

1 **Discrimination of textures with spatial**
2 **correlations and multiple gray levels**

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10 **Abstract:** Analysis of visual texture is important for many key steps in early vision. We study
11 visual sensitivity to image statistics in three families of textures that include multiple gray
12 levels and correlations in two spatial dimensions. Sensitivities to positive and negative
13 correlations are approximately independent of correlation sign, and signals from different
14 kinds of correlations combine quadratically. We build a computational model, fully
15 constrained by prior studies of sensitivity to uncorrelated textures and black-and-white
16 textures with spatial correlations. The model accounts for many features of the new data,
17 including sign-independence, quadratic combination, and the dependence on gray level
18 distribution.

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20 **1. Introduction**

21 One of the strategies that the visual system uses to grapple with the complexity of analyzing
22 natural sensory signals is to organize this analysis according to groups of attributes – for
23 example, orientation, color, motion, and depth [2]. For these classical submodalities of spatial
24 vision, this organizational strategy has well-recognized anatomical underpinnings, both at the
25 level of specialization of cortical areas and the tuning properties of their component neurons
26 [2-6].

27 Although the specialization of visual areas and the independence of processing within
28 submodalities is far from absolute [7-10], it is clear that computational “factoring” is an
29 important principle. That is, while a neuron may be tuned to more than one submodality of
30 spatial vision (e.g., its response may depend both on color and orientation), its selectivity can
31 often be understood by considering one submodality at a time. Conversely, it is rare to find a
32 neuron whose preferred spatial orientation changes as a function of the chromaticity of the
33 grating used to probe it. Intuitively, this arrangement is a natural consequence of parallel
34 visual streams and simplifies the logic needed to read out a pattern of neural activity.

35 Here, we ask whether this computational principle generalizes to another aspect of spatial
36 vision – visual texture. There are two ways in which texture differs from the classic
37 submodalities, and thus, two reasons that this generalization is not a foregone conclusion.
38 First, the connection between perceptual sensitivities and tuning properties of individual
39 neurons is likely to be less direct than for the classic submodalities: texture, by its nature,
40 cannot be signaled by a small number of localized receptive fields, as it is a statistical
41 characterization of an image across an extended region.

42 Second, the domain of visual texture is high-dimensional. The reason for this is that any
43 statistic that measures the joint probability of a set of luminance values in any given spatial
44 configuration is, potentially, a perceptual dimension for texture, i.e., a parameter for which
45 visual sensitivity may be tuned. Within this vast range of possibilities, visual sensitivity is

46 highly selective – but nevertheless, there are a large number of such image statistics for which
47 visual sensitivity is substantial. [11-14].

48 To address whether computational “factoring” extends to texture, we measure visual
49 sensitivity to image statistics that incorporate two aspects of texture that are typically studied
50 separately: the distribution of luminance levels, and the spatial organization of the
51 correlations. We then construct a model for these sensitivities. The model has the familiar
52 “back-pocket” structure [15], but each channel of the model posits a specific way in which
53 analysis of image statistics can be separated into a component that is sensitive to the
54 distribution of luminance levels, and a component that is sensitive to spatial configuration.
55 The model’s parameters are then constrained by requiring it to account for two
56 complementary, pre-existing psychophysical datasets that do not overlap the current study:
57 sensitivity to differences in the luminance histogram in textures with no spatial structure [14,
58 16, 17], and sensitivity to differences in spatial configuration in textures with only two
59 luminance levels [13, 18]. Because of the model’s simple structure, it can be fully constrained
60 by this requirement, with no free parameters. We find that the model provides an approximate
61 account of the new psychophysical measurements, in terms of relative sensitivities to different
62 kinds of image statistics and how different image statistics combine.

63 **2. Materials and methods**

64 Our overall experimental strategy is to use synthetic visual textures to measure visual
65 sensitivity to image statistics and their combinations. As in previous work, a texture is
66 formally defined as an ensemble of infinitely large images, with the requirement that its
67 statistics can be equivalently estimated either by averaging a single sample over all of space,
68 or averaging across many examples of a finite patch[18, 19]; our stimuli consist of random
69 samples drawn from such an ensemble. The textures we consider here are all composed of
70 monochrome checks, and the statistics we consider are all local correlations, i.e., the average
71 value, across the ensemble, of a product of luminances of checks at specific relative
72 displacements.

73 Despite these restrictions, a practical challenge remains: the number of image statistics
74 required to specify a texture is enormous [20, 21]. This challenge, along with a range of
75 theoretical considerations [18, 22-25], motivates the adoption of the “maximum-entropy”
76 approach used here: a small number of image statistics are specified explicitly, and the
77 texture ensemble is constructed to be as random as possible, given these constraints.

78 In this work, the constraints are the luminance distribution and correlations of checks
79 within a 2×2 neighborhood. We use a 2×2 region (here, and in previous studies that this
80 work builds on [13, 18, 26-28]) because it is the smallest region that enables specification of
81 textures with contours and corners in multiple directions, as well as T-junctions and X-
82 junctions.

83 This approach provides a practical dimension reduction and also one which, perhaps
84 surprisingly, is related to the statistics of natural images[24, 25]. Our approach is related to,
85 but distinct from, the “FRAME” approach to texture synthesis of Zhu et al. [22]. While both
86 are maximum-entropy approaches, FRAME uses constraints that are neurally-inspired linear
87 spatial filters applied to the image (and thus, also encompasses the original texton approach of
88 Julesz [29, 30]); here, the constraints are nonlinear combinations of local luminances.

