2004). These instances arise either when spatial or temporal separation of the textures prevents their segmentation, or by the presence of a texture difference that is not well suited for the filter-rectify-filter process. The mechanisms underlying this process are described as being *region-based* and require the integration of spatially distributed local signals to attain an informative statistical measurement of the composition (Dakin & Watt, 1997; Wolfson & Landy, 1998). This statistical analysis is essential to our consistent perception of visual texture more generally, as comparison on a pixel-by-pixel basis would be too unreliable and heavily dependent on various viewing conditions (e.g. viewing angle, lighting, and distance; Adelson, 2001) if we are to recognise one instance of texture as belonging to a particular category (e.g. sand, granite or woodchip). Indeed, Portilla and Simoncelli (2000) have shown that new instances of a particular texture can be successfully generated on the basis of statistical representations garnered from a sample image (e.g. from the responses of orientation and spatial frequency filters and correlations between such filters). One example of a simple image statistic that has been studied in relation to visual texture is that of orientation variance. Spatial discontinuities in orientation variance are detected poorly by a filter-rectify-filter process (Wolfson & Landy, 1998), as the average orientation on either side of the border is constant. Dakin and colleagues (Dakin & Watt, 1997; Dakin, 2001) have shown that observers' judgments of orientation variance were both accurate and flexible, being dependent on the characteristics of what is being perceived. Additionally, Morgan, Chubb, and Solomon (2008) have outlined a 'dipper' function in the representation of orientation variance in visual texture that may be evidence of intrinsic noise resulting from a dedicated mechanism in the visual system for the computation of visual texture. Thus, two very distinct mechanisms appear to exist; one which prioritises the extraction of texture-defined contours, and one which estimates statistical properties within a region.

Wolfson and Landy (1998) took the approach of directly comparing and contrasting these mechanisms. They showed that when two patches of texture differed in mean orientation, then observers were more sensitive to the difference if the patches were abutting than if they were separated. When the patches differed in variance, however, no such effect was observed. This is indicative of a second-order image statistic (i.e. orientation variance) being associated with a region-based mechanism; in other words not related to texture segmentation, but more related to the discrimination of a texture's *appearance.* A trend was also found in a subset of their participants that discriminations based on differences in variance were actually greater when the patches were *separated.* This was theorised to be due to the role that a separating boundary might have played in delineating the areas on which to perform the regional analysis (in this instance, variance estimation).

The aim of the first experiment was to replicate the findings of Wolfson and Landy (1998) but also to correct for a potential confound in their experiment: their stimuli were composed of randomly positioned line segments and thus were allowed to overlap. This created a larger quantity of "line crossings" in textures of high variance, a cue that observers could have used to discern variance independently of any computation of orientation statistics (Julesz, 1981). Although Wolfson and Landy (1998) discussed this and dismissed it, no experimental evidence has yet to be presented which directly addresses this point, and data collected from experiments using such stimuli may reveal more clearly the workings of region-based texture analysis mechanisms. This confound is prevented in the present study by using structurally placed Gabor patches that do not overlap. It is predicted that for odd-one-out judgments based on a difference-in-mean, accuracy would be higher for abutting patches than for separated patches of texture. Conversely, no effect is predicted for discrimination based on a difference-in-variance. In addition, the first experiment extends Wolfson and Landy's (1998) findings by measuring reaction times (RTs) on the same task, predicting that when accuracy is greatest for abutting textures relative to separated textures in the case of detecting a difference-in-mean, RTs would also be shorter. Conversely, no decrease in RTs for detecting a difference-in-variance is expected, although RTs are expected to be faster for separated textures, as the separation may serve to clearly define the regions on which to perform regional estimations of variance.

2. Experiment 1

2.1. Material and methods

2.1.1. Participants

Twenty participants (11 male, 9 female) took part in all conditions of this study. All subjects had normal or corrected-to-normal vision. All gave written informed consent to take part and were compensated financially for their time.

2.1.2. Stimuli

The display monitor was viewed at a distance of 41 cm (subjects rested their head on a chin rest). Stimuli were presented on the uniform grey background of a gamma-corrected ViewSonic 17″ (1254 × 877 pixels) colour monitor positioned on its side and driven by a Cambridge Research Systems VSG 2/5 Graphics System.

The experimental stimuli consisted of three regions of texture presented in a vertical alignment 0.5° to the right of fixation (a fixation cross subtending 0.3° × 0.3°). Each was constructed of 240 evenly positioned Gabor patches in a 24 (across) × 10 (down) rectangular arrangement. Each individual Gabor patch had a spatial frequency of 3 cycles/° and was generated with a common cosine phase such that the pivotal centre of each Gabor patch contained a dark band. Each measured 0.5° in diameter and was separated from its neighbours by a distance of 0.3°. Thus, each patch of texture covered a total area of 27.0° × 17.7°. Gabors had a 100% luminance contrast. It was decided that the locations of the Gabors were to be fixed rather than randomly distributed to avoid any potential confounds of "line crossings" that would occur with an increase in variance.

The orientation of each individual Gabor patch was independently drawn from a Gaussian distribution of a particular mean (μ) and variance (σ^2) associated with its relative texture patch. In all trials, a 'pedestal' patch was created with the parameters $\mu = \alpha$ (where α is a randomly determined orientation between 0° and 360° cycle) and $\sigma^2 = 5^2$. In a difference-in-mean trial, a second patch was created with the parameters $\mu = \alpha \pm x$ and $\sigma^2 = 5^2$ (where x is the degree of orientation difference for that trial, i.e. $x = 2, 5, 8, 11, 15$ or 20). In a difference-in-variance trial, the second patch was created with the parameters $\mu = \alpha$ and $\sigma^2 = (5 + y)^2$ (where y determines the degree of variance difference for that trial, i.e. $y = 0.75, 1.25, 2, 3.75, 5$ or 7.5, thus creating variance differences of 8.1, 14.1, 24, 51.6, 75 and 131.3). In both types of trial, the third patch was constructed with the same parameters as either the pedestal patch or the second patch such that the odd texture was equally likely to be the pedestal patch or not.

