THE
ROYAL
SOCIETY
PUBLISHING

Texton Segregation by Associated Differences in Global and Local Luminance Distribution
Author(s): H. C. Nothdurft
Source: *Proceedings of the Royal Society of London. Series B, Biological Sciences*, Vol. 239, No. 1296 (Apr. 23, 1990), pp. 295-320
Published by: Royal Society
Stable URL: http://www.jstor.org/stable/49462
Accessed: 10-01-2017 11:28 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms

Royal Society is collaborating with JSTOR to digitize, preserve and extend access to *Proceedings of the Royal Society of London. Series B, Biological Sciences*

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Proc. R. Soc. Lond. B **239**, 295–320 (1990)
Printed in Great Britain

Texton segregation by associated differences in global and local luminance distribution

BY H. C. NOTHDURFT

Department of Neurobiology, Max Planck Institute for Biophysical Chemistry, P.O. Box 2841, *D*-3400 *Göttingen, F.R.G.*

(*Communicated by H. B. Barlow, F.R.S. – Received* 17 *April* 1989)

Perceptual segregation of visual textures has been attributed to certain features ('textons') such as (elongated) blobs of given size and orientation, line crossings, and line ends. Differences in the spatial distribution of these features were assumed to be detected pre-attentively and to provide the instantaneous impression of segregating texture areas and of borders between them. This paper questions the validity of this general view and, in particular, the role of some of these features in texture discrimination. It is demonstrated that for some textons, perceptual segregation is independent of detection and discrimination of the texton itself. In addition, segregation can be strongly affected by positional or luminance jitter of texture elements or by other modifications that change the luminance distribution in the pattern but do not affect the supposed texton differences. From the textons reported in the literature, only differences in orientation were found to be fairly robust against such modifications.

1. INTRODUCTION

Figure–ground discrimination is an important task in vision. In human perception it can be achieved through any of at least five different visual properties, namely luminance or colour contrast, relative motion, and differences in interocular disparity or texture. Despite detailed knowledge of the spatial-filter properties of neurons in the early visual system (for reviews see Orban (1984) and Von der Heydt (1987)) and of their texture sensitivity (Hammond & MacKay 1977; Nothdurft & Li 1985; Van Essen *et al.* 1989), the physiological basis of texture segregation and, in particular, of perception of texture borders is not yet clear.

The observation that the human visual system can pre-attentively segregate certain pairs of textures but fails with others (Olson & Attneave 1970) has led to many attempts at a systematic explanation (see, for example, Beck (1972, 1982, 1983); Julesz (1975, 1984); Rentschler *et al.* (1988)). According to the texton theory of Julesz (Julesz 1981*a*,*b*, 1984, 1986; Julesz & Bergen 1983), a pattern is pre-attentively analysed for certain visual features (textons), whose first-order statistics then provide the information necessary to segregate areas and to establish texture borders between them. Textures differing only in non-texton properties do not segregate. Features considered to be textons are 'elongated blobs': 'for example rectangles, ellipses, line segments, with specific colours, angular orientations, widths and lengths'), 'terminators (i.e. ends of lines) of line segments'

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

and 'crossings of line segments' (Julesz 1984, p. 42, table 1). Examples of texture pairs each differing in at least one supposed texton feature are shown in figure 1*a–d*.

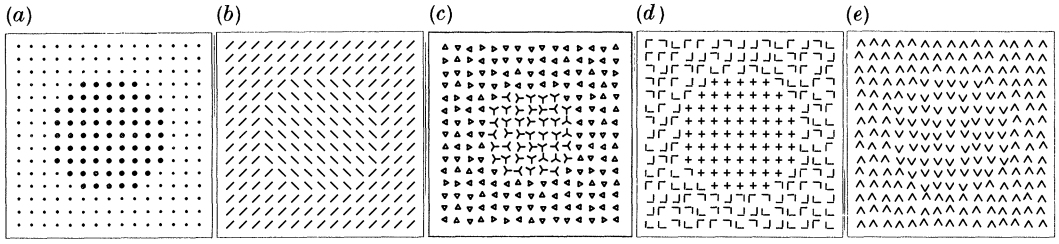

FIGURE 1. Texture segregation by texton differences. (*a–d*) In each pattern, texture areas segregate instantaneously and produce the effect of a global disc popping out from the rest of the pattern. Texture areas in (*e*) do not segregate and the global figure can only be reconstructed by detailed scrutiny of the texture. According to the texton theory (Julesz 1984), texture segregation is mediated by a limited set of visual features ('textons'), whose different spatial distribution can be detected pre-attentively. Such textons are 'blobs' of a certain size (*a*) or orientation (*b*), line ends or 'terminators' (*c*), and line 'crossings' (*d*). The orientation of the angle between lines is not a texton; textures differing only in this property do not segregate (*e*).

The texton theory evoked wide interest, especially in the light of new concepts of a modular representation of visual information in perception (Treisman 1985; Treisman & Gelade 1980). It has some pitfalls, however. First, its application to natural scenes is difficult as texton features are not well defined in such patterns (cf. Caelli 1982; Bergen & Adelson 1988). Further, textons are defined *posthoc* by studying the segregation of various configurations of a presumed texton feature. Perceived segregation in these patterns is not necessarily due to differences in the spatial distribution of these features but could also be a consequence of unintended variation of other visual cues. This paper discusses some other visual cues possibly contributing to the segregation of typical texton differences, and suggests control experiments for separating them. As will be seen from a series of demonstrations, first-order differences of supposed textons are often associated with global or local luminance variations or variations in the homogeneity of light distribution. If these are minimized by appropriate modifications of the texture pattern, the strength of segregation decreases even when the distribution of supposed textons is not changed.

2. Evidence for non-texton segregation of texture pairs

Some of our recent experiments have cast doubt on the concept that textures segregation is based on textons, in particular on those given in the literature. When the segregation of oriented line textures was measured for various orientation differences, line lengths and raster widths, it was found that to segregate, small orientation differences required closer arrangement of small texture elements than large ones (Nothdurft 1985*b*). Further elaboration of this phenomenon established that segregation is based on local discontinuities; continuous changes in texture

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

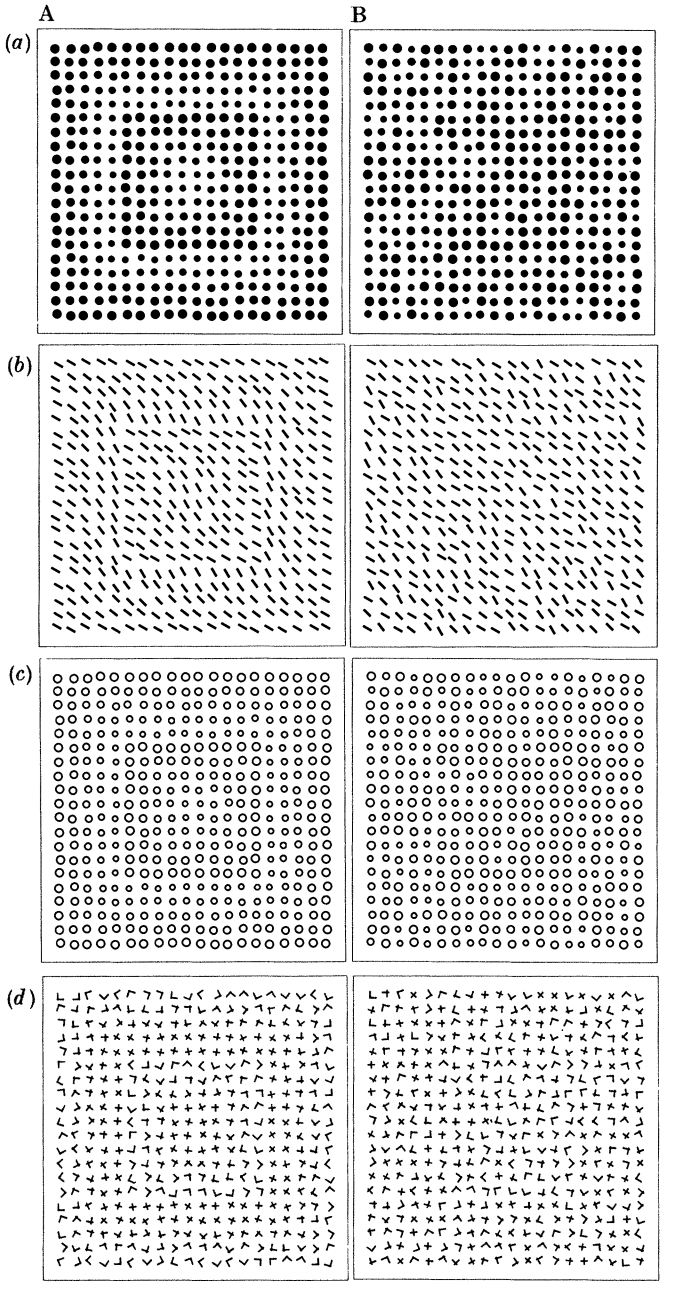

FIGURE 2. Texture segregation is linked to (local) texture contrast. The patterns in (A) perceptually dissect into two distinct texture areas although both areas contain, on average, similar texture elements. To perceive segregation, local differences of sufficient amplitude are required; continuous variations (as shown within each texture area) can be recognized but do not provide segregation. Textures are formed from (*a*) blobs of various sizes, (*b*) oriented lines, (*c*) circles, and (*d*) crossing and non-crossing line pairs. In (A), texture elements were arranged to form a sharp local contrast that produces the impression of a texture border. In (B), the same texture elements were randomly redistributed separately for each 'texture area'. Without sufficient texture contrast across the border, areas do not segregate.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

do not segregate even though they can be recognized (figure 2). This is contrary to the texton concept according to which segregation is based on the spatial distribution of discrete features.

Secondly, both neurophysiological and psychophysical experiments have provided evidence that texture segregation and the detection and identification of supposed textons are mediated, to some extent, by different mechanisms. For example, when cells in the cat lateral geniculate nucleus (LGN) were tested with crossed and non-crossed line-pair textures, they would differentially respond to texture areas or transmit the spatial details necessary for subsequent texton analysis. However, an individual cells would not usually do both simultaneously (Nothdurft 1990*a*). Correspondingly, in masking experiments with band-limited visual noise, performance in texture segregation and texton analysis were predominantly affected at different spatial frequency bands, indicating that these tasks are mediated by groups of cells with different sensitivities (Nothdurft 1990*b*). This also becomes evident when looking at texture pairs in figure 1 from a distance. Many patterns segregate even when spatial details, and in particular the supposed textons, can hardly be identified. Note that this is not true for differences in line orientation (figure 1*b*, cf. Nothdurft 1985*a*).