89 Psychophysical measurements of sensitivity to individual image statistics and their
90 combinations were made by using the texture segmentation task introduced by Chubb et al.
91 [17] and used in many previous studies in our lab [13, 18, 26-28] for black-and-white
92 textures. Here we describe an extension of this approach to multiple gray levels. We then
93 detail the psychophysical task, experimental procedure, and data analysis. Construction of the
94 textures is detailed in the Supplemental Document (“Specification and construction of
95 textures”). This construction maintains the maximum-entropy property of the black-and-white

96 construction [18]: textures are as random as possible for the image statistics that are specified.
97 Because of this maximum-entropy property, the textures contain the minimal visual structure
98 that is required to achieve the specified image statistics.

99 A portion of the psychophysical data presented in Experiments 1 and 2 has also been
100 presented in [23], but without many of the experimental details.

101 2.1 Stimuli for experiments 1 and 2

102 Experiments 1 and 2 extend the analysis of black-and-white textures [18] to textures with
103 three luminance levels. In the binary context, we developed a coordinate system for image
104 statistics that comprehensively described all kinds of correlations within a 2×2
105 neighborhood of checks; we now expand the coordinate system to take into account multiple
106 luminance levels.

107 In the case of black-and-white textures, image statistics are grouped according to “order”,
108 i.e., the number of checks that are multiplied to calculate the statistic. For example, the first-
109 order statistic specifies the luminance distribution of individual checks, and the second-order
110 statistics describe the pairwise correlation of luminances in a pair of checks. There are four
111 second-order statistics, since there are four kinds of two-check correlations to be considered:
112 between two checks that are adjacent horizontally, vertically, and along each of the two
113 diagonals. Each statistic thus specifies the expected value of the product of the luminances of
114 horizontally adjacent, vertically adjacent, or diagonally adjacent check pairs, averaged across
115 all samples of the texture. Similarly, there are four third-order statistics, corresponding to the
116 four ways of selecting three checks within a 2×2 neighborhood; each statistic specifies the
117 expected value of the product of three luminances. Finally, there is one fourth-order statistic;
118 it specifies the correlation among all four checks, i.e., the product of the four luminances.

119 To extend this scheme to multiple luminance levels, we group image statistics according
120 to order (the number of checks whose luminances are multiplied), and subdivide each order
121 according to the spatial configuration of the checks. However, each of these subdivisions now
122 becomes a family of statistics, as more than one parameter is needed to describe the
123 correlations among checks in a given configuration (Table 1). Furthermore, each family (other
124 than first-order) subdivides into independent genera based on the rule that links the luminance
125 values within each configuration; each genus in turn contains several species -- the individual
126 statistics that specify the distribution of values created by this rule. (We are borrowing the
127 standard taxonomic nomenclature – order, family, genus, and species -- for a hierarchy that
128 arises out of mathematical considerations, but we do not intend to imply a hierarchical
129 structure for the visual computations). The need for this structure becomes apparent when we
130 consider three or more luminance levels and statistics of order two or more; these play a key
131 role in the first two experiments.

132 First-order statistics

133 First-order statistics describe the distribution of luminance level values assigned to each
134 check. When three levels are present, the distribution is specified by the probability that a
135 check is black (0), gray (1), or white (2). This is a three-element vector, $(p(0), p(1), p(2))$,
136 which we denote as $\vec{\sigma}_{(1)}$. Since the probabilities of black, gray, and white checks must sum to
137 1, there are two degrees of freedom, so this family requires two image statistics – the
138 “species” within this family.

139 We represent these two degrees of freedom as barycentric coordinates (page 216 of [1]) of
140 a triangular domain (Fig. 1), whose vertices correspond to textures that are all black
141 $\vec{\sigma}_{(1)} = (1, 0, 0)$, all gray $\vec{\sigma}_{(1)} = (0, 1, 0)$, or all white $\vec{\sigma}_{(1)} = (0, 0, 1)$. The centroid of the

142 triangle, $\bar{\sigma}_{(1)} = (1/3, 1/3, 1/3)$, corresponds to a texture in which each gray level occurs
 143 1/3 of the time, and there are no spatial correlations. Note that in the black-and-white case,
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Table 1. Texture Coordinates