2.1.3. Procedure

Trials were completed in two blocks, each defined by the adjacency of the textures: in one block (the *abutting* condition), the patches were adjoining such that the distance between each patch of texture equated the distance between the Gabor patches within each texture patch (0.3°). In another block (the *separated* condition), the patches of texture were separated vertically by a distance of 0.5° between each one, thus creating the impression that there were three isolated patches of texture one atop the other (see Fig. 1). Additionally, on each trial, the position of the stimuli was randomised such that the whole display was equally likely to be shifted 0.9° either above or below fixation level or not at all. This was designed to prevent the observer from anticipating the exact location of the textures and thus from pre-empting the position of the border.

In each trial, two of the textures were given the same appearance (by drawing their composite orientations from the same Gaussian distribution as one another). The third texture (the 'odd' texture) was equally likely to appear at the top or bottom of the arrangement, but never in the centre. This patch of texture was made conspicuous compared to the others by changing either the *mean* or *variance* of the distribution from which its orientations were drawn. See Fig. 1 for examples of each type. For each type of texture difference (difference-in-mean/variance), there were six difference levels. They were, for a difference in mean, 2°, 5°, 8°, 11°, 15° and 20°, and, for a difference in variance 8.1, 14.1, 24, 51.6, 75 and 131.3. For each block of trials corresponding to each condition of texture adjacency (abutting/separated) there were two conditions of texture difference (difference-in-mean/difference-in-variance) × 6 difference levels × 8 repetitions. Thus there

were 96 trials per block per subject. It should be noted that the order of trials was randomised within each block, ensuring that for each given trial subjects could not anticipate the type of parameter that was to define the "odd" texture from the rest (i.e. whether it was a difference-in-mean or difference-in-variance). This adds a particular level of task uncertainty for the subjects and so reduces any variation in how they might approach the different discrimination types; in other words, they are not able to adopt a preferred strategy over the course of one block of trials that would selectively appeal to discriminating difference-in-mean or difference-in-variance textures. The presentation order of the blocks was also counterbalanced across participants.

Thus, there were four conditions of the experiment, with each containing six levels of difference

1. Patches are abutting, with a difference in mean.
2. Patches are abutting, with a difference in variance.
3. Patches are separated, with a difference in mean.
4. Patches are separated, with a difference in variance.

Fig. 1 shows examples of each of these four types of stimuli.

The stimuli were presented for 5 s or until a response was made. A fixation cross appeared 2 s prior to the onset of the stimuli and remained until a response was made. Subjects were instructed to fixate the cross whenever it was present and to respond as accurately and as quickly as possible in a two-alternative forced choice paradigm by pressing the appropriate key (top or bottom) to indicate the odd texture. Responses were made on a 5-button Cedrus Response Box (Cambridge Research Systems) with the subject's right hand. The next trial would not begin until a response had been collected and a 2 s inter-trial interval was included. Accuracy and reaction times were measured. Stimuli were presented to the right of fixation.

2.2. Results

Fig. 2 shows the data from Experiment 1. To reduce the noise in the data, the lowest two difference levels were excluded for both the difference-in-mean and difference-in-variance conditions, as participants' accuracy did not rise above chance performance, leaving four levels of difference in each condition. RTs that exceeded 4 s were removed from analysis along with any remaining values that fell outside two standard deviations of the mean per condition per subject. This removed no more than 9.5% of all cases. Planned comparisons were performed by isolating either the mean or variance discriminations for either the accuracy or RT measurements. Thus, four 2 × 4 within-subject ANOVAs were carried out on these data with the factors of texture adjacency ('abutting' vs. 'separated') and level of difference, respectively. Each of these will be discussed in turn. In all of these analyses, the main effect of difference level reached significance (all F values > 20) and thus is omitted in all cases from the report to aid concision.

Accuracy data for difference-in-mean stimuli (Fig. 2a): No significant effect of texture adjacency emerged ($F(1, 19) = 3.365$, $p = 0.082$), but there was a significant interaction between the two main effects ($F(3, 57) = 3.159$, $p = 0.031$). As subsequent paired t-tests showed, no difference in accuracy was found between odd-one-out judgments of abutting and separated textures at the lower levels of difference, specifically 8° ($t(19) = 1.20$, $p = 0.245$) and 11° ($t(19) = -1.555$, $p = 0.137$). Higher accuracy rates, however, were found for judgments of abutting- relative to separated-textures at 15° ($t(1, 19) = 2.106$, $p = 0.049$) and 20° ($t(1, 19) = 2.963$, $p = 0.008$) with differences of 8.2% and 6.8%, respectively.