3. Luminance cues that could provide texton segregation

Differences in mean luminance

As figure 1 illustrates, variation in blob size (figure 1*a*) is accompanied by a variation in mean luminance, suggesting that segregation could also be based on global luminance contrast. The perception of segregating texture areas might therefore be based on the parallel representation of different aspects of a pattern. Neurons with large receptive fields respond to mean luminance contrast and represent the texture border; neurons with smaller receptive fields transmit details of the pattern, such as the form of individual elements, but themselves cannot encode the border between texture areas (Nothdurft 1990*a*).

Luminance homogeneity and differences in spatial frequency composition

Texture pairs such as those in figure 1*b–d* do not differ in mean luminance and, therefore, perceptual segregation with these patterns must be based on a different mechanism. Inspection of figure 1*d*, for example, suggests that areas with crossed line pairs display a more regular light distribution than those with non-crossed line pairs and that the light energy of crosses (if lines are bright on dark background) is more locally concentrated than that of non-crosses. These differences become evident from the power spectra of such textures that notably vary at low spatial frequencies (figure 3). Local, and in particular nonlinear filters, such as cells with a spatially limited receptive field and a firing threshold, would enhance the discriminability of such differences (for the functional importance of local filters in texture segregation see Julesz & Caelli (1979)).

Whereas differences in the spatial frequency composition are easy to detect between crossed and non-crossed line-pair textures, they may be less obvious with other texton differences. To enhance the visibility of such differences and of other

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

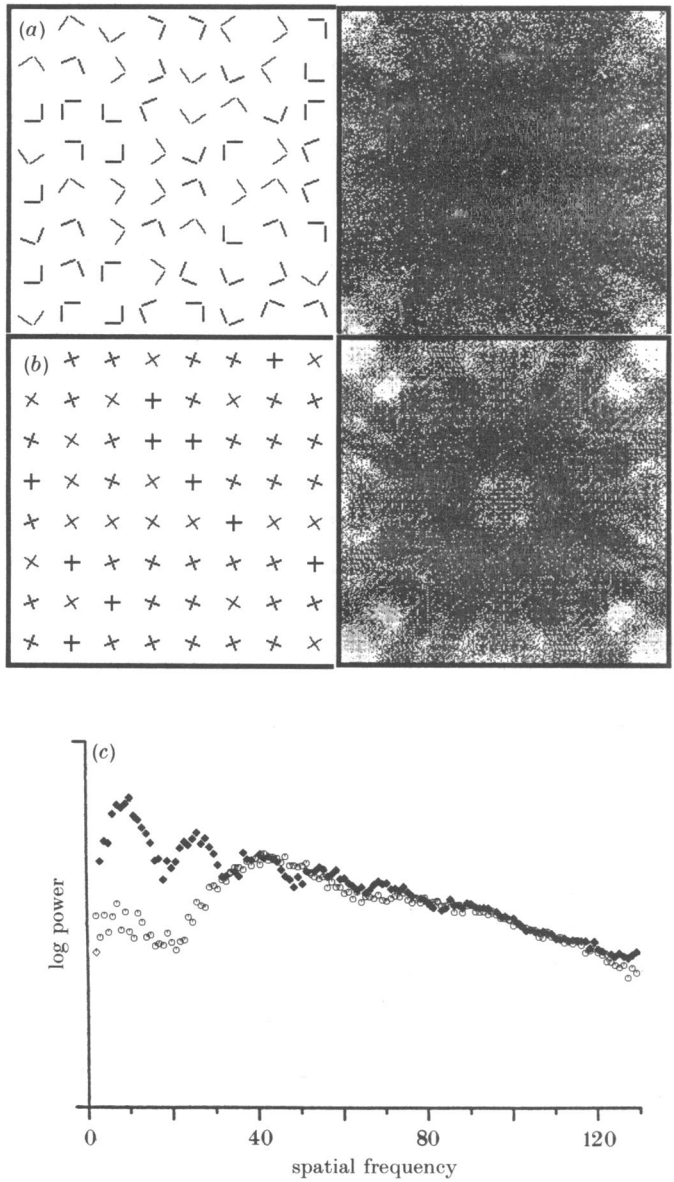

FIGURE 3. Differences in the spatial frequency composition of crossed and non-crossed line-pair textures. (*a*, *b*) Textures (left-hand column) and their two-dimensional power spectra (right-hand column). Energy amplitudes are shown on a logarithmic scale. From these data, (non-oriented) circular power spectra were calculated (*c*) by averaging identical spatial frequency bands at all orientations in *a* (filled symbols) and *b* (open symbols). Note the differences in spatial frequency composition between the textures.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

possible cues for segregation, the density of texture elements is varied in figure 4 (cf. Nothdurft 1985*b*; Sagi & Julesz 1987). With each texture pair, segregation is strongest when elements are densely packed (left column) and decreases rapidly with increased spacing. The strength of this effect varies considerably between features; for example, increasing the spacing between texture elements has a less pronounced effect on the strength of segregation of orientation (figure 4*d*) than terminator differences (figure 4*b*).

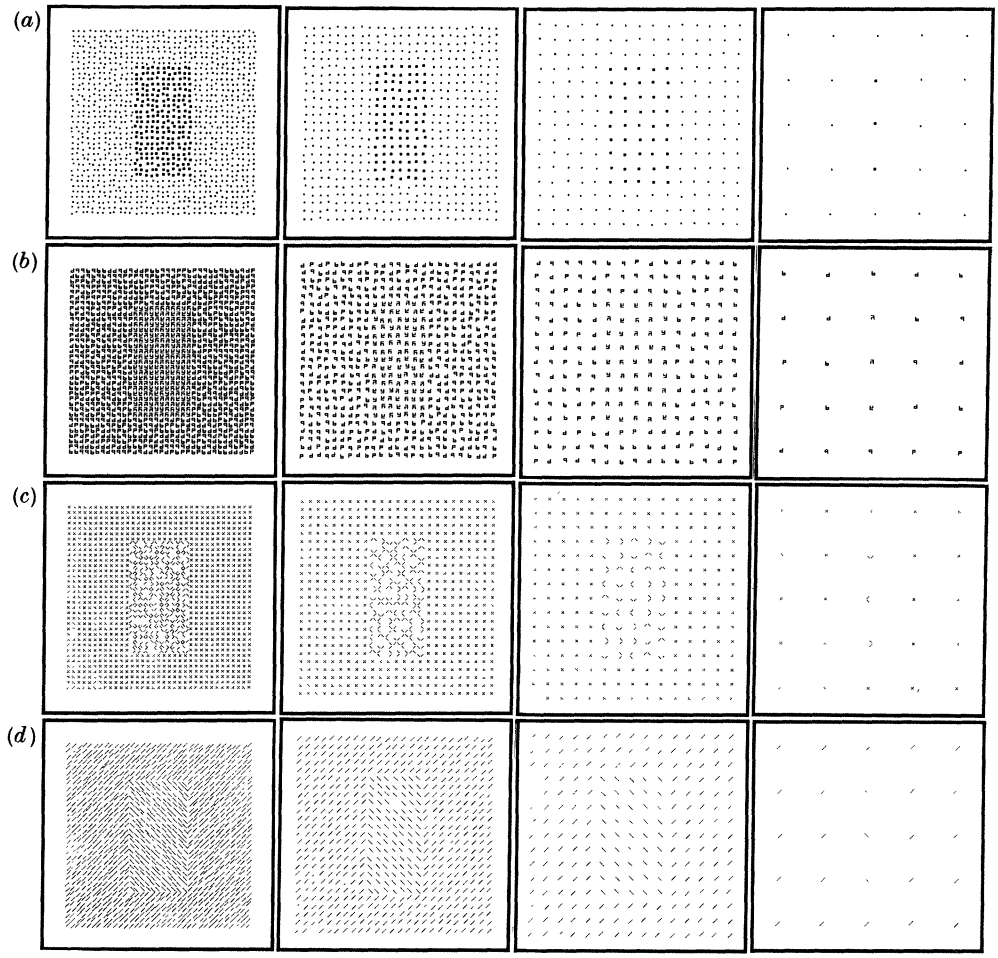

FIGURE 4. The effect of element density on texture segregation. Segregation of supposed texton differences ((*a*), 'blob size'; (*b*), 'terminators'; (*c*), 'crossings'; (*d*), 'line orientation') depends on the spacing of texture elements; it is strongly reduced when they are widely spaced (right-hand column). In dense arrangements (left-hand columns), other visual cues on top of the assumed texton differences become obvious, such as differences in the homogeneity of light distribution.

In the densest arrangement shown, all examples of texton differences, except line orientation, display obvious differences in the spatial homogeneity of light distribution. In figure 4*b*, for example, the outer texture area (with one line end per micropattern) contains small gaps between texture elements that are absent

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

from the central texture area (with three line ends per micropattern). Perceived segregation of these areas is therefore not necessarily based on differences in the distribution of terminators but could also be due to associated differences in the homogeneity of light distribution.

In summary, the inspection of typical texton examples shows a variety of visual cues that vary between texton-rich and texton-free texture areas and could also explain the perceived segregation of these patterns. These are: (i) texture areas have different mean luminance; (ii) texture areas differ in luminance homogeneity, i.e. in the (local) spatial frequency spectrum; (iii) texture border regions stand out from either texture area because of local luminance variations (this particular cue has not been demonstrated here). If segregation of so-called texton differences is based on one of these coincident variations in luminance distribution, compensation of these variations alone should render segregation difficult.

4. Masking of textons

Compensation of mean luminance differences

The possibility that segregation of blob size differences is achieved through the associated mean luminance contrast can easily be tested by compensating for the latter. This is demonstrated in figure 5. When the luminance contrast of the larger elements is decreased so that both texture areas display similar mean luminance, segregation is weakened although the differences in blob size can still be recognized (figure 5*b*). Small differences of element size, though visible, do not cause segregation if the global luminance gradient is too small to activate individual neurons, e.g. in coarse textures (figure 5*c*). None of these effects could be explained with the concept that segregation is based on the first-order statistics of blob-size textons.

In dense arrangements of texture elements (figure 5*d*) and in textures with large blobs, adjustment of blob luminance may not be sufficient to suppress segregation completely (figure 5*e*). This could be the result of different effects. As the mean luminance gradient is increased with texture elements lying close together, not only neurons with large but also those with medium-sized receptive fields would detect the differences in mean luminance and hence encode the texture border. The difficulty in masking the perception of texture borders in these patterns may thus reflect the impossibility of compensating luminance variations for all cells simultaneously, especially if these show non-linearities such as a firing threshold and response saturation. When luminance of the individual texture elements is randomized so that the signal-to-noise ratio of remaining luminance variations across the texture border is decreased, segregation of texture areas is rendered more difficult (figure 5*f*).