order	block probabilities	Fourier coordinates	reduced Fourier coordinates	barycentric coordinates	binary coordinates
1	$p \begin{pmatrix} A_1 & A_2 \\ A_3 & A_4 \end{pmatrix}$	$\varphi \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}$	$\varphi(s_1)$	$\bar{\sigma}_{(1)}$	$\bar{\sigma}_{(1)} = \left(\frac{1-\gamma}{2}, \frac{1+\gamma}{2} \right)$
2			$\varphi(s_1 \ s_2)$	$\bar{\sigma}_{(1 \ s_2)}$	$\bar{\sigma}_{(1 \ s_2)} = \left(\frac{1+\beta_-}{2}, \frac{1-\beta_-}{2} \right)$
			$\varphi \begin{pmatrix} s_1 \\ s_3 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 \\ s_3 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} 1 \\ s_3 \end{pmatrix}} = \left(\frac{1+\beta_+}{2}, \frac{1-\beta_+}{2} \right)$
			$\varphi \begin{pmatrix} s_1 & \\ & s_4 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 & \\ & s_4 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} 1 & \\ & s_4 \end{pmatrix}} = \left(\frac{1+\beta_\perp}{2}, \frac{1-\beta_\perp}{2} \right)$
			$\varphi \begin{pmatrix} & s_2 \\ s_3 & \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} & 1 \\ s_3 & s_4 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} & 1 \\ s_3 & s_4 \end{pmatrix}} = \left(\frac{1+\beta_l}{2}, \frac{1-\beta_l}{2} \right)$
3			$\varphi \begin{pmatrix} s_1 & s_2 \\ s_3 & \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_3 & \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_3 & \end{pmatrix}} = \left(\frac{1-\theta_\perp}{2}, \frac{1+\theta_\perp}{2} \right)$
			$\varphi \begin{pmatrix} s_1 & s_2 \\ & s_4 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 & s_2 \\ & s_4 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} 1 & s_2 \\ & s_4 \end{pmatrix}} = \left(\frac{1-\theta_\perp}{2}, \frac{1+\theta_\perp}{2} \right)$
			$\varphi \begin{pmatrix} s_1 & \\ & s_4 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 & \\ & s_4 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} 1 & \\ & s_4 \end{pmatrix}} = \left(\frac{1-\theta_\perp}{2}, \frac{1+\theta_\perp}{2} \right)$
			$\varphi \begin{pmatrix} & s_2 \\ s_3 & s_4 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} & 1 \\ s_3 & s_4 \end{pmatrix}}$	$\bar{\sigma}_{\begin{pmatrix} & 1 \\ s_3 & s_4 \end{pmatrix}} = \left(\frac{1-\theta_\perp}{2}, \frac{1+\theta_\perp}{2} \right)$
4				$\varphi \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}$	$\bar{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_3 & s_4 \end{pmatrix}}$
parameter count	G^4 real	G^4 complex	$G(G-1) \times (G^2 + G - 1)$ complex	$G \times (G^2 + G - 1)$ barycentric vectors	10
random texture	all $\frac{1}{G^4}$	all 0 except $\varphi \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} = 1$	all 0	all $\frac{1}{G}$	all 0

147 Parameterization of local image statistics in terms of block probabilities. G (columns 2 through and 5) is the number
 148 of gray levels. For $G = 3$, the barycentric coordinates correspond to triangular domains, as shown in Figs. 1-3. For
 149 $G = 2$, these domains are one-dimensional, and correspond to the image statistics of [18], as shown in the
 150 rightmost column. The rows of the last three columns correspond to families of statistics.

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there was only one degree of freedom for first-order statistics— since the fraction of black and white checks must sum to 1. This single degree of freedom was captured by a single parameter γ , where $(1+\gamma)/2$ is the probability of white checks, and $(1-\gamma)/2$ is the probability of black checks. The final two columns of Table 1 specify the correspondence between the barycentric coordinates, which apply to any number of gray levels, and the binary coordinates introduced in [18] and used in previous studies.

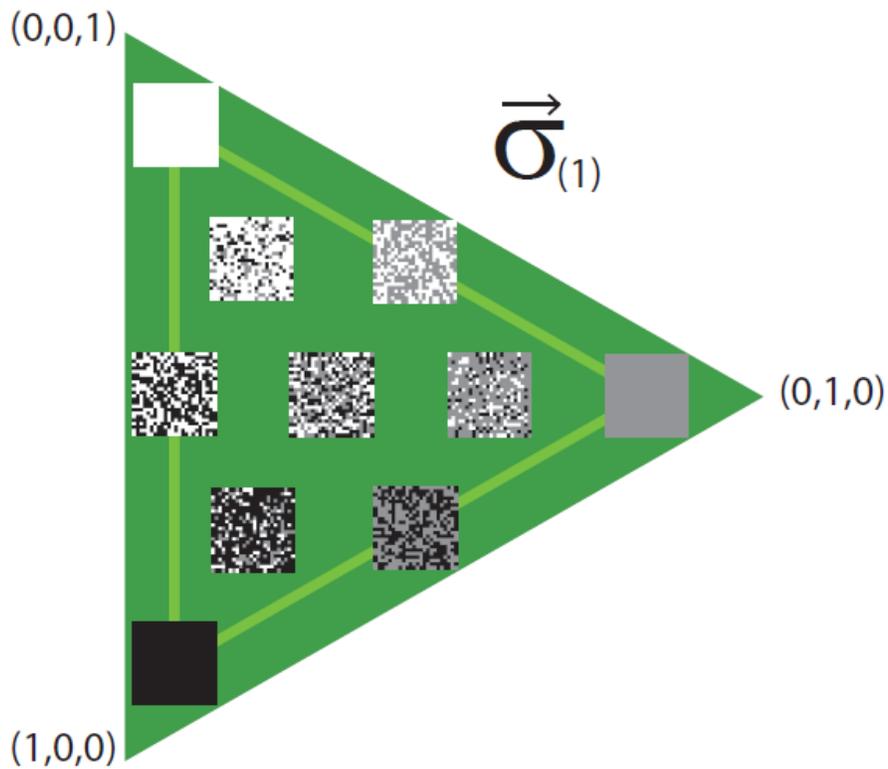


Fig. 1. The domain of the first-order statistic $\vec{\sigma}_{(1)}$ for three-level textures. $\vec{\sigma}_{(1)}$ is a three-element vector whose entries correspond to the probability of black, gray, and white checks, respectively. Since these three values must sum to 1, they can be considered as barycentric coordinates [1] (page 216) for a triangle. The vertices of the triangle are the extreme points of the domain, and correspond to the probability distributions that are all black $\vec{\sigma}_{(1)} = (1,0,0)$, all gray $\vec{\sigma}_{(1)} = (0,1,0)$, or all white $\vec{\sigma}_{(1)} = (0,0,1)$. The centroid of the triangle, which corresponds to $\vec{\sigma}_{(1)} = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$, corresponds to a random texture.

160

161 Second-order statistics

162 For second-order statistics, we detail the family of statistics that describe correlations
 163 between two horizontally-adjacent checks; the other three families of second-order statistics,
 164 which describe correlations in vertical and diagonal directions, are handled similarly.