Accuracy data for difference-in-variance stimuli (Fig. 2b): No significant effect of texture adjacency emerged ($F(1, 19) = 0.142$, $p = 0.710$) and there was no evidence of an interaction
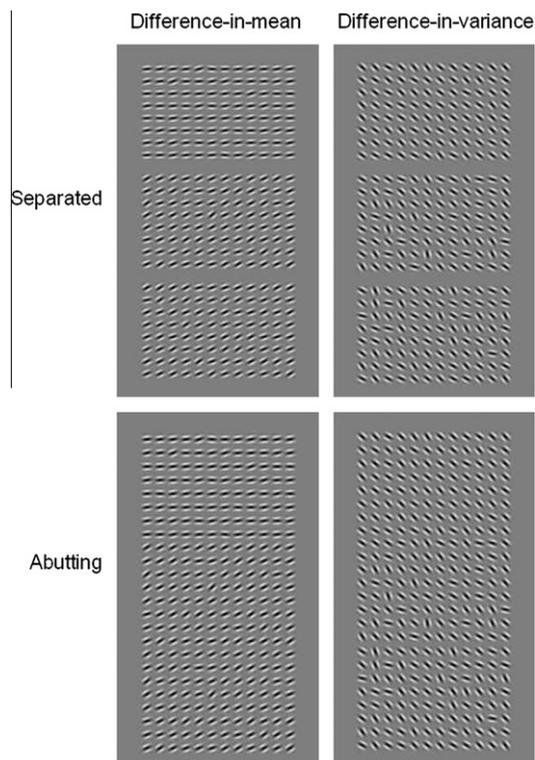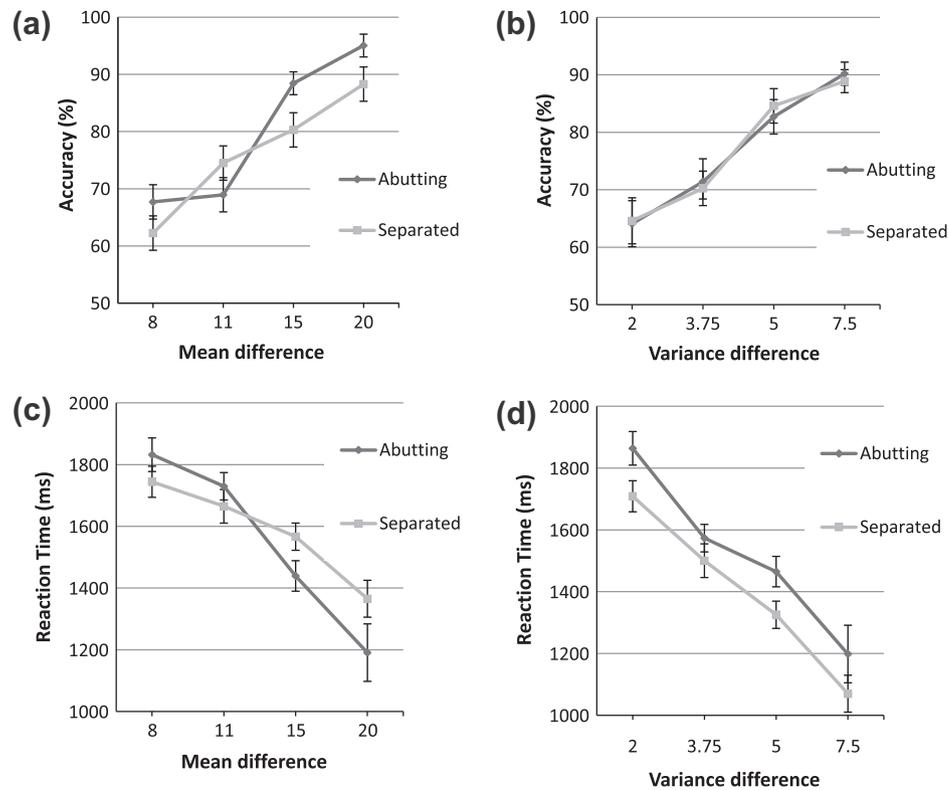

Fig. 1. Replications of the stimuli used in the four conditions of Experiment 1. Each window shows three equally sized textures either *abutting* or *separated* vertically from one another. The task required observers to indicate the "odd-one-out". The odd texture would either be due to a *difference-in-mean* or a *difference-in-variance* in the orientation statistics used to generate each texture. Thus, in the figure, the top texture in each of the quadrants is the odd-one-out. Stimuli were presented slightly to the right of a small fixation cross. Note that the textures in the illustration are a reduction in size of the actual stimuli used.

Fig. 2. Results from Experiment 1. (a and c) Accuracy and RT data for difference-in-mean discriminations for either abutting or separate textures. (b and d) Accuracy and RT data for difference-in-variance discriminations for either abutting or separated textures. All are shown as a function of increasing difference level. Error bars show ±1 SEM with between-subject variance omitted.

($F(3, 57) = 0.112$, $p = 0.947$). Note the extreme similarity between the plots in Fig. 2b compared to those in Fig. 2a. These data indicate that subjects' accuracy for odd-one-out judgments based on orientation variance did not improve with abutting textures relative to separated textures.

RT data for difference-in-mean stimuli (Fig. 2c): No significant effect of texture adjacency ($F(1, 19) = 0.213$, $p = 0.649$) was found, but a significant interaction emerged ($F(3, 57) = 3.334$, $p = 0.026$). Subsequent paired sample t-tests revealed no difference in RT for odd-one-out judgments of abutting and separated textures at any level of the difference in mean orientation (all p values > 0.1), however, although Fig. 2c clearly shows a trend that is consistent with the accuracy data (Fig. 2a); at higher difference levels (15° and 20°) responses were faster when the textures abutted compared to when they were separated, but this effect was not present at lower levels of difference, which in fact show the opposite effect. It is important to note at this point that there is no evidence that subjects showed a speed-accuracy trade-off; neither did they make more accurate judgments by delaying their RT and nor did they make quicker decisions through sacrificing accuracy.