Also for textures on a large scale (close viewing distance), segregation often does not completely disappear with the compensation of global luminance differences. Differences in spatial frequency composition and effects from the alignment of texture elements (Beck *et al.* 1989) may also contribute to the perceived segregation in these cases.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

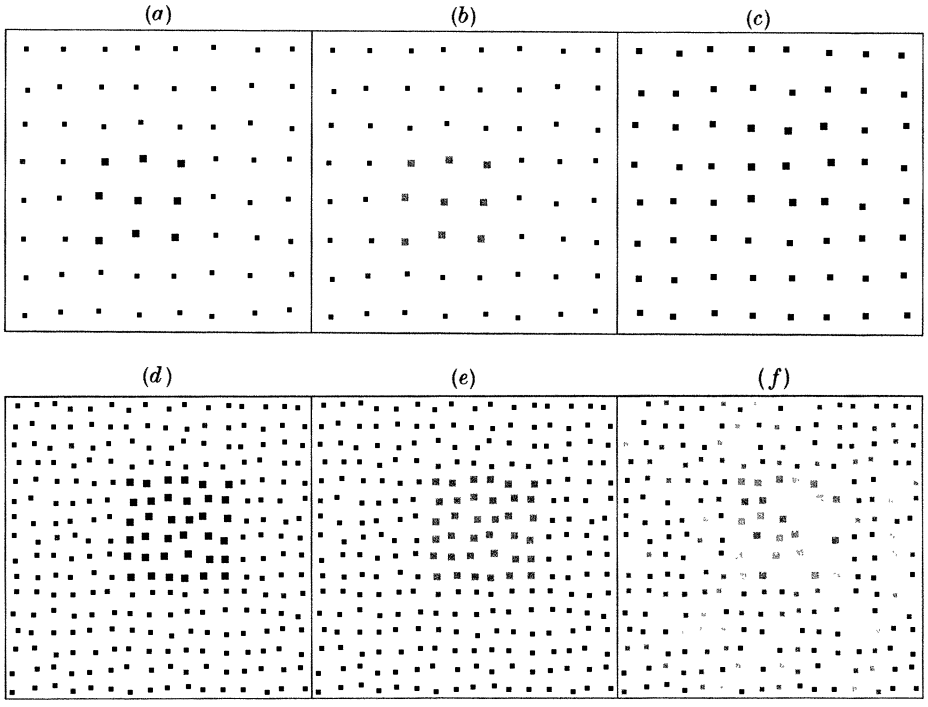

FIGURE 5. Masked segregation of textures with blobs (squares) of different size. Segregation of squares of different size (*a*) is impaired when the global variation of mean luminance is minimized by the reduction of the contrast of larger blobs (*b*) or when the global luminance gradient is too small to activate cells (*c*). In dense textures with a large luminance gradient (*d*), segregation cannot be masked completely by the compensation of differences in mean luminance (*e*). However, the perception of the texture border is reduced when individual squares vary randomly in luminance (*f*).

Randomization of element position (positional jitter)

In figure 4*b*, *c*, inhomogeneities in luminance distribution, e.g. holes between texture elements, are present in one but not in the other texture area. One way to achieve an unbiased and more uniform distribution of holes over the pattern is to randomize element position. In the following examples, texture elements, instead of being drawn on a regular raster, are plotted at a random position within a given area around the regular raster point. The size of this area, i.e. the maximal amplitude of the positional jitter, is varied between figures.

Figures 6–9 illustrate the effect of positional jitter on texture segregation. For better quantification, some texture differences were shown with varying texture contrast; in these patterns the strength of segregation increases continuously from left to right (figures 6 and 9). When positional jitter is applied to texture elements (figure 6*b*, *c*), the position at which the central texture bar (crossed to non-crossed lines) appears to segregate from the adjacent texture bands (crossed lines) shifts towards the right. This is particularly evident when the onset of segregation is estimated parafoveally, e.g. by fixating the frame around each texture plot, or when the right half (or more) of figure 6 is covered. However, positional jitter

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

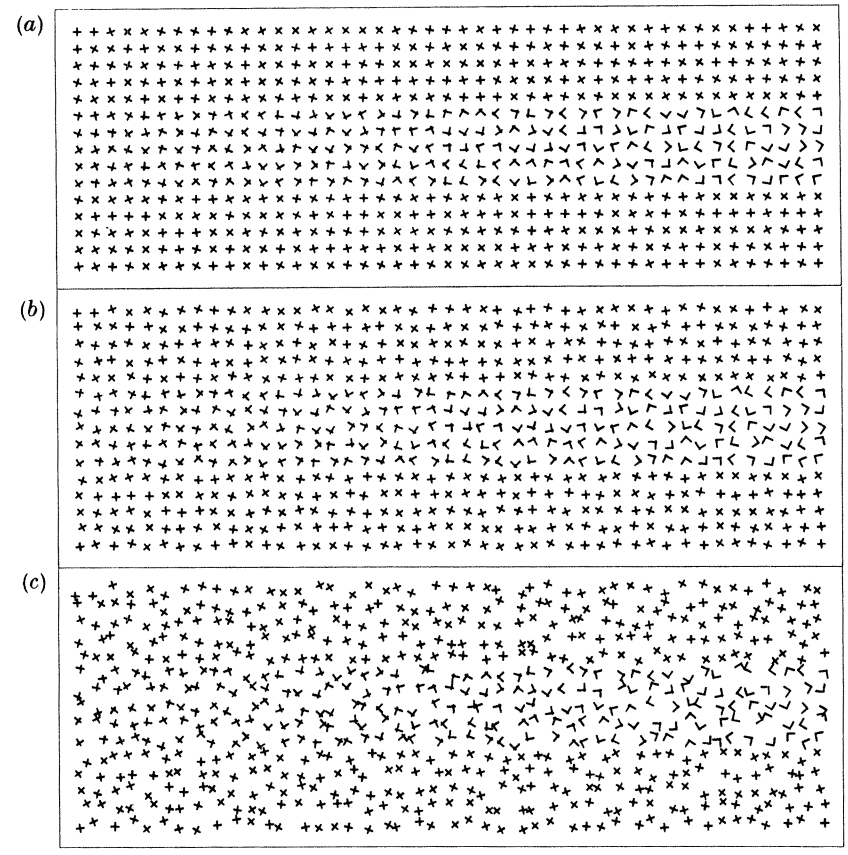

FIGURE 6. Positional jitter affects segregation of crossed and non-crossed line-pair textures. (*a–c*) Texture bands with increasing texture contrast from left to right. In each pattern, two texture bands with crosses surround a central texture band in which the intersection point of line pairs changes continuously from line centre ('crosses', on the left) to line end ('L's, on the right). In a regular arrangement of texture elements (*a*), these bands already segregate at a point where all line pairs are crossed. With increasing positional jitter of texture elements (*b*, *c*), the onset of perceived segregation shifts towards the right (this is most clearly seen when viewing the texture border parafoveally, e.g. by fixating the picture frame, or when covering the right half of the figure). The position of texture elements is scattered within amplitudes of 0 % (*a*), 25 % (*b*), or 67 % (*c*) of the raster width around the regular raster point. (A larger positional jitter though further reducing segregation produces unwanted crossings between originally non-crossing line pairs and is not shown.) Decreased segregation by increased positional jitter indicates that segregation may be based on differences in luminance homogeneity rather than first-order texton statistics.

alone cannot mask segregation completely, especially when element positions are randomized only up to amplitudes small enough to avoid accidental intersections of originally non-crossing lines (maximal jitter, in figure 6*c*, is 67 % of the raster width). On the right of figure 6, texture areas still differ in the homogeneity of light distribution and further modifications of the texture pattern would be necessary to suppress perceived segregation.

Note that in a regular arrangement of texture elements (figure 6*a*), even areas

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

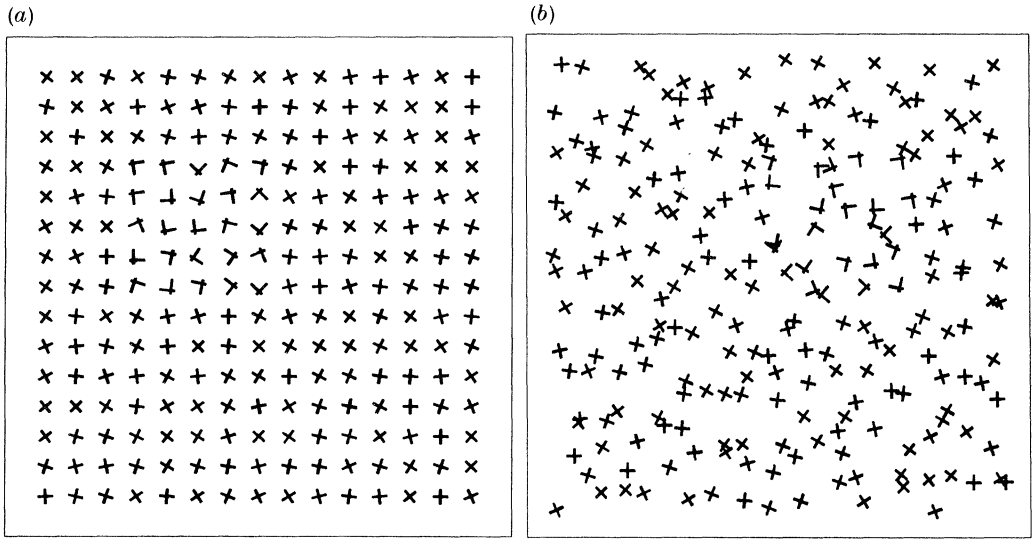

FIGURE 7. Crossed lines may segregate from other crossed lines of identical length and orientation. (*a*) Textures with line pairs intersecting at different eccentricities from the line midpoint. Note that these textures segregate although texture elements do not differ by any of the supposed texton features 'crossing', 'terminator', 'line size' or 'orientation'. Positional jitter is 0% of the raster width. (*b*) With increased jitter in element position (100% of raster width), segregation is suppressed. Both segregation in (*a*) and decreased segregation in (*b*) suggest influences from luminance inhomogeneities rather than texton analysis.