165 There are nine ways that a pair of horizontally-adjacent checks can be colored by three

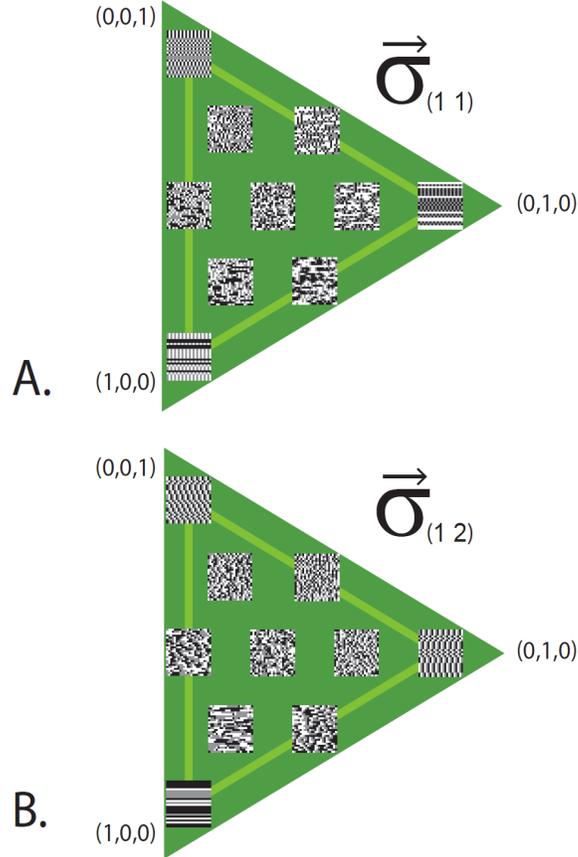


Fig. 2. The domains of the second-order statistics $\vec{\sigma}_{(1\ 1)}$ (A) and $\vec{\sigma}_{(1\ 2)}$ (B) that capture the pairwise correlation of luminance levels in horizontally-adjacent checks. Within each domain, a three-element vector $\vec{\sigma}_{(1\ s)}$ ($s = 1$ in panel A, $s = 2$ in panel B) describes the kind of horizontal correlation. Specifically, the elements of $\vec{\sigma}_{(1\ s)}$ give the probability distribution of $A_1 + sA_2 \pmod{3}$, where A_1 and A_2 are the luminance values of the checks (0 for black, 1 for gray, 2 for white). Since the three values of each $\vec{\sigma}_{(1\ s)}$ are a probability distribution and therefore sum to 1, the domain of each vector forms a triangle (as in Fig. 1). The vertices of the triangle, $\vec{\sigma}_{(1\ s)} = (1, 0, 0)$, $\vec{\sigma}_{(1\ s)} = (0, 1, 0)$, and $\vec{\sigma}_{(1\ s)} = (0, 0, 1)$, correspond to textures in $A_1 + sA_2$ is either always 0, always 1, or always 2. Therefore, the textures at the vertices have rows that are completely determined by their initial check. Also as in Fig 1. (and as in all other triangular domains), the centroid of the triangle corresponds to a random texture.

166 luminance levels. We denote these nine probabilities by $p(A_1 A_2)$, where A_1 and A_2
 167 denote the luminances (0,1, or 2) assigned to the two checks. These nine probabilities must
 168 sum to 1. There are additional constraints implied by the first-order statistics. For example,
 169 summing $p(A_1 A_2)$ over A_2 must yield $p(A_1)$, and summing $p(A_1 A_2)$ over A_1
 170 must yield $p(A_2)$. Consequently (see Supplemental Document), there are four degrees of
 171 freedom for the second-order statistics that describe horizontal correlations.

172
 173 These four parameters can be grouped into two independent triangular domains (Fig. 2),
 174 the “genera” for this family. The first domain (Fig. 2A) links luminance values by
 175 constraining the distribution of $A_1 + A_2 \pmod{3}$ (here, as is standard, “mod n ” denotes the
 176 remainder after division by n); the second (Fig. 2B) links luminance values by constraining
 177 the distribution of $A_1 + 2A_2 \pmod{3}$. In each case, the possible values of the sum are 0, 1,
 178 or 2, so the distribution of the sum is described by a three-element vector of elements that sum
 179 to 1. We denote these vectors as $\vec{\sigma}_{(1\ 1)}$ for $A_1 + A_2$ and $\vec{\sigma}_{(1\ 2)}$ for $A_1 + 2A_2$: the
 180 subscripts indicate the values of the multipliers and their positions within the 2×2
 181 neighborhood. As for the first-order statistic $\vec{\sigma}_{(1)}$, the vertices of each triangle correspond to
 182 extremes of the distribution, in which only one value of the sum occurs. The centroid of the
 183 triangle corresponds to the random texture, where each value of the sum has probability $1/3$.

184 Inspection of the texture samples at the vertices of these triangular domains shows that
 185 $\vec{\sigma}_{(1\ 1)}$ and $\vec{\sigma}_{(1\ 2)}$ describe quite different aspects of pairwise correlations. For $\vec{\sigma}_{(1\ 1)}$ (Fig.
 186 2A), each extreme texture consists of two kinds of rows: rows that contain only one
 187 luminance level, and rows that contain alternation of the other two levels. For example, for
 188 $\vec{\sigma}_{(1\ 1)} = (1, 0, 0)$ (bottom vertex of the triangle in Fig. 2A), luminance values of
 189 horizontally-adjacent check pairs must sum to 0 (mod 3). Thus, the only allowed pairs are
 190 $(0, 0)$, $(1, 2)$, and $(2, 1)$, so every row is either only black, or alternating white and gray.
 191 Similarly, for $\vec{\sigma}_{(1\ 1)} = (0, 0, 1)$ (top vertex of the triangle in Fig. 2A), luminance values of
 192 horizontally-adjacent checks must sum to 2 (mod 3). Thus, the allowed pairs are $(1, 1)$,
 193 $(2, 0)$, and $(0, 2)$ and every row is either only gray, or alternating white and black.