RT data for difference-in-variance stimuli (Fig. 2d): A significant effect of texture adjacency ($F(1, 19) = 4.437$, $p = 0.049$) was found, in which subjects were, on average, quicker by 124.01 ms to judge separated textures than abutting textures. No significant interaction emerged ($F(2.061, 39.16) = 0.190$, $p = 0.83$; Greenhouse–Geisser corrected). Again, no evidence of a speed-accuracy trade-off was found.

3. Interim discussion

The results support Wolfson and Landy's (1998) conclusions by showing that accuracy increased for judgments made based

on mean orientation when the textures abutted compared to when they were separated (although only at the higher levels of difference). This was further supported by the finding that when accuracy was greater for abutting textures, RT was also faster, rather than subjects trading speed for accuracy. Contrarily, when subjects were not significantly more accurate, they were, if anything, slower. This is consistent with the detection of a difference in mean orientation being well suited for a fast contour-detection system that has been outlined in both the psychophysical and neurophysiological literature (e.g. Motoyoshi, 1999; Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999; Romani et al., 1999). Importantly, however, there was no such elevation in accuracy for judgments based on variance; performance was remarkably similar between the two conditions. This is because on either side of the boundary between the textures, the average orientation is the same and so a filter-rectify-filter process tuned to orientation would elicit very weak responses at this location of contrast. Perhaps the most intriguing finding, however, is that judgments based on differences-in-variance were made more rapidly for separated textures compared to those abutting. Wolfson and Landy (1998) briefly discussed that it might be expected that subjects would perform better on judgments of variance if the patches were separated, suggesting that the separation of the textures serves to clearly delineate the regions to be discerned. The flexible "region of integration" of orientation signals associated with variance estimation (Dakin & Watt, 1997; Dakin, 2001) may indeed benefit from the clear border definitions offered by the separation of the textures. In the present experiment, however, this is an effect which manifested clearly in measurements of RT but not accuracy. Given different instructions, and perhaps limited stimulus presentation durations, subjects may have shown significantly greater accuracies in the separated relative to the abutting condition.

The notion of a fast edge-based mechanism of texture segmentation is explored further in experiments two and three. Specifically, is rapid texture segmentation by orientation contrast a result of phase-insensitive magnocellular processes? The cells of the magnocellular subdivision of visual processing (M cells) exhibit high temporal and low spatial sensitivity, as well as being adept at discriminating motion but being blind to colour identity. This is in stark contrast to the slower parvocellular system, which is more attuned to spatial detail and chromatic information (Schiller & Logothetis, 1990). One important aspect of M cells is that they have the capacity to detect chromatic contrast despite their colour-insensitivity (Saito et al., 1989). So an intriguing question is whether the border that is perceived between two regions of texture that differ in mean orientation is generated by a magnocellular mechanism that signals orientation contrast without signalling the identity of the orientations themselves.

The second experiment investigated this possibility using "flicker-defined form". Using such stimuli, Rogers-Ramachandran and Ramachandran (1998) demonstrated that when two abutting fields of dots (one consisting entirely of white dots, the other black; see Fig. 3) are flickered in counter-phase above a particular frequency (roughly 7 Hz), the resultant perception is that of an implicit border separating two indistinguishable regions. Up to roughly 15 Hz (depending on various stimulus attributes), this perception of the border remains despite no conscious access to the surface information (i.e. which side is black, which is white). This particular type of stimulus is thought to isolate the phase-insensitivity of magnocellular mechanisms and has been used as a diagnostic test for its improper functioning (e.g. in cases of dyslexia, Sperling et al., 2003). The absolute effectiveness of this type of stimuli in isolating magnocellular functioning, however, is slightly contentious (see Section 7, and Skottun & Skoyles, 2006).

Assuming that texture segmentation is governed by the magnocellular system, if the orientations of two textures are reversed above a particular frequency, the texture border should be visible at a higher frequency than is possible to discern the regional texture information (i.e. the identity of the orientation either side of the border). This was assessed in the second experiment by requiring observers to locate a texture border defined by a difference in mean orientation in both the presence and absence of a coincidental black border, which masks the perception of an implicit contour that may be formed between the two regions. Thus, it is assumed that two processing mechanisms exist: *edge-* and *region-*based texture analysis, and that these processes can be dissociated in the case of the difference-in-mean condition by showing that edge-based mechanisms operate at a higher speed than their region-based counterpart. As a control, no such dissociation should exist for textures differing in variance, as judgments based on this statistic are not governed by the fast contour-extraction (edge-based) mechanism.
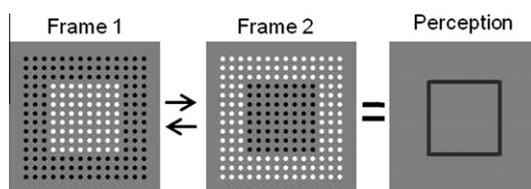

Fig. 3. Example of flicker-defined form. When the two frames shown above are presented in high frequency alternation, an implicit border can be seen between the inner and outer regions despite it being impossible to tell at any given time which is dark and which is light. Thus, when an intervening black border is placed between the two regions, the viewer cannot perceive a difference between the two regions at such high frequencies. Note that the perception shown in the figure is just an illustration, black lines are not seen.

4. Experiment 2

4.1. Material and methods

4.1.1. Participants

Three naive observers (two male) as well as one of the authors (male) took part in all conditions of the experiment. All had normal or corrected-to-normal vision and gave their full written informed consent.

4.1.2. Stimuli

This display set-up and equipment used were identical to the previous experiment.