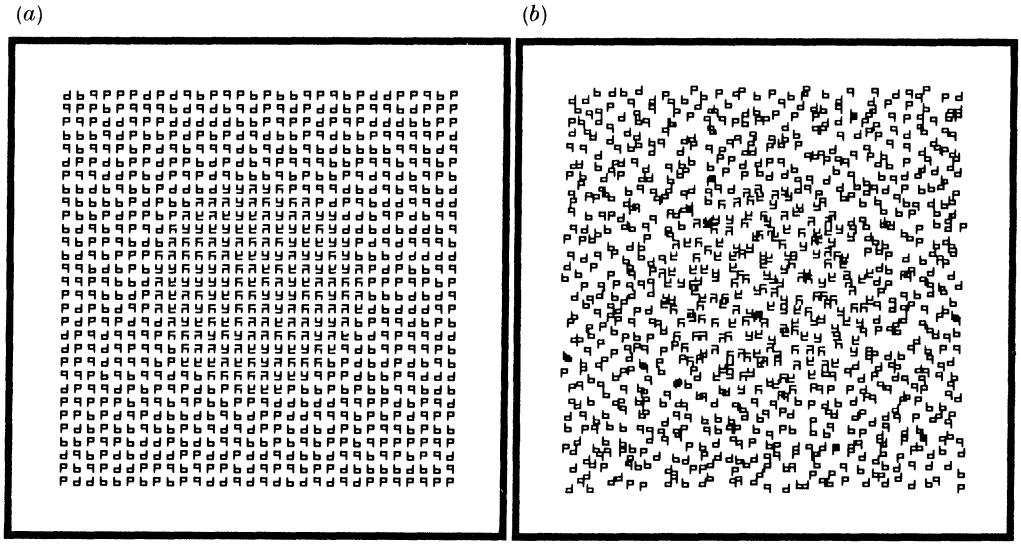

FIGURE 8. Positional jitter affects segregation of 'terminator' differences. (*a*) Textures with a different distribution of free line ends may segregate when the texture elements lie close together. Segregation could be based on terminator differences or on the difference in luminance distribution between texture areas. (*b*) Randomization of element positions (positional jitter) up to 100% of the raster width, which changes the distribution of luminance inhomogeneities but not that of the supposed texton, renders segregation difficult.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

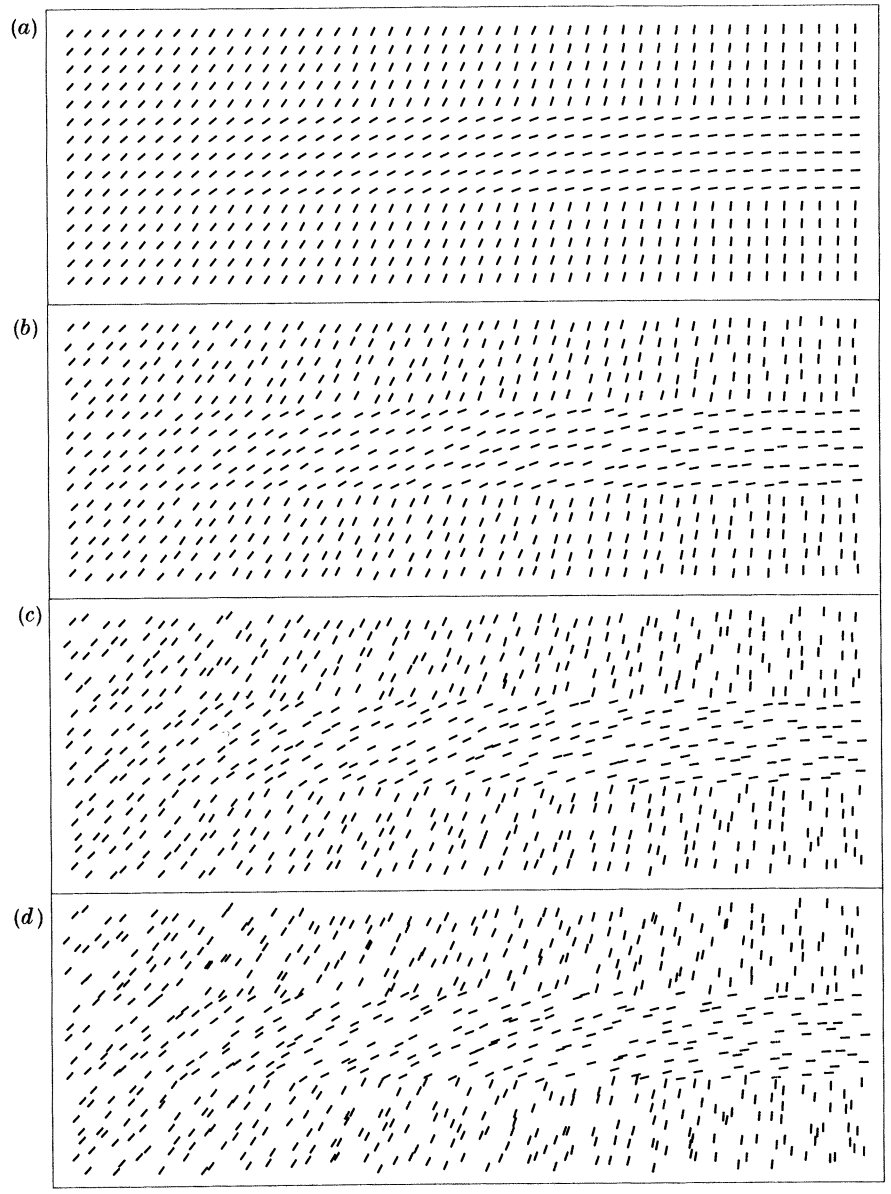

FIGURE 9. Positional jitter does not affect segregation of orientational differences. (*a–d*) Texture bands with differences in line orientation increasing from left to right. The point at which texture bands start to segregate does not markedly change with positional jitter (*b–d*). Position of texture elements varies within 5% (*a*), 25% (*b*), 65% (*c*), and 100% (*d*) of the raster width around the regular raster.

of crossed line-pairs segregate from each other if lines intersect at different distances from their midpoints. This is further illustrated in figure 7. The texture areas in figure 7*a* segregate spontaneously, although they are made of identical line elements with no differences in supposed crossing or terminator textons.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

However, the segregation is strongly masked by positional jitter of texture elements (figure 7*b*).

Texture pairs differing in the number of *line ends* fail to segregate in the presence of positional jitter, at least in the example of figure 8. It should be stressed that positional jitter does not change the differential distribution of terminators even if elements happen to fall upon each other as is here the case. Therefore, if terminators were textons, segregation should not be affected. In contrast to these observations, segregation of *orientation* differences is not reduced by positional jitter of texture elements; for the example given here, increased positional jitter may, in fact, even increase the strength of segregation (figure 9).

Variations of element density and size

Figures 10–12 show further examples of segregation of texture areas being rendered difficult by modifications that change the luminance distribution of textures but not the spatial distribution of supposed textons. In crossing and non-crossing textures, shortening of the non-crossed lines (Bergen & Adelson 1988), or increasing the length of crossed lines (figure 10), makes the luminance distributions in the texture areas more similar and (hence) reduces the strength of segregation. Except for a few holes between non-crossing texture elements, the distribution of lines in figure 10*c* appears to be homogeneous and areas are hard to discriminate when additional lines are drawn into these holes (figure 10*d*). Note that none of these modifications changed the distribution of crossings and therefore should not have affected segregation if crossings were textons.

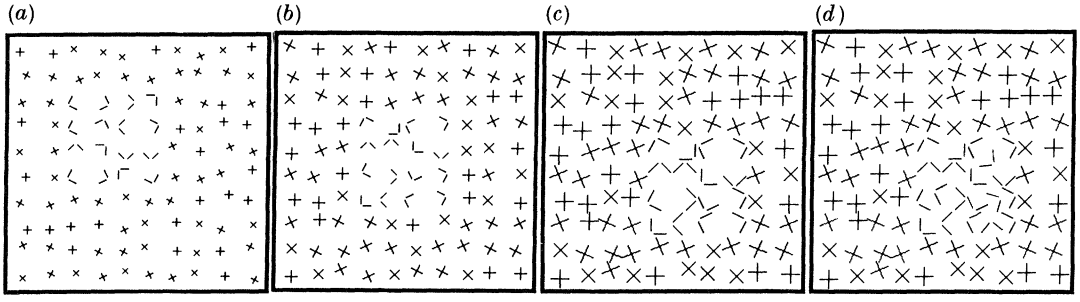

FIGURE 10. Reduced segregation of crossed and non-crossed line-pair textures with a more homogeneous light distribution. (*a*) Textures differ in the spatial extent over which the light (here, black ink) from each element is distributed. (*b*) Segregation of crosses from non-crosses is reduced when these distributions become similar even thought the supposed texton differences are not affected. (*c*) With large texture elements, only the 'holes' between non-crossing line pairs provide some segregation. (*d*) Texture areas fail to segregate when these holes are filled with additional (non-crossing) lines.

Positional jitter can only mask differences in the homogeneity of light distribution which are due to the arrangement of texture elements; it cannot compensate for differences in light distribution in the elements themselves. One way to minimize such differences, without changing the supposed texton distribution, is the variation of line length and thickness (figures 11 and 12). Randomizations of the intersection point of crossings (figure 11*b*) or of the length of line elements in

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

both texture areas (figure 11*c*) render segregation (figure 11*a*) difficult; variations of line length, line width and the intersection point together suppress it (figure 12*b*). Although some crosses are still easily detected in these patterns (probably because their local luminance peaks in certain spatial frequency bands stand out from the rest of the pattern), outlines of the texture areas appear to be poorly defined.

All these examples indicate that modifications that change the luminance distribution in a pattern and thereby affect the output of filters with a spatially restricted but otherwise not highly form-specific sampling window (such as LGN cells) may strongly affect the segregation of crossing differences even when the supposed texton distribution itself was not changed. Variations of line length and width in textures that differ in line orientation do not affect perceived segregation (figure 12*c*).

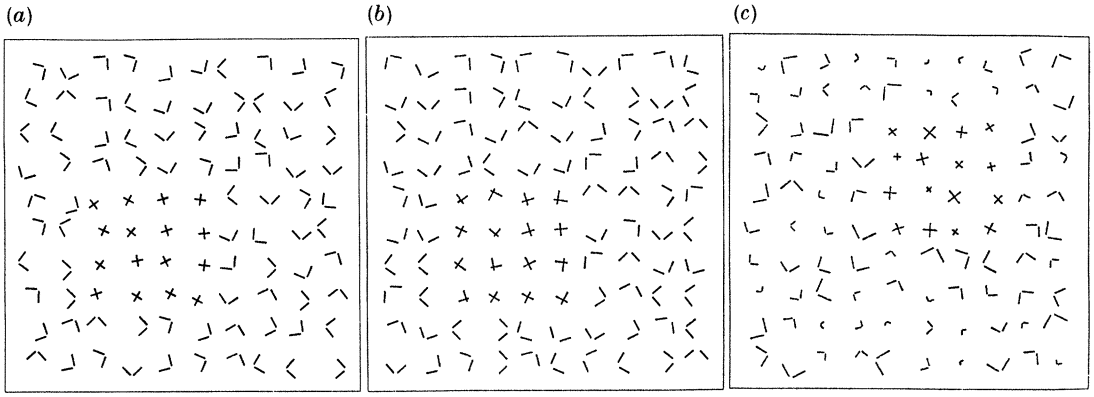

FIGURE 11. Modification of texture elements themselves can mask segregation of crossing textures. Instantaneous segregation of a crossing from a non-crossing texture area (*a*) is affected by variations of the intersection point (*b*) or random variations of line length (*c*) both of which do not affect the distribution of the supposed texton 'crossing'.