194 In contrast, the textures for $\vec{\sigma}_{(1\ 2)}$ have very different characteristics (Fig. 2B). At the
 195 bottom vertex, $\vec{\sigma}_{(1\ 2)} = (1, 0, 0)$ specifies that $A_1 + 2A_2$ is always equal to 0 (mod 3). This
 196 is equivalent to $A_1 = A_2 \pmod{3}$, so all rows contain just one luminance level. The other
 197 two vertices of the domain correspond to rows that cycle between the colors. For the right
 198 vertex, $\vec{\sigma}_{(1\ 2)} = (0, 1, 0)$, the coloring (reading from left to right) cycles from white to gray
 199 to black, since $\vec{\sigma}_{(1\ 2)} = (0, 1, 0)$ means that $A_1 + 2A_2 = 1 \pmod{3}$, so
 200 $A_2 = A_1 - 1 \pmod{3}$ and the allowed pairs are $(2, 1)$, $(1, 0)$, and $(0, 2)$. For the top
 201 vertex, $\vec{\sigma}_{(1\ 2)} = (0, 0, 1)$, the coloring cycles in the opposite order, since $\vec{\sigma}_{(1\ 2)} = (0, 0, 1)$
 202 means that $A_1 + 2A_2 = 2 \pmod{3}$, so $A_1 = A_2 + 2 = A_2 - 1 \pmod{3}$, yielding the
 203 allowed pairs $(0, 1)$, $(1, 2)$, and $(2, 0)$.

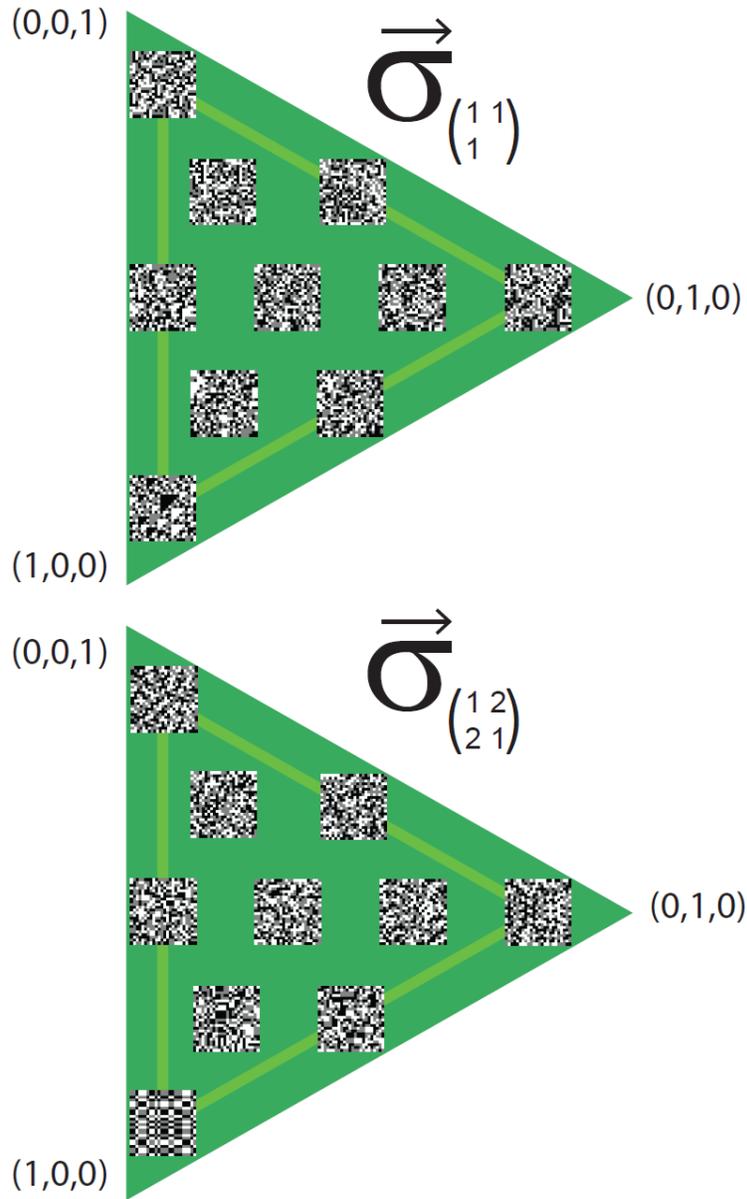


Fig. 3. A. The domain of the third-order statistics $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 \end{pmatrix}}$ that describes the correlation among the three checks

$\begin{pmatrix} A_1 & A_2 \\ A_3 \end{pmatrix}$, according to the distribution of $A_1 + A_2 + A_3 \pmod{3}$. B: The domain of the fourth-order statistics $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$

that describe correlations of luminance levels among the four checks $\begin{pmatrix} A_1 & A_2 \\ A_3 & A_4 \end{pmatrix}$ according to the distribution of $A_1 + 2A_2 + 2A_3 + A_4 \pmod{3}$. Other notations and plotting conventions as in Figs. 1 and 2.