A black fixation cross was present in the centre of the screen before and after the presentation of the stimuli. The experimental stimuli consisted of a lattice of 20×20 uniformly positioned Gabor patches (each measuring 0.6° in diameter and separated from its neighbours by 0.2°). In total, the lattice measured 14.8° in width and in height. All Gabor patches had a spatial frequency of 3 cycles/° and were each given a randomly determined phase from the full 0–360° cycle. Gabors had a 100% luminance contrast.

The textures' statistics were determined by independently drawing each composite orientation value from a Gaussian distribution with a particular μ and σ^2. For one half (the "pedestal" texture), orientations were drawn from a distribution with a randomly determined μ for that trial and a σ^2 of 10^2. In the difference-in-mean sessions, the remaining half of the lattice (the second texture) would differ in μ with a magnitude of 90°. In the difference-in-variance sessions, μ would be the same but the second texture would differ in σ^2 by a magnitude of $+26^2$.

4.1.3. Procedure

Trials were divided into four blocks. In each block, the subject's task was to identify how the lattice was bisected (vertically vs. horizontally), which was determined randomly with equal probability on each trial. Subjects completed two blocks of trials in which the lattice was divided by a difference in the mean orientation between the two textures (see top row of Fig. 4) and two in which the lattice was divided by a difference in the orientation variance (see bottom row of Fig. 4). For each of these types of stimuli, one of the two blocks of trials included the addition of two intervening black borders (separators) dividing the lattice both
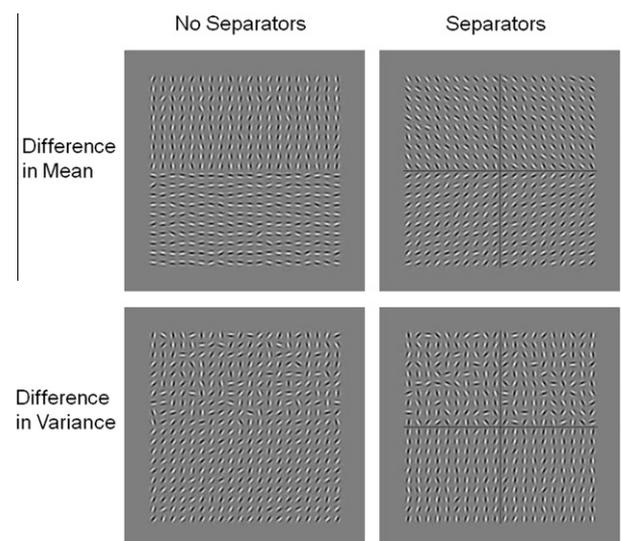

Fig. 4. Example stimuli used in Experiment 2 for each of the four conditions. In each case, the texture is divided horizontally.

vertically and horizontally at the locations at which the change in orientation statistics would coincide (see right column of Fig. 4). The separators measured only 1 pixel in thickness and 15.1° in length. This masked the effect of any subjective contour that may have been brought about by an orientation contrast. Unlike the previous experiment, the stimuli were to be placed in the centre of the visual field, so the decision was taken in this experiment to use black borders to separate the textures, as opposed to the spatial separation used in the first experiment, to control for effects of eccentricity. Thus, the four trial blocks were, with the order being counterbalanced across participants:

1. Difference-in-mean, abutting.
2. Difference-in-mean, separated.
3. Difference-in-variance, abutting.
4. Difference-in-variance, separated.

Fig. 4 shows illustrations of the stimuli used in each of the above conditions.

In each trial, two frames of stimuli were generated and presented in alternation at different levels of frequency. The first frame was generated by constructing the textures through the methods described above. The second frame, however, was generated by exchanging the orientation statistics of the two halves of texture. Note, however, that the two frames were not simply mirror images of one another; the two frames contained exactly the same orientation values, though their positions were randomised within each texture. This randomisation was designed to prevent observers from using the Gestalt principal of "common fate" to infer how the lattice was divided. For example, by witnessing a particular cluster of orientations moving together in a particular direction (e.g. left to right, or top to bottom), the way in which the textures were bisected (horizontal vs. vertical) could be inferred. This ensured that the task could only be performed on the basis of statistical computations of the orientations.

Fig. 5 shows an illustration of the sequence of events for one trial. The subject fixated centrally on the black cross before each trial. Each trial was preceded by a warning tone, after which (250 ms) the fixation cross would disappear and a mask would appear at the centre of the screen consisting of a lattice of equal size as the stimuli but consisting of randomly determined orientations. This mask would last for 25 ms before being replaced by the stimuli. The stimuli would last on screen for 800 ms, with the two textures continually flickering (appearing to change positions) at a particular frequency until the offset of the stimuli. This was followed by a second mask identical to the first one.

Following this (500 ms), a second tone signalled to the participant to make a response. Participants made a two alternative forced-choice decision, pressing one key if they thought the lattice was divided vertically and pressing another if they thought the lattice was divided horizontally. Subjects were encouraged to guess if they were unsure. Responses were made on a 5-button Cedrus Response Box (Cambridge Research Systems). No time limit was set for the collection of the response, but the next trial would not begin until a response had been collected. A 1 s interval was included between the period of collecting the response and the warning tone for the following trial, during which only the fixation cross was present.

Each block of trials consisted of four interleaved one-down two-up staircases that each began at a low frequency (4 Hz) that increased in frequency following two correct responses and decreased following 1 incorrect response. This method estimates the 70.7% correct level on the subject's psychometric function. The magnitude of the frequency increment/decrement was fixed at 1 Hz for the first 10 trials in each staircase, and then at 0.4 Hz in all subsequent trials. The staircases each terminated after 14 reversals in performance.