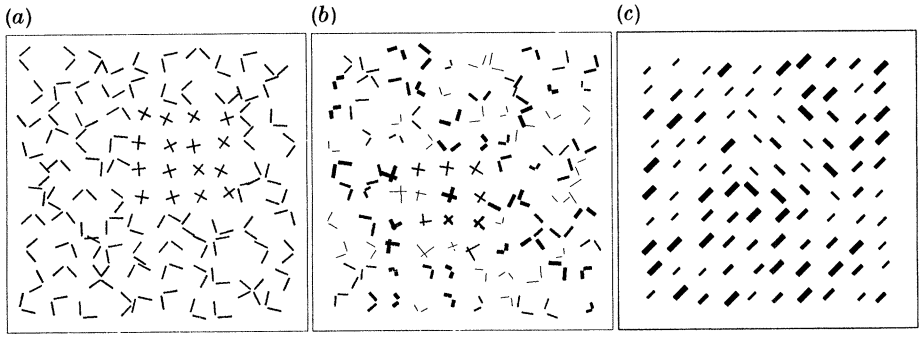

FIGURE 12. Reduced segregation from variations in line length and width with crossing but not orientation differences. (*a*) Texture differences provide the perception of texture borders and of a square segregating from the background. (*b*) Random variations of line length, line width and the relative positions of crossing of crossed line pairs and separation of uncrossed line pairs render the perception of texture borders difficult. (*c*) Similar variations of line length and width in textures of different orientation do not affect segregation.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Randomization of element contrast (luminance jitter)

Texture segregation, if based on local variations in luminance homogeneity, should be strongly affected by inhomogeneities of the background illumination, as was found in masking experiments (Nothdurft 1990*b*). A, to some extent, similar effect can be obtained by varying texture elements themselves in luminance (figures 13 and 14).

Luminance jitter of texture elements can have a pronounced effect on the perceived segregation of texture areas (figure 13). Although it obviously cannot mask the 'pop-out' of individual large blobs (figure 13*a*) or crossings (figure 13*b*), it suppresses the instantaneous perception of texture borders in these patterns. In the given example of terminator differences, luminance jitter alone can mask the segregation of texture areas completely (figure 13*c*). Note that there is almost no effect from luminance jitter on the segregation of textures differing in line orientation (figure 13*d*).

One may argue that reduced segregation in figure 13 is due to reduced contrast, and hence reduced visibility, of some texture elements. Although this could not account for the differential effect of masking in figures 13*a–d*, a different demonstration of luminance jitter is given in figure 14. In the middle and right-hand columns, texture elements have random luminance polarity against the background; luminance contrast itself is the same over all. This, too, has a strong effect on segregation. Texture areas differing in the number of line ends (figure 14*c*) do not segregate at all. For differences in blob size (figure 14*a*) or crossing (figure 14*b*), evaluation of the exact course of the texture border is not easy and requires some scrutiny, though the supposed features themselves can easily be detected. This indicates that, in texture-discrimination tasks, the visual system cannot analyse these features independent of their luminance contrast. Note that the segregation of orientation differences (figure 14*d*) is, again, less disturbed by random luminance reversal of individual texture elements. This becomes most evident when the segregation of modified patterns (columns B and C) is compared with that of non-modified patterns (column A). Without modification (A), differences in blob size and crossing segregate more strongly than differences in line orientation; after luminance randomization (B and C), orientation differences segregate best.

It is important to distinguish two mechanisms that could lead to these masking effects: (i) interferences between luminance and supposed texton features in establishing the texture border itself and (ii) interactions between correctly identified borders (e.g. from size or luminance differences) at a higher level. In the second case, reduced segregation of texture elements at randomized luminance polarity does not exclude the existence of supposed texton filters. The fact, however, that clustering of bright and dark elements affects segregation of orientation differences to a smaller degree than that of differences in size, crossings or terminators, suggests a direct interference by luminance cues with the evaluation of texture borders in these patterns.

In some patterns of figure 14, individual texture elements, or patches of texture at one contrast polarity, pop-out from the pattern. This could be a result of the very limited luminance randomization (texture elements are shown at only two

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

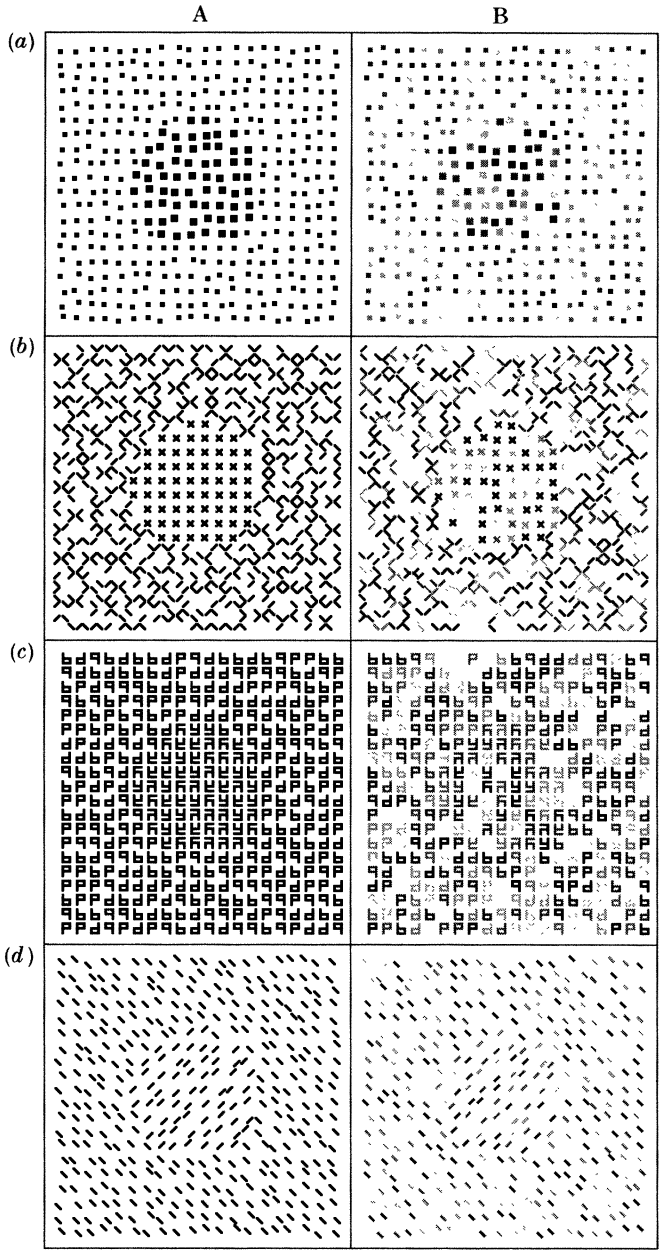

FIGURE 13. Luminance jitter of texture elements affects segregation. Random variation of element luminance contrast (right column, B) weakens the segregation of 'blob size' (*a*), 'crossing' (*b*) and 'terminator' (*c*) differences but less so that of differences in 'line orientation' (*d*). The left-hand column (A) shows the same texture differences with a fixed contrast.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

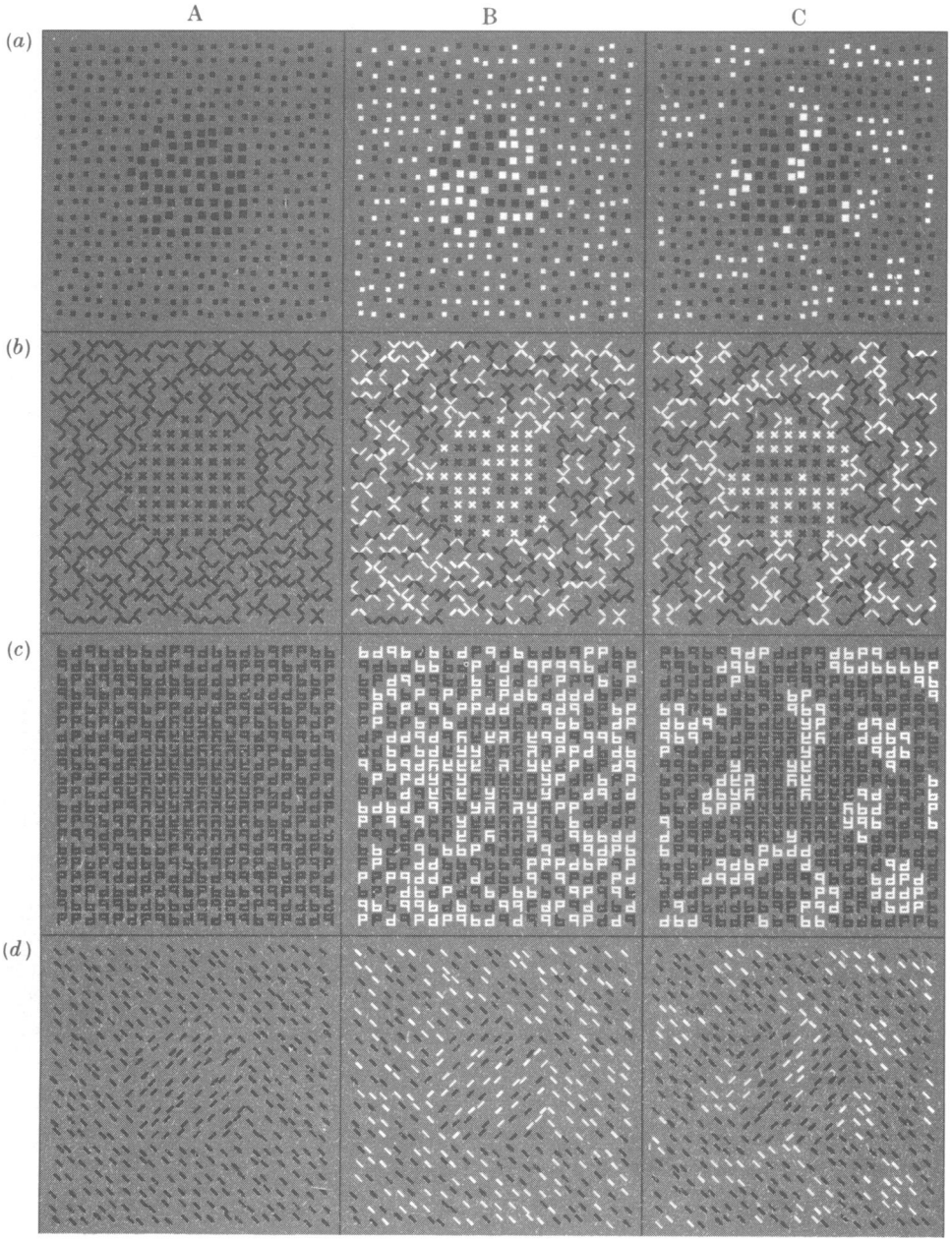

FIGURE 14. Contrast reversal of individual texture elements affects segregation. Contrast reversal of randomly chosen, individual texture elements reduces segregation of 'blob size' (*a*), 'crossing' (*b*), and 'terminator' (*c*) differences but not that of differences in 'line orientation' (*d*). (A) Texture elements at half contrast of earlier patterns which is the maximal contrast in (B) and (C). (B) Randomization of contrast polarity of individual elements, (C) with adjacent elements tending to be similar to their neighbours (see text). In (*a*) and (*b*), evaluation of the texture border is rendered difficult with random contrast reversal of individual texture elements. Segregation is completely masked in (*c*) but only mildly affected in (*d*).