204 Because the two combinations $A_1 + A_2$ (Fig. 2A) and $A_1 + 2A_2$ (Fig. 2B) that define the
 205 two genera are linearly independent, their probability distributions can be specified
 206 independently; we exploit this in Experiment 2.

207 The same parameterization strategy can be applied in the other grid directions, yielding a
 208 pair of vectors $\vec{\sigma}_{\binom{1}{1}}$ and $\vec{\sigma}_{\binom{1}{2}}$ for the genera within the family of correlations between pairs
 209 of checks that are vertically adjacent, the vectors $\vec{\sigma}_{\binom{1}{1}}$, $\vec{\sigma}_{\binom{1}{2}}$ for the genera within the
 210 family of correlations in the upper-left to lower-right direction, and $\vec{\sigma}_{\binom{1}{1}}$, and $\vec{\sigma}_{\binom{1}{2}}$ for
 211 the genera within the family of correlations in the upper-right to lower-left direction. We refer
 212 to $\vec{\sigma}_{\binom{1}{s}}$ and $\vec{\sigma}_{\binom{1}{s}}$ as “cardinal second-order correlations,” and to $\vec{\sigma}_{\binom{1}{s}}$ and $\vec{\sigma}_{\binom{1}{s}}$ as
 213 “diagonal second-order correlations.” Each of these eight genera have two degrees of freedom
 214 (“species”), corresponding to the triangular domain of the distribution of values for its linear
 215 combination. Thus, there are a total of 16 free parameters for the second-order correlations:
 216 four families of vectors $\vec{\sigma}_{\binom{1}{s}}$, $\vec{\sigma}_{\binom{1}{s}}$, $\vec{\sigma}_{\binom{1}{s}}$, $\vec{\sigma}_{\binom{1}{s}}$, each with two genera ($s = 1$ and
 217 $s = 2$), and these eight vectors each occupy a triangular domain. This is a substantial
 218 expansion compared to the black-and-white case, where there were a total of 4 free
 219 parameters (β_{-} , β_{+} , β_{\setminus} , and $\beta_{/}$; see Table 1).

220 We also mention the correspondence to the notation of [23] for second-order statistics: the
 221 subscripts 1 or 2 of $\vec{\sigma}$, used here, correspond to the subscripts + and - of β in [23]. The
 222 numerical notation used here generalizes more readily to multiple gray levels.

223 Third- and fourth-order statistics

224 The analogous approach provides a parameterization of third- and fourth-order
 225 correlations. For example, there is a family of third-order statistics corresponding to the

226 correlations among the three checks in the \sqcap -shaped region $\begin{pmatrix} A_1 & A_2 \\ A_3 & \end{pmatrix}$. This family is
 227 subdivided into four genera, corresponding to the distributions of the four sums
 228 $A_1 + A_2 + A_3 \pmod{3}$, $A_1 + A_2 + 2A_3 \pmod{3}$, $A_1 + 2A_2 + A_3 \pmod{3}$, and
 229 $A_1 + 2A_2 + 2A_3 \pmod{3}$, which are linearly independent. As in the second-order case,
 230 each of these genera is a triangular domain, whose coordinates indicate the probability that the
 231 sum $A_1 + s_2A_2 + s_3A_3$ is 0, 1, or 2.

232 Fig. 3A shows the domain parameterized by $\vec{\sigma}_{\binom{1}{1}}$, the vector that specifies the distribution
 233 of the sum $A_1 + A_2 + A_3 \pmod{3}$. At the bottom vertex of the triangle, $\vec{\sigma}_{\binom{1}{1}} = (1, 0, 0)$,
 234 so $A_1 + A_2 + A_3 = 0 \pmod{3}$. Since this relationship holds whenever the three A_k 's are
 235 equal, the resulting texture contains \sqcap -shaped regions uniformly black, gray, or white. At the
 236

237 other two vertices, $A_1 + A_2 + A_3 = 1 \pmod{3}$ or $A_1 + A_2 + A_3 = 2 \pmod{3}$. Every Γ -
 238 shaped region therefore must contain at least two different luminance levels. Since there are
 239 four possible orientations of a Γ -shaped region, there are four such families of third-order
 240 statistics (each with the analogous four genera, and two degrees of freedom in each genus),
 241 for a total of 32 independent third-order statistics.

242 At fourth-order, there is a single family, corresponding to the entire 2×2 neighborhood.
 243 Fig. 3B shows an example domain, corresponding to the genus $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$, which specifies the

244 distribution of $A_1 + 2A_2 + 2A_3 + A_4 \pmod{3}$. At the bottom vertex of this domain, where
 245 $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}} = (1, 0, 0)$, the texture has uniform 2×2 regions of all luminance levels. This is

246 because $A_1 + 2A_2 + 2A_3 + A_4 = 0 \pmod{3}$ is equivalent to
 247 $A_1 + A_4 = A_2 + A_3 = 0 \pmod{3}$, which holds for any constant value of the A_k . In total,
 248 there are 16 independent fourth-order statistics, corresponding to the eight genera, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}}$,

249 $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 1 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 2 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 1 & 2 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}}$, and $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 2 \end{pmatrix}}$, each of which is a

250 triangular domain with two free parameters. For further details and correspondences to the
 251 black-and-white case, see Table 1 and the Supplemental Document (“Specification and
 252 construction of textures”).
 253

254 Experiment 1: Individual texture statistics, three luminance levels

255 Experiment 1 quantifies sensitivity within each of the triangular domains (genera)
 256 described above: one first-order domain (Fig. 1), eight second-order domains (two examples
 257 shown in Fig. 2), 16 third-order domains (an example shown in Fig. 3A), and eight fourth-
 258 order domains (an example shown in Fig. 3B). The burden of studying these 33 domains, each
 259 containing two degrees of freedom, may be reduced by recognizing that many of them are
 260 interrelated by spatial symmetries. For example, exchanging horizontal and vertical axes

261 interconverts $\vec{\sigma}_{\begin{pmatrix} 1 & s \\ s & s \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 \\ s \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_3 & s_3 \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_2 & s_3 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & s_3 \\ s_2 & s_3 \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 & s_2 \\ s_3 & s_4 \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 & s_3 \\ s_2 & s_4 \end{pmatrix}}$, etc.