4.2. Results

Fig. 6 shows the data collected from Experiment 2. Data were collected at frequency levels (measured in Hz) at which subjects' accuracy at successfully judging the division of the lattice rested at 70.7%. Each staircase estimated this threshold by averaging the final 6 reversal points in performance (after a total number of 14 reversals). The values shown in Fig. 6 are the average threshold
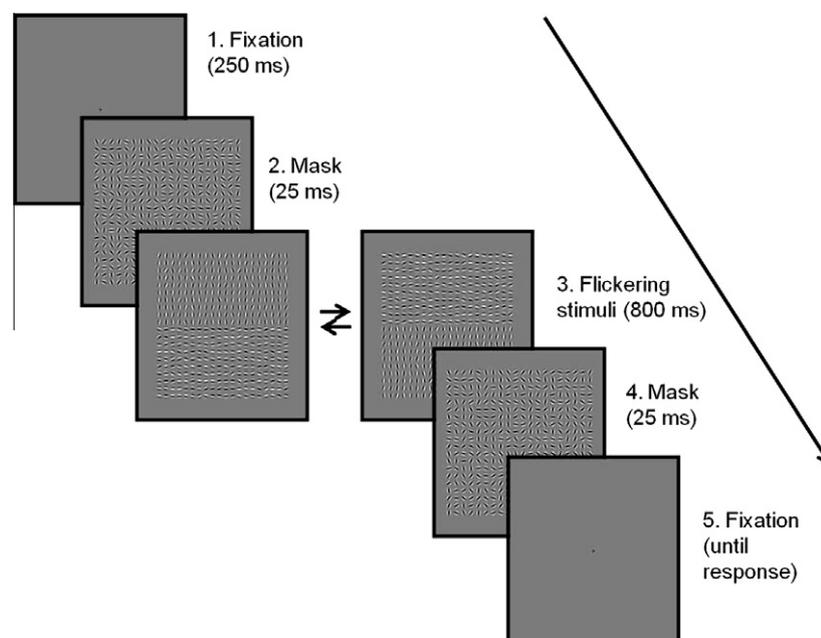

Fig. 5. The presentation of the stimuli in each trial for Experiment 2. The illustration shows an example of a trial in which a lattice was presented with a difference in mean orientation between the left and right regions. For the duration that the stimuli were displayed (in stage 3 of the illustration), the two frames were presented in alternation at a particular frequency, as indicated by the double arrow. Subjects were required to indicate whether the lattice was divided horizontally (as in this case) or vertically.
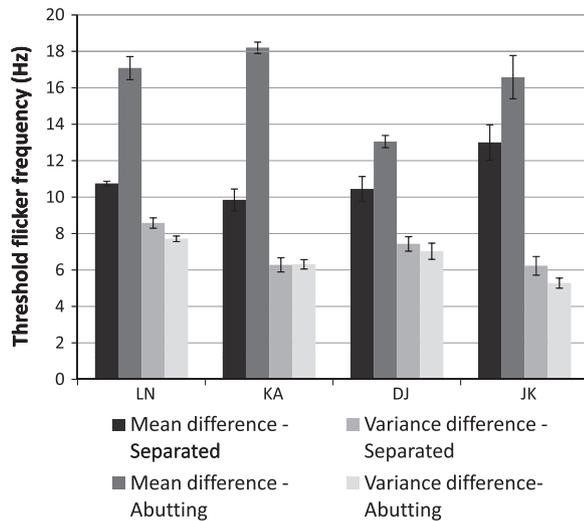
Fig. 6. Results from Experiment 2. Estimates of threshold flicker frequency for each condition per subject. Values show the frequency level at which subjects performed at 70.7% in judging the difference between two textures either based on a difference-in-mean or a difference-in-variance and either with or without the inclusion of coincident black borders at the locations of contrast. Error bars represent ±1 SEM, taken from four staircase estimates of threshold.

estimates taken from the four staircase procedures in each condition for each subject.

It is clear from Fig. 6 that, for the difference-in-mean condition, all subjects could identify the division of the abutting textures at a higher frequency compared to those that were separated with black lines. Importantly, for the difference-in-variance condition, no similar effect was observed; subjects either performed comparably in the abutting and separated conditions or reached a higher frequency, albeit marginally, in the separated condition. Because these difference-in-variance results were not found consistently for all four subjects, however, no strong inferences can be made as to whether they truly suggest better performance in the separated relative to the abutting condition. Experiment 1, however, does suggest that this is possible.

Most importantly, however, the present results strongly indicate that, like the two textures composed of black and white spots used by Rogers-Ramachandran and Ramachandran (1998), when two textures composed of orientation signals have a difference in mean orientation, the perception of an implicit border between these regions can be dissociated from that of the actual orientations on either side of the border. The fact that the perception of the border persisted to a higher frequency than that of the regional qualities is potential evidence of magnocellular processing underlying the perception of orientation contrast.

5. Interim discussion

Evidence that texture segmentation may be the result of magnocellular processing has also come from findings that the rapid detection of a figure defined by texture contrast increases with non-foveal viewing (Joffe & Scialfa, 1995; Saarinen, Rovamo, & Virsu, 1987). Generally, most visual discriminations diminish with peripheral viewing, but one characteristic of peripheral vision relative to central vision is the abundance of M cells in comparison to P cells in the retina (de Monasterio & Gouras, 1975).

The third experiment aims to show that the perception of the border alone defined by a difference in mean orientation is more readily perceived in the periphery compared to the fovea, whereas

this is not true for the perception of the regions of texture that constitute the border.