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

luminance levels) and separate analysis by on and off channels. Large white and dark blobs in figure 14B*a* resemble peaks and troughs in mean luminance and, on that score, may segregate from the rest of the pattern. In the right-hand column of figure 14, texture elements are also randomized in luminance polarity but with a tendency of neighbouring elements to have identical values. (This is achieved by multiplying the contrast of the individual elements by the sign of a two-dimensional noise pattern of limited spatial frequency.) Depending on the spatial frequency of such global luminance modulations and the size and form of texture areas, segregation may be more strongly masked by spatially correlated than by random luminance jitter of texture elements. In the given examples, segregation deteriorates when superimposed variations in mean luminance affect the same spatial frequency bands that represent information about the texture border. This stresses the role of spatial frequency components, rather than supposed textons, in the analysis of texture borders. Luminance jitter at spatial frequency bands that are irrelevant for the evaluation of texture borders, has no or only little effect on segregation.

5. Discussion

From the beginning, the texton concept (Julesz 1980) provided a close link between perceptually observed phenomena of texture discrimination and feature properties of neural filters in the visual system. Some of the first features found to segregate resembled known receptive-field properties of visual neurons (see, for example, Beck (1966, 1967); Julesz *et al.* (1973), or the 'quasi-collinearity detectors' postulated by Caelli & Julesz (1978)), although a simple isomorphism between textons and neural units had been rejected (Julesz & Bergen 1983, p. 1633). Segregation of textures that could not be explained by known features led to postulation of additional textons (Julesz 1982; Julesz & Bergen 1983). However, the apparent absence of some of these filters in the neurophysiological literature raised the question of whether all such features are indeed textons providing instantaneous segregation. It is shown in this paper that segregation of many supposed textons is affected by variations in the arrangement, density, size or contrast of texture elements and can be rendered difficult even when the spatial distribution of supposed texton features is not changed.

Non-texton cues in segregation of texton differences

Blob size

The fact that compensation of associated differences in mean luminance renders segregation of blob textures difficult, emphasizes the role of luminance cues for segregation. Beck and co-workers (Beck *et al.* 1983, 1987; Sutter & Beck 1989; see also Graham (1989)), studying (tripartite) segregation of orientational differences that were generated by the arrangement of blobs of different size ('higher-order textures', cf. Nothdurft 1985*c*), found that their subjects were unable to perform the task if large and small blobs displayed identical areal contrast. That is, segregation of differences in size could be cancelled by differences in contrast. If blob size differences segregate by virtue of the associated differences in mean luminance, higher-order textures of this sort are simply first-order textures in low

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

spatial-frequency channels (cf. Graham 1989). The role of low spatial-frequency bands for many visual tasks including texture segregation was postulated earlier (see, for example, Ginsburg (1982, 1984)). However, apparent nonlinearities in texture discrimination (Julesz & Caelli 1979) and the fact that the segregation of some texture differences cannot be fully explained by low spatial-frequency analysis (Jáñez 1984) indicate some limitations of this approach.

The observation that the segregation of size differences with large blobs cannot be completely masked by the compensation of luminance differences is interesting and indicates that luminance differences are not the only cue for segregating these textures. Segregation may also arise from differences between the spatial frequency composition of texture areas that could be detected by LGN cells or cells in the striate cortex (Campbell *et al.* 1969; Maffei & Fiorentini 1973; Movshon *et al.* 1978) and from the alignment of texture elements along the texture border (Beck *et al.* 1989).

Crossings

Although the segregation of crossed and non-crossed line-pair textures is convincingly demonstrated in the literature (see, for example, Beck (1966); Julesz & Bergen (1983)), the existence of a 'crossing' texton has repeatedly been questioned. Gurnsey & Browse (1987) showed that certain modifications of the texture elements, even if they did not change the original texton distribution, reduced segregation. In experiments on visual search, Treisman & Gormican (1988) did not find pre-attentive detection of crosses within non-crosses and, in general, failed to establish any combination of line elements as an independent feature. Kröse (1987) has shown that the perceptual segregation of crosses from non-crosses is a monotone function of the eccentricity of the intersection point from the line centre (cf. figure 6). Segregation of crossed and non-crossed line textures can be masked by noise that has only a small effect on the perception of the intersection of lines (Nothdurft 1990*b*). All of these observations suggest that the existence of crossings in a pattern and its perceptual segregation are to some extent functionally independent aspects. This view is supported by recent computational studies in which segregation of texture differences in the crossing domain has been achieved without using crossing filters (Kröse 1987; Griffiths *et al.* 1988; Fogel & Sagi 1989; Malik & Perona 1989).

Recently, Bergen & Adelson (1988) and Voorhees & Poggio (1988), also arguing against the texton quality of the crossing feature, suggested that size differences between crossed and non-crossed texture elements (from identical lines) are the distinguishing cue. Considering that size differences themselves (when matched in mean luminance) are only a weak cue for segregation, it remains unclear whether the segregation of crossed and non-crossed line-pair textures could be explained by such a mechanism alone. Contributions from spatial frequency differences (figure 3), in general, seem to play a role in segregation. For large and widely spaced elements, the most pronounced variations in spatial frequency come from the different sizes of texture elements; minimization of these differences by adjusting their sizes renders segregation difficult (Bergen and Adelson's demonstration). With more closely arranged texture elements, size adjustment alone may be insufficient to mask segregation.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Terminators

The fact that segregation of terminator differences is strongly affected by positional or luminance jitter of texture elements, casts doubt on the special role of line ends in texture segregation. Many examples of terminator differences, which are carefully designed to avoid other cues for segregation (in particular differences in mean luminance to which LGN cells would strongly respond), are difficult to discriminate. Other examples (e.g. figure 1*c*) are reminiscent of properties of crossed and non-crossed line textures and similar visual cues as discussed for those patterns could also account for segregation here. The textures in figure 4*b* segregate only for closely arranged elements, i.e. when the differences in spatial luminance distribution become evident. Segregation decreases rapidly with increased element spacing (figure 4*b*) or with positional jitter (figure 8), i.e. when the differences in spatial luminance distribution (but not the terminators) are hard to recognize. This suggests that segregation is based on these visual cues rather than on line ends.

One might speculate whether segregation, if based on a categorical judgment (no versus some features) rather than a relative one (some versus many), might show less dramatic effects from luminance or positional jitter. Because most demonstrations of supposed terminator differences provide strong segregation even of non-categorical differences, such an argument is not really sound. Moreover, examples of categorical differences are frequently imperfect as other visual cues (e.g. differences in mean luminance) are invariably present and segregation may be caused by these rather than the categorical judgment of terminator distribution.

Cells in the cat LGN were found to distinguish terminator textures on the basis of differences in mean luminance, or luminance patches that were present in one but not the other texture area (Nothdurft 1990*a*), but not by true responses to terminators. When these cues are removed from a pattern, differential responsiveness is reduced, as also the perceived segregation of texture area. Enns (1986) showed that certain modifications of texture elements that, in fact, change their spatial frequency composition but not the supposed texton difference, may suppress segregation. Even in an early example of supposed terminator differences (Julesz 1980, figure 5), segregation was strongly affected by modifications that reduce the difference in light distribution between texture areas but do not change the distribution of terminators (Julesz 1980, figure 8). Also in this example, positional jitter of texture elements was seen to reduce the apparent strength of segregation.

Contrary to the effect seen in figures 13*c* and 14*c*, Taylor & Stanley (1986) found a small improvement of terminator segregation by luminance jitter. Also Treisman & Souther (1985), though failing to establish connectedness as a functional feature, reported evidence for the special role of terminators in visual search. However, these findings rather than arguing against the conclusions made in this paper may underline the principal difficulty in isolating supposed texton differences from other cues. That the segregation of terminator differences can be strongly affected by the modification of non-texton cues is in favour of such an interpretation.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Remaining and emerging texton properties

Orientation

Among the texton features studied in this paper, orientation was the only one for which segregation could not be linked to coincident global or local luminance variations. With regular patterns, luminance variations at the texture border are inevitable, and these variations are indeed detected at early processing stages (Nothdurft 1990*a*). In the cat, LGN cells also show some degree of orientational bias (Daniels *et al.* 1977; Creutzfeldt & Nothdurft 1978; Vidyasagar & Urbas 1982; Vidyasagar & Heide 1984) but no pronounced differences in mean responsiveness were found when such cells were stimulated with line textures at orthogonal orientation (Nothdurft 1990*a*). If perceived segregation of oriented textures were based upon response differences at the LGN, it should, in fact, be strongly affected by random luminance variations of texture elements, as LGN cells are not driven by one specific stimulus property alone. The observation from this study that segregation of oriented textures is not cancelled by positional or luminance jitter whereas such effects were certainly stronger with other features, suggests that segregation cannot be based on LGN response differences alone.

Although cortical cells could act as texton filters for orientation, as they have been shown to analyse texture patterns for the orientation of individual line elements (Nothdurft & Li 1985), recent psychophysical studies indicate a very limited contribution of the orientation feature itself to texture segmentation (cf. figure 2).

Spatial frequency

The segregation of crossing and terminator textures and textures with closely arranged blobs of different size was found to be influenced by local peaks and troughs in the luminance distribution (which were present in one but not the other texture area), i.e. by differences in the spatial-frequency composition.

That the human visual system can segregate textures that differ in their spatial frequency composition, has been known for some time (Julesz 1980; Caelli 1982), although the limitations of a global Fourier analysis have been stressed (Mayhew & Frisby 1978) and local features of granularity had been postulated (Julesz 1980). Caelli & Moraglia (1985) studying segregation of Gabor functions (i.e. oriented stimuli with luminance modulation at defined spatial frequencies) found differences in spatial frequency as well as differences in orientation provide strong segregation. According to their results, these two properties are not processed separately. Gabor functions have been shown to resemble a powerful set of filters for texture discrimination (Turner 1986; Clark *et al.* 1987; Griffiths *et al.* 1988; Fogel & Sagi 1989). Interestingly, the segregation of spatial frequency differences at high frequency bands requires a closer arrangement of elements than that of differences at low frequency bands (Sagi 1990). Together with the interdependence of spatial frequency sensitivity and tuning width for orientation (which is an intrinsic property of the Gabor function), this could explain why small differences in orientation need closer arrangement of line elements for segregation than do large orientation differences (Nothdurft 1985*b*).