262 Additional symmetries include mirror-flips and 90-deg rotations. Previous work with black-
 263 and-white textures showed that statistics related by these symmetries had the same thresholds
 264 [13], and, in preliminary experiments, we verified that this equivalence held for the cardinal
 265 second-order correlations in the textures with three luminance levels. We therefore limited our
 266 analysis to 12 domains, from which all other domains could be obtained via a symmetry

267 operation. These domains were: the first-order domain $\vec{\sigma}^{(1)}$; the second-order domains
 268 $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 1 & 2 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 2 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}}$, and $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 2 \end{pmatrix}}$;

269 and the fourth-order domains $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 2 \end{pmatrix}}$, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}}$, and $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$.

270

271 To measure sensitivity to these statistics, we determined psychophysical thresholds in a
 272 standard texture-segmentation task ([17], described below) via a method of constant stimuli.
 273 For each threshold measurement, stimuli were defined by equally-spaced points lying along
 274 12 rays in the triangular domain. Each ray began at the origin of the domain (the random
 275 texture) and extended either towards a vertex, or to points that were equally spaced along the
 276 edges of the domain. The distances of the endpoints from the origin were chosen based on
 277 pilot experiments so that the texture contrasts would capture the transition between
 278 subthreshold and suprathreshold performance. For the first-order statistics, an additional set
 279 of 12 rays were interleaved to better delineate the threshold behavior. These specifics are
 280 detailed in the Supplemental Document, Figure S1.

281 For construction of psychophysical curves and quantification of thresholds, the texture
 282 contrast c is defined as the distance from the origin (i.e., the centroid of the domain), scaled
 283 so that the vertices of each domain have a texture contrast of 1.

284 Experiment 2: Pairs of texture statistics, three luminance levels

285 Experiment 2 quantifies sensitivity to combinations of image statistics drawn from
 286 different triangular domains (genera). We focused on combinations of cardinal second-order
 287 statistics, as sensitivity to these statistics was high, and included interactions between image
 288 statistics that specify correlations in the same spatial orientation (i.e., between two image
 289 statistics from the $\vec{\sigma}_{(1\ s)}$ -family) as well as interactions between image statistics that specify
 290 correlations in different orientations (i.e., between the $\vec{\sigma}_{(1\ s)}$ -family and the $\vec{\sigma}_{\begin{pmatrix} 1 \\ s \end{pmatrix}}$ -family).

291 Fig. 4A,B shows stimuli that probe interactions between correlations in the $\vec{\sigma}_{(1\ s)}$ -family,
 292 but drawn from different genera: $\vec{\sigma}_{(1\ 1)}$ (along the abscissae of the panels) and $\vec{\sigma}_{(1\ 2)}$ (along
 293 the ordinates of the panels). The panels differ in terms of the species of the $\vec{\sigma}_{(1\ 1)}$ genus that
 294 lies along the abscissa: in Fig. 4A, it is in the direction of the $(1, 0, 0)$ -vertex of the $\vec{\sigma}_{(1\ 1)}$ -
 295 domain; in Fig. 4B, it is in the direction of the $(0, 0, 1)$ -vertex. In both cases, the ordinate is
 296 in the direction of the $(1, 0, 0)$ -vertex of the $\vec{\sigma}_{(1\ 2)}$ -domain. Not all combinations of
 297 coordinates are represented in these panels, because extreme values of one coordinate limit
 298 values of the other – but these limits were beyond the range needed to determine thresholds.
 299

300 Fig. 4C,D shows stimuli that probe interactions in different spatial directions: $\vec{\sigma}_{\begin{pmatrix} 1 \\ 2 \end{pmatrix}}$, along
 301 the ordinate, and $\vec{\sigma}_{(1\ 2)}$, along the abscissa. In both cases, the ordinate is in the direction of
 302 the $(1, 0, 0)$ -vertex of the $\vec{\sigma}_{\begin{pmatrix} 1 \\ 2 \end{pmatrix}}$ -domain. In Fig. 4C, the abscissa is in the direction of the
 303 $(1, 0, 0)$ -vertex in the $\vec{\sigma}_{(1\ 2)}$ -domain; in Fig. 4D, the abscissa is in the direction of the
 304 $(0, 1, 0)$ -vertex of that domain.

305 Experiments were organized into four groups. Group I examined interactions between
 306 different statistics with the same family ($\vec{\sigma}_{(1\ 1)}$ and $\vec{\sigma}_{(1\ 2)}$), as in Fig. 4A,B); the other
 307 groups probed interactions between statistics from different families, describing correlations