6. Experiment 3

6.1. Material and methods

6.1.1. Participants
The participants were those from Experiment 2.

6.1.2. Stimuli
The stimuli and set-up were the same as the previous experiment, although only the "difference-in-mean" conditions (with and without the separators) were used. Also, the lattice contained 10×10 uniformly positioned Gabor patches, rather than 20×20, thus measuring 8.0° in width and in height. For blocks of trials in which the subjects viewed the stimuli peripherally, the lattice would appear 5.6° to the left of the fixation cross (as measured from centre-to-centre).

6.1.3. Procedure
The general procedure was the same as the previous experiment, except that subjects completed two blocks viewing the stimuli centrally and two blocks viewing the stimuli in the periphery. As in the previous experiment, one of the blocks in each of these conditions would present the stimuli with the black separators (8.0° in length) that bisected the texture horizontally and vertically. Thus, the four trial blocks were, with the order being counterbalanced across participants:

1. Foveal viewing, abutting.
2. Peripheral viewing, abutting.
3. Foveal viewing, separated.
4. Peripheral viewing, separated.

6.2. Results

Thresholds were estimated in the same way as in the previous experiment. Fig. 7 shows these data. For all subjects, in the
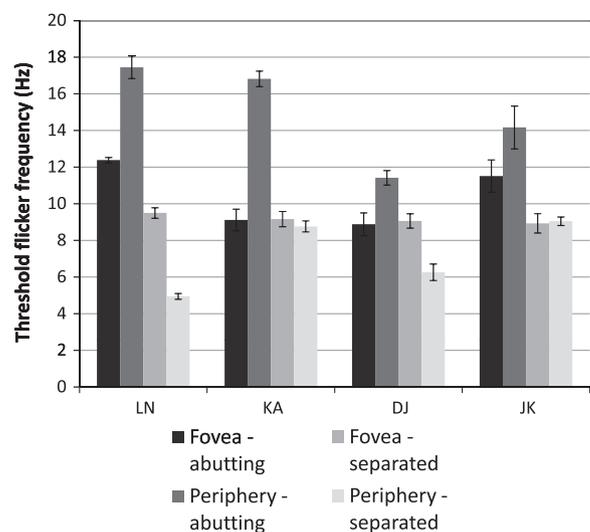

Fig. 7. Results from Experiment 3. Estimates of threshold flicker frequency for each condition per subject. Values show the frequency level at which subjects performed at 70.7% in judging the difference between two textures that differed in mean orientation either in the fovea or at 5.6° in the periphery and either with or without the inclusion of coincident black borders at the locations of contrast, taken from four staircase estimates of threshold.

abutting condition frequency thresholds were higher when the stimuli were viewed peripherally compared to when they were viewed foveally. Contrastingly, in the separated condition, for two of the subjects (KA and JK) thresholds were comparable and for the other two (LN and DJ) performance was poorer (lower frequency threshold) in the periphery. On no occasion did performance improve in the periphery relative to the fovea for separated textures, whereas it did so consistently for abutting textures.

As there are fewer M cells found in the fovea compared to the surrounding retinal area (de Monasterio & Gouras, 1975), this finding is consistent with the notion that the ability of the visual system to signal a texture border defined by orientation contrast is mediated by the magnocellular system, whereas the perception of the regions of the texture is governed by a separate, possibly parvocellular, system.

7. General discussion

The results gained from these three experiments highlight a fast, edge-based texture segmentation mechanism responsible for signalling the location of a border between two textures defined by a difference in mean orientation. Performance was more accurate and more rapid for abutting textures relative to separated ones (at high levels of difference). Additionally, when the textures were rapidly phase-reversed, the implicit border formed by the orientation contrast could be readily perceived at a much higher frequency than the perception of the orientations either side of the border. Furthermore, experiment three showed that the perception of such contours improved with non-foveal viewing, whereas the perception of the regions constituting such contours did not. This corroborates previous work that has shown texture segmentation more generally to improve in the periphery (Joffe & Scialfa, 1995; Saarinen, Rovamo, & Virsu, 1987), but additionally demonstrates that it is the perception of the texture *contour* alone that underlies this effect. These dissociations suggest separable mechanisms of edge- and region-based texture perception, and potential magnocellular involvement in the former, as some M cells have been shown to signal properties such as chromatic contrast and luminance contrast whilst remaining insensitive to the identity of the stimulus properties either side of the border (Saito et al., 1989; Rogers-Ramachandran & Ramachandran, 1998), and their relative number increases in the periphery.

It is partly questionable, however, as to whether flicker-defined-form does indeed isolate magnocellular processing. Indeed, this can only be speculated, as no study has yet recorded selective activity from an M cell in response to such stimuli. This principle is merely the result of observing the similarities between the perception of flicker-defined-form and the responses of M cells (i.e. they improve with lower spatial frequencies, are phase insensitive and improve or are more numerous in the periphery, Rogers-Ramachandran & Ramachandran, 1998; Schiller & Logothetis, 1990; Saito et al., 1989; de Monasterio & Gouras, 1975). Despite this, Skottun and Skoyles (2006) have speculated that the disparity between flicker frequencies associated with the perceptions of surface and contour information in flicker-defined-form is too large to imply a distinction between parvo- and magno-cellular processes. Rather, it is perhaps indicative of a cortical distinction, rather than a subcortical one. Lamme and colleagues (1999) and Romani and colleagues (1999) certainly found a temporal enhancement of the processing of texture edges relative to homogenous regions in the *cortex*. It is not clear, however, whether this represents a cortical distinction independent of magno- and parvo-cellular processes or simply reflects the relative activity of the pathways which project onto the cortical

regions in question. Clearly more physiological recording needs to be carried out if we are to answer this question fully and understand the relationship between the perception of flicker-defined-form and the magnocellular pathway. Whether or not the method of using flicker-defined-form in Experiments 2 and 3 indeed isolated a magnocellular process of texture segmentation is clearly important, but regardless of the answer to this question, it does not detract away from the observation that texture segmentation can be achieved through rapid, phase-insensitive processes, regardless of their neural substrates.