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

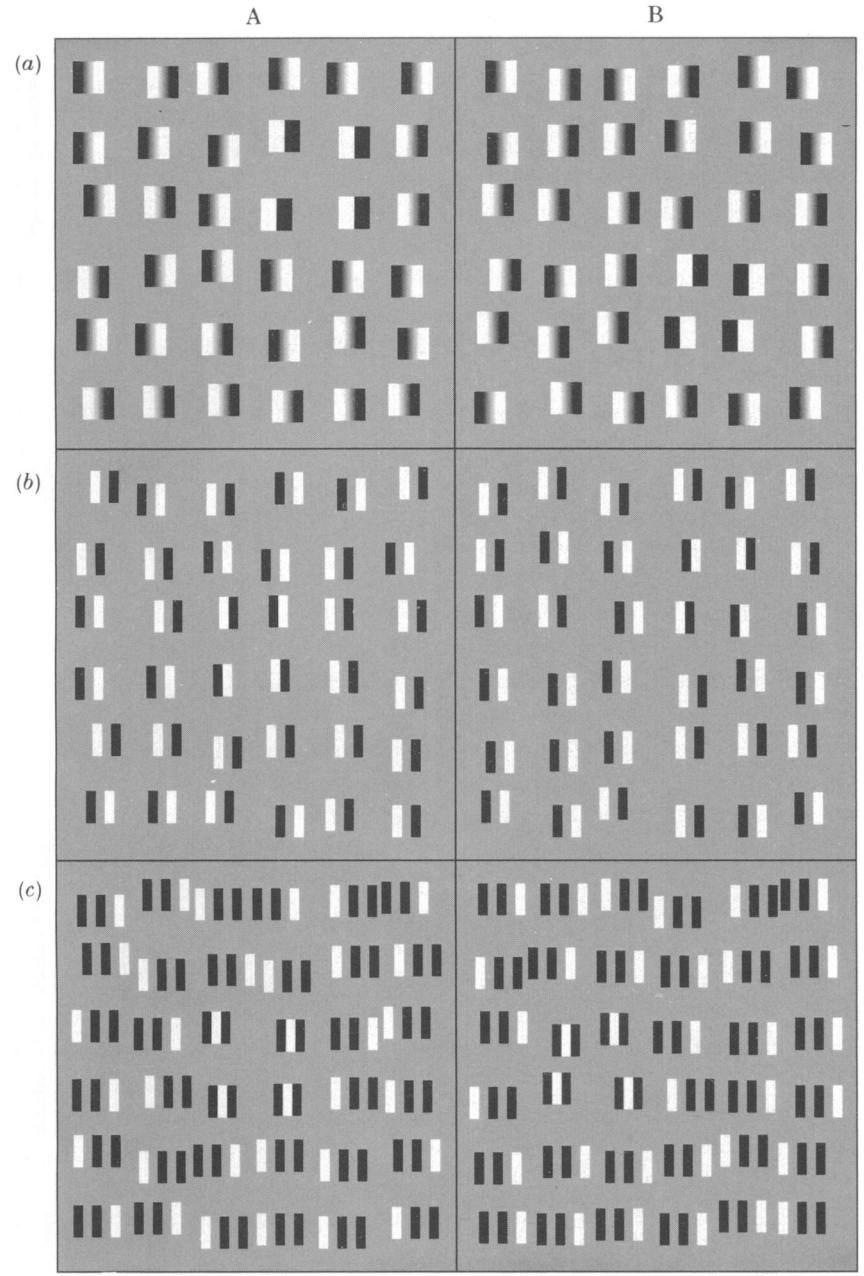

FIGURE 15. New textons from spatial-frequency combinations? A (*a*) Differences based on a different luminance gradient of texture elements segregate despite the absence of known textons. However, segregation could be easily explained on the basis of differences in the spatial frequency composition or differential activation of LGN cells by these micropatterns. (*b*) Segregation of 'edges'. From all possible combinations of two (elongated) blobs at different contrast, only adjacent pairs ('edges') were found to provide segregation and hence to constitute texton features (Caelli *et al.* 1986). (*c*) Segregation of 'bars'. From the possible combinations of three blobs, only 'bar' arrangements segregate (Caelli *et al.* 1986). (B) When the contrast of segregating texture elements is reduced, the strength of segregation is decreased. This indicates that segregation is to some extent based on luminance contrast cues (as, for example, represented in cells of the LGN) rather than on true analysis of line or spatial-frequency combinations.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

New textons from spatial frequency combinations?

Textures differing in the combination of spatial frequencies may also segregate. An example is shown in figure 15A*a*, where the micropatterns differ in the luminance gradient from bright to dark (a sharper luminance gradient is obtained by simply adding appropriate higher spatial-frequency components). An explanation of this perceptual phenomenon by the texton theory would lead to the postulation of a new texton 'contrast gradient'. However, segregation could also be related to differences in the spatial-frequency composition, or to response variations with sharp and blurred edges at early processing levels, for example the LGN (Siguenza *et al.* 1987). For an individual cell, these differences (a stronger response to sharp than to blurred edges) could be compensated by decreasing the contrast amplitude of the sharp edges. When micropatterns are modified in this way, segregation is indeed reduced (figure 15B*a*).

Segregation based on phase differences between identical spatial frequency samples is rather limited. Rentschler *et al.* (1988), investigating this in detail, found that only those combinations of micropatterns segregate whose phase differences produced sufficient variation in local luminance modulation. Micropatterns with smaller phase differences and mirror images, though easily discriminable by scrutiny, did not segregate. In related experiments (Caelli *et al.* 1986), these authors also studied configurations of pairs or triplets of elongated blobs and found only a few such configurations to provide segregation (figure 15A*b*, *c*). However, with all of these new textons, segregation is reduced when the local luminance contrast is modified (figure 15B), as would be expected if segregation is based upon response variations from differences in local luminance contrast.

The neural basis of texture segregation

Cells in the primary visual cortex respond well to oriented stimuli of a certain spatial frequency (Campbell *et al.* 1969; Maffei & Fiorentini 1973; Movshon *et al.* 1978; Pollen & Ronner 1981; Kulikowski & Vidyasagar 1986). Many of them have sensitivity profiles similar to Gabor functions (Kulikowski & Vidyasagar 1986; Hawken & Parker 1987; Webster & De Valois 1985) and are sensitive to orientation contrast (Van Essen *et al.* 1989) that provides a better description of perceived segregation than sensitivity to line orientation does. Response differences at this level could thus resemble the neuronal basis of texture segregation and of the evaluation of texture borders. Interestingly, segregation based on interocular disparity (Poggio & Poggio 1984) or relative motion (Nothdurft 1987) also seems to be linked to response properties of cells in the primary visual cortex. However, differences in spatial-frequency composition also cause response variation in cells at earlier processing stages and segregation is not necessarily based on cortical mechanisms alone. In fact, recordings in the cat have revealed remarkable parallels between the strength of response variation of LGN cells and perceived segregation (Nothdurft 1990*a*). This could explain why bilateral lesions of area 17 in cats do not abolish the animals' abilities to segregate certain textures (Berlucchi 1988).

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

6. Conclusion

This paper provides evidence that texture segregation is not based upon the analysis of complex features, particularly not of different combinations of line elements, such as crossed or non-crossed line pairs or different arrangements of blobs (an obvious exception, however, is provided by examples of texture elements resembling depth cues; cf. Ramachandran (1988)). Segregation of supposed texton differences could rather be achieved from a series of other visual cues many of which are known to evoke differential responses at early levels of the visual system. Because segregation was not resistant against luminance variations or related modifications, texture discrimination is likely to be initiated at a level at which response variations due to luminance contrast interfere with response variations related to texture. This does not imply that segregation is exclusively based on luminance cues.

The observations also do not, in general, support the assumed role of texton features for segregation. Even with classical textons (except orientation), segregation could often be related to associated differences in luminance distribution and the supposed textons could not reliably predict segregation. In fact, different patterns with the same texton differences were seen to segregate well, weakly, or not at all. In addition, strength of segregation was found to change continuously with increasing texture gradient, indicating that texture segregation is related to continuously defined visual properties rather than discrete textons, which opens the way to texture analysis in photographs and natural scenes in which some of the supposed textons (e.g., crossings, terminators) are hard to define.

In a recent discussion on an earlier version of this manuscript, B. Julesz (personal communication) decided to remove crossings and terminators from his list of textons and strengthen the role of (elongated) blobs of a given size (and orientation). Interestingly, these two parameters have come out of one of his early studies as the most important ones for segregation (Julesz 1967). The limited contribution from true size differences to segregation, as shown in this paper, together with the fact that segregation of orientation differences is linked to orientation contrast, not orientation *per se*, necessitates further modifications of the texton concept.

I am grateful to O. Creutzfeldt, T. R. Vidyasagar, A. Lüschow and anonymous referees for helpful comments on an earlier version of the manuscript, and to Dr Vidyasagar and C. Maelicke for correcting the English. I also like to thank K. H. Fuchs, R. Klement, K.-F. Lehmann, U. Lüthje, D. Michael, H. Schucht and H. Sebesse for their help in producing half-tone demonstrations of sufficient quality.

This work was supported by the Deutsche Forschungsgemeinschaft (Az.: Cr/30-18). Parts of this paper were presented at the '9. Kybernetik Kongreß' (Göttingen, March 1986), at the EBBS workshop on 'Visual processing of form and motion' (Tübingen, March 1988) and at the 11th ECVP (see Nothdurft 1988).

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

References

Beck, J 1966 Effect of orientation and of shape similarity on perceptual grouping. *Percept. Psychophys.* **1**, 300–302.

Beck, J. 1967 Perceptual grouping produced by line figures. *Percept. Psychophys.* **2**, 491–495.

Beck, J. 1972 Similarity grouping and peripheral discriminability under uncertainty. *Am. J. Psychol.* **85**, 1–19.

Beck, J. 1982 Textural segmentation. In *Organization and representation in perception* (ed. J. Beck), pp. 285–317. Hillsdale, New Jersey and London: Erlbaum.

Beck, J., Prazdny, K. & Rosenfeld, A. 1983 A theory of textural segmentation. In *Human and machine vision* (ed. J. Beck, B. Hope, & A. Rosenfeld), pp. 1–38. New York: Academic Press.

Beck, J., Sutter, A. & Ivry, R. 1987 Spatial frequency channels and perceptual grouping in texture segregation. *Comput. Vis. Graph. Image Process.* **37**, 299–325.

Beck, J., Rosenfeld, A. & Iury, R. 1989 Line segregation. *Spatial Vis.* **4**, 75–101.

Bergen, J. R. & Adelson, E. H. 1988 Early vision and texture perception. *Nature, Lond.* **333**, 363–364.