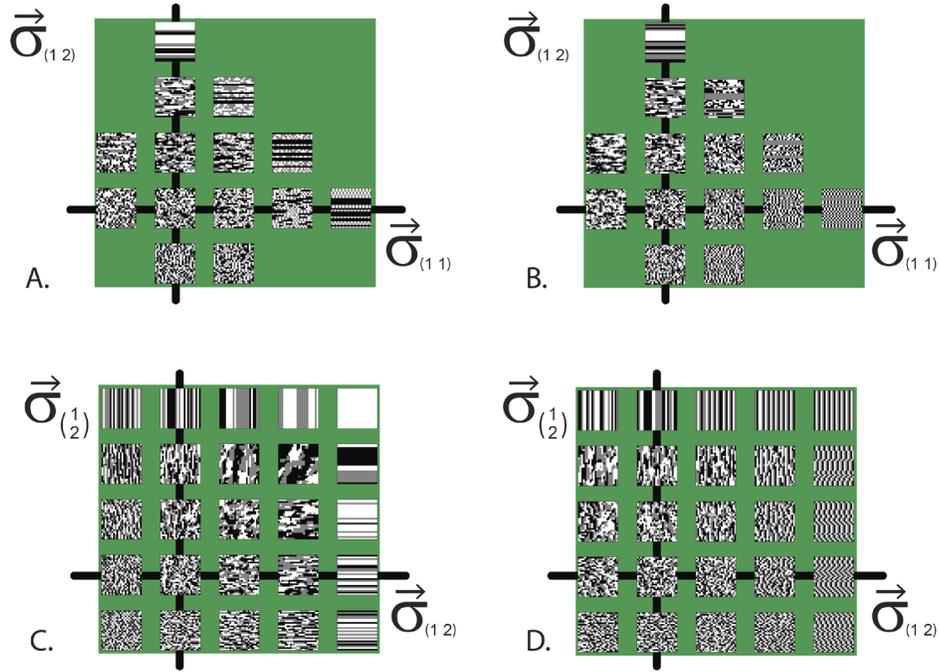


Fig. 4. The domain generated by specifying a pair of cardinal second-order statistics. In each case, the random texture is at the origin, indicated by the intersection of the two solid black lines. Panels A and B: The statistics are $\bar{\sigma}_{(1,1)}$ and $\bar{\sigma}_{(1,2)}$, both specifying horizontal correlations. In A, the abscissa indicates values of $\bar{\sigma}_{(1,1)}$, ranging from $(\frac{1}{9}, \frac{4}{9}, \frac{4}{9})$ to $(1, 0, 0)$; this corresponds to the ray pointing towards the lower vertex of Fig. 2A. The ordinate indicates values of $\bar{\sigma}_{(1,2)}$ over the same range; this corresponds to the ray pointing towards the lower vertex of Fig. 2B. Steps along each axis are equal to $(\frac{2}{9}, -\frac{1}{9}, -\frac{1}{9})$. In B, the ordinate is the same as in A, but the abscissa now indicates values of $\bar{\sigma}_{(1,1)}$ ranging from $(\frac{4}{9}, \frac{4}{9}, \frac{1}{9})$ to $(0, 0, 1)$, corresponding to the ray pointing towards the upper vertex in Fig. 2A. Here, abscissa steps are equal to $(-\frac{1}{9}, -\frac{1}{9}, \frac{2}{9})$. Panels C and D: The statistics are $\bar{\sigma}_{(1,2)}$ and $\bar{\sigma}_{(2)}$, specifying horizontal and vertical correlations, respectively. In C, the abscissa indicates values of $\bar{\sigma}_{(1,2)}$, ranging from $(\frac{1}{9}, \frac{4}{9}, \frac{4}{9})$ to $(1, 0, 0)$; this corresponds to the ray pointing towards the lower vertex of Fig 2B. The ordinate indicates values of $\bar{\sigma}_{(2)}$ over the same range; this corresponds the same kind of correlation, but now in the vertical direction. Steps along each axis are equal to $(\frac{2}{9}, -\frac{1}{9}, -\frac{1}{9})$. In D, the ordinate is the same as in C but the abscissa now indicates values of $\bar{\sigma}_{(1,2)}$ ranging from $(\frac{4}{9}, \frac{1}{9}, \frac{4}{9})$ to $(0, 1, 0)$, corresponding to the ray pointing towards the right vertex in Fig. 2B. Here, abscissa steps are equal to $(-\frac{1}{9}, \frac{2}{9}, -\frac{1}{9})$. In all panels, the coordinates at the origin are equal to $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$, corresponding to the random texture.

308 in orthogonal directions, $\bar{\sigma}_{(1,s)}$ and $\bar{\sigma}_{(1,s')}$: with $(s, s') = (1, 1)$ in group II, $(s, s') = (1, 2)$

309 in group III, and $(s, s') = (2, 2)$ in group IV (the latter shown in Fig. 4C,D). These domains
 310 included 22 pairs of statistics, each sampled along rays in 12 equally-spaced directions. As
 311 was the case for Experiment 1, the positions of the three points sampled along each ray were
 312 determined by pilot studies to ensure that they would be effective for measuring thresholds;
 313 further details are provided in the Supplemental Document, Figure S2 and Table S1. Also as
 314 in Experiment 1, texture contrast c is defined as the distance from the origin, scaled so that
 315 the vertices of each domain have a texture contrast of $c = 1$.

316 2.2 Stimuli for experiment 3

317 The last set of experiments makes use of textures with up to 11 luminance levels. We focused
 318 on second-order statistics that provided tests of the computational model complementary to
 319 the data of Experiments 1 and 2. Specifically, we selected members of the second-order
 320 families $\vec{\sigma}_{(1\ s)}$ and $\vec{\sigma}_{\binom{1}{s'}}$ that specify progressively smoother gradients as further gray levels

321 were added, and a contrasting set of statistics that does not specify gradients.

322 The textures that probe these statistics are shown in Fig. 5, for the number of gray levels
 323 (3, 4, 5, 7, and 11) used in these experiments. Within each of the “gradient” stimuli (the
 324 individual patches in Fig. 5A), luminances tend to increase gradually in one direction (