On a related note, in addition to orientation contrast, texture segmentation based on spatial frequency would also be an interesting consideration for phase-insensitive texture segmentation. Bergen and Adelson (1988) have shown how the automatic segregation of textures based on element shape ('X's vs. 'L's) diminishes following the equating of spatial frequency content across the border. Such perceptual computations may be undertaken by early mechanisms in the visual brain, found in the lateral geniculate nucleus and layer 4 of the primary visual cortex (Landy & Graham, 2004), and so may be susceptible to the effects shown in the present study.

In comparison to the rapid edge-based texture segmentation mechanism, some texture discriminations require a more regional, statistical analysis and are not well suited for the processing of edge-based mechanisms. This was shown in the case of orientation variance judgments in the present study. In Experiment 1, unlike judgments of mean orientation, those of orientation variance were not more accurate when the patches were abutting compared to when they were separated. This is in line with Wolfson and Landy's (1998) findings and their interpretation of edge- and region-based texture analysis mechanisms, but the present study removed the confound of an increase in the quantity of line crossings in textures with greater variance. Interestingly, however, in the present experiment, judgments were actually more rapid when the patches were separated than when they were abutting. Wolfson and Landy (1998) offered the possibility that the separation serves to clearly delineate the regions on which to perform the regional analysis. This is certainly a possibility, given that the work of Dakin and colleagues (Dakin & Watt, 1997; Dakin, 2001) has outlined a flexible region of integration which is applied by an observer when required to perform spatial estimations of variance. In Experiment 1, when the textures were not clearly separated, observers may have applied regions of integration that were inaccurately scaled to the sizes of the patches of texture. Given the relatively long presentation duration of the stimuli, however, observers were able to successfully rescale the regions, resulting in longer RTs than in the separated condition but no reduction in accuracy. Given different instructions, and perhaps limited stimulus presentation durations, subjects may have shown significantly greater accuracies in the separated relative to the abutting condition.

This finding was not entirely observed in Experiment 2, however, which found that only two out of the four observers reached higher flicker frequency thresholds in the separated condition relative to the abutting condition for textures that differed in variance. The remaining two showed comparable thresholds in the two conditions. Why then does Experiment 2 not clearly corroborate the findings of Experiment 1? It is important to outline some differences between the experiments which may have accounted for this. One explanation is that it is only spatial *separation* that facilitates discriminations of orientation variance, rather than the presence of a coincidental black border between the textures. Alternatively, the black borders used in the second experiment not only separated the textures, but also bisected each one orthogonally, essentially dividing each texture further into two regions (see Fig. 4, bottom right). This may have impeded the

process of orientation variance estimation, which would have worked in opposition to the facilitation effect provided by the separation of the textures, thus resulting in an overall null or very weak effect. Additionally, the stimuli in Experiment 2 were fixed (i.e. appeared always in the same location) whereas those in Experiment 1 were randomly positioned in one of three locations on each presentation. This may have increased the observer's uncertainty as to where to apply the region of integration. These are only speculations, however, and regardless of the interpretation, there is no evidence from either of these experiments of edge-based facilitation for discriminations of variance.

One peculiarity of the results which deserves to be addressed, however, is the finding that in Experiment 3, for foveally viewed stimuli, higher frequency thresholds for abutting relative to separated textures were found only in two of the four observers. This does not at first sight concur with the findings from the previous experiment, which found with similar stimuli higher frequency thresholds in all subjects for the abutting relative to the separated condition. One important discrepancy between these two experiments, however, was the reduction in the size (by half) of the stimuli from Experiments 2 to 3. This was done to allow for more sensitive placement of the stimuli both in the centre and in the periphery of the visual field. In doing this, the stimuli in Experiment 3 were more concentrated in the centre of the visual field for the fovea condition, and thus did not extend into the periphery as much as in Experiment 2. If we are to take the conclusions from the third experiment that texture segmentation improves in the periphery whereas discrimination does not, we may also speculate that the relevant results in Experiment 2 were more evident due to the fact that the stimuli extended into the periphery, thus aiding segmentation and not discrimination.

More generally, however, these results highlight a dissociation between the processing of border information and that of surface properties, a distinction which has been at the centre of both psychophysical and neuropsychological interest for several decades. Indeed, the macro-geometry (i.e. shape) of an object appears to be processed by a separable anatomical system to that of the same object's surface properties (e.g. colour or texture; Cavina-Pratesi et al., 2010). Furthermore, neuropsychological cases are often presented in which a patient is unable to reliably distinguish surfaces based on some featural property but can nevertheless locate a border defined by that same property, or vice versa. Cases of achromatopsia (cortical colour-blindness) are a striking example of this, in which the ability to use colour-opponent mechanisms is retained to the extent at which chromatic contrast can be detected, but not colour identity (Kentridge, Heywood, & Cowey, 2004). So far, however, no comparable evidence has been presented for texture processing, likely to be a consequence of the highly specific brain-damage that would be required to produce such selective visual dysfunction. Nevertheless, the results gained from the present study lend well to the prediction that, at least theoretically, this could be a possibility.

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