Berlucchi, G. 1988 New approaches to the analysis of the function of visual cortical areas in the cat with the lesion method. Lecture held at the EBBS-Workshop *Visual Processing of form and motion*, Tübingen.

Caelli, T. 1982 On discriminating visual textures and images. *Percept. Psychophys.* **31**, 149–159.

Caelli, T. & Julesz, B. 1978 On perceptual analyzers underlying visual texture discrimination: part I. *Biol. Cyber.* **28**, 167–175.

Caelli, T. & Moraglia, G. 1985 On the detection of Gabor signals and discrimination of Gabor textures. *Vision Res.* **25**, 671–684.

Caelli, T., Hübner, M. & Rentschler, I. 1986 On the discrimination of micropatterns and textures. *Hum. Neurobiol.* **5**, 129–136.

Campbell, F. W., Cooper, G. F. & Enroth-Cugell, C. 1969 The spatial selectivity of visual cells in the cat. *J. Physiol., Lond.* **203**, 223–235.

Clark, M., Bovik, A. C. & Geisler, W. S. 1987 Texture segmentation using Gabor modulation/demodulation. *Patt. Recog. Lett.* **6**, 261–267.

Creutzfeldt, O. D. & Nothdurft, H. C. 1978 Representation of complex visual stimuli in the brain. *Naturwissenschaften* **65**, 307–318.

Daniels, J. D., Normal, J. L. & Pettigrew, J. D. 1977 Biases for oriented moving bars in lateral geniculate nucleus neurones of normal and stripe-reared cats. *Expl Brain Res.* **29**, 155–172.

Enns, J. 1986 Seeing textons in context. *Percept. Psychophys.* **39**, 143–147.

Fogel, I. & Sagi, D. 1989 Gabor filters as texture discriminator. *Biol. Cyber.* **61**, 103–113.

Ginsburg, A. P. 1982 On a filter approach to understanding the perception of visual form. In *Recognition of pattern and form* (ed. D. G. Albrecht), pp. 175–192. Berlin, Heidelberg and New York: Springer-Verlag.

Ginsburg, A. P. 1984 Visual form perception based on biological filtering. In *Sensory experience, adaptation, and perception* (ed. L. Spillmann & B. R. Wooten), pp. 53–72. Hillsdale, New Jersey: Erlbaum.

Graham, N. 1989 Low-level visual processes and texture segregation. *Phys. Script.* **39**, 147–152.

Griffiths, E., Troscianko, T. & Knapman, J. 1988 A computational model of texture perception. *Perception* **17**, 356.

Gurnsey, R. & Browse, R. A. 1987 Micropattern properties and presentation conditions influencing visual texture discrimination. *Percept. Psychophys.* **41**, 239–252.

Hammond, P. & MacKay, D. M. 1977 Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Expl Brain Res.* **30**, 275–296.

Hawken, M. J. & Parker, A. J. 1987 Spatial properties of neurons in the monkey striate cortex. *Proc. R. Soc. Lond.* B **231**, 251–288.

Jáñez, L. 1984 Visual grouping without low spatial frequencies. *Vision Res.* **24**, 271–274.

Julesz, B. 1967 Some recent studies in vision relevant to form perception. In *Models for the perception of speech and visual form* (ed. W. Whaten-Dunn), pp. 136–154. Cambridge, Massachusetts: MIT Press.

Julesz, B. 1975 Experiments in the visual perception of texture. *Scient. Am.* **232/4**, 34–43.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Julesz, B. 1980 Spatial nonlinearities in the instantaneous perception of textures with identical power spectra. *Phil. Trans. R. Lond.* B **290**, 83–94.

Julesz, B. 1981*a* A theory of preattentive texture discrimination based on first-order statistics of textons. *Biol. Cyber.* **41**, 131–138.

Julesz, B. 1981*b* Textons, the elements of texture perception, and their interactions. *Nature, Lond.* **290**, 91–97.

Julesz, B. 1982 The role of terminators in preattentive perception of line textures. In *Recognition of pattern and form* (ed. D. G. Albrecht), pp. 33–58. Berlin, Heidelberg and New York: Springer-Verlag.

Julesz, B. 1984 A brief outline of the texton theory of human vision. *Trends Neurosci.* **7**, 41–45.

Julesz, B. 1986 Texton gradients: the texton theory revisited. *Biol. Cyber.* **54**, 245–251.

Julesz, B. & Bergen, J. R. 1983 Textons, the fundamental elements in preattentive vision and perception of textures. *The Bell System tech. J.* **62**, 1619–1645.

Julesz, B. & Caelli, T. 1979 On the limits of Fourier decompositions in visual texture perception. *Perception* **8**, 69–73.

Julesz, B., Gilbert, E. N., Shepp, L. A. & Frisch, H. L. 1973 Inability of humans to discriminate between visual textures that agree in second-order statistics – revisited. *Perception* **2**, 391–405.

Kröse, B. J. A. 1987 Local structure analyzers as determinants of preattentive pattern discrimination. *Biol. Cyber.* **55**, 289–298.

Kulikowski, J. J. & Vidyasagar, T. R. 1986 Space and spatial frequency: analysis and representation in the macaque striate cortex. *Expl Brain Res.* **64**, 5–18.

Maffei, L. & Fiorentini, A. 1973 The visual cortex as a spatial frequency analyser. *Vision Res.* **13**, 1255–1268.

Malik, J. & Perona, P. 1989 A computational model of texture perception. Computer Science Division (EECS), University of California, Berkeley, California 94720, report no. UCB/CSD 89/491.

Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. 1978 Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol., Lond.* **283**, 101–120.

Mayhew, J. E. W. & Frisby, J. P. 1978 Texture discrimination and Fourier analysis in human vision. *Nature, Lond.* **275**, 438–439.

Nothdurft, H. C. 1985*a* Orientation sensitivity and texture segmentation in patterns with different line orientation. *Vision Res.* **25**, 551–560.

Nothdurft, H. C. 1985*b* Sensitivity for structure gradient in texture discrimination tasks. *Vision Res.* **25**, 1957–1968.

Nothdurft, H. C. 1985*c* Discrimination of higher-order textures. *Perception* **14**, 539–53.

Nothdurft, H. C. 1987 Perceptive fields of direction selective neurones in the human visual system. In *New frontiers in brain research* (ed. N. Elsner & O. Creutzfeldt), p. 180. Stuttgart and New York: Thieme.

Nothdurft, H. C. 1988 Texton properties associated with differences in spatial-frequency distribution. *Perception* **17**, 361.

Nothdurft, H. C. 1990*a* Texture discrimination by cells in the cat lateral geniculate nucleus. *Expl Brain Res.* (Submitted.)

Nothdurft, H. C. 1990*b* Different effects from spatial frequency masking in texture segregation and texton detection tasks. *Vision Res.* (Submitted.)

Nothdurft, H. C. & Li, C. Y. 1985 Texture discrimination: representation of orientation and luminance differences in cells of the cat striate cortex. *Vision Res.* **25**, 99–113.

Olson, R. K. & Attneave, F. 1970 What variables produce similarity grouping? *Am. J. Psychol.* **83**, 1–21.

Orban, G. A. 1984 *Neuronal operations in the visual cortex.* Berlin, Heidelberg, New York and Tokyo: Springer-Verlag.

Poggio, G. F. & Poggio, T. 1984 The analysis of stereopsis. *A. Rev. Neurosci.* **7**, 379–412.

Pollen, D. A. & Ronner, S. F. 1981 Phase relationship between adjacent simple cells in the visual cortex. *Science, Wash.* **212**, 1409–1411.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms

Ramachandran, V. S. 1988 Perceiving shape from shading. *Scient. Am.* **259**/2, 76–83.
Rentschler, I., Hübner, M. & Caelli, T. 1988 On the discrimination of compound Gabor signals and textures. *Vision Res.* **28**, 279–291.
Sagi, D. 1990 Detection of an orientation singularity in Gabor textures: effect of signal density and spatial-frequency. *Vision Res.* (Submitted.)
Sagi, D. & Julesz, B. 1987 Short-range limitations on detection of feature differences. *Spatial Vis.* **2**, 39–49.
Siguenza, J., Heide, W. & Creutzfeldt, O. D. 1987 Representation of edges of variable blur by neuronal responses in the lateral geniculate body and the visual cortex of cats: limits of linear prediction. *Vision Res.* **27**, 1701–1717.
Sutter, A., Beck, J. & Graham, N. 1989 Contrast and spatial variables in texture segregation: testing a simple spatial-frequency channels model. *Percept. Psychophs.* **46**, 312–332.
Taylor, S. & Stanley, G. 1986 Contrast and conspicuity in preattentive texture perception. *Percept. Psychophys.* **40**, 287–289.
Treisman, A. 1985 Preattentive processing in vision. *Comp. Vis. Graph. Image Process.* **31**, 156–177.
Treisman, A. & Gelade, G. 1980 A feature integration theory of attention. *Cognit. Psychol.* **12**, 97–136.
Treisman, A. & Gormican, S. 1988 Feature analysis in early vision: evidence from search asymmetries. *Psychol. Rev.* **95**, 15–48.
Triesman, A. & Souther, J. 1985 Search asymmetry: a diagnostic for preattentive processing of separable features. *J. Expl Psychol.* **114**, 285–310.
Turner, M. R. 1986 Texture discrimination by Gabor functions. *Biol. Cyber.* **55**, 71–82.
Vidyasagar, T. R. & Urbas, J. V. 1982 Orientation sensitivity of cat LGN neurones with and without inputs from visual cortical areas 17 and 18. *Expl Brain Res.* **46**, 157–169.
Vidyasagar, T. R. & Heide, W. 1984 Geniculate orientation biases seen with moving sine wave gratings: implications for a model of simple cell afferent connectivity. *Expl Brain Res.* **46**, 157–169.
Van Essen, D. C., De Yoe, E. A., Olavarria, J., Knierim, J., Sagi, D., Fox, J. & Julesz, B. 1989 Neural responses to static and moving texture patterns in visual cortex of the macaque monkey. In *Neural mechanisms of visual perception* (ed. D. M. K. Lom & C. D. Gilbert), pp. 137–154. Woodlands, Texas: Portfolio publishing.
Von der Heydt, R. 1987 Approaches to visual cortical function. *Rev. Physiol. Biochem. Pharmacol.* **108**, 69–150.
Voorhees, H. & Poggio, T. 1988 Computing texture boundaries from images. *Nature, Lond.* **333**, 364–367.
Webster, M. A. & De Valois, R. L. 1985 Relationship between spatial frequency and orientation tuning of striate-cortex cells. *J. opt. Soc. Am.* A**2**, 1124–1132.

This content downloaded from 134.76.223.157 on Tue, 10 Jan 2017 11:28:52 UTC
All use subject to http://about.jstor.org/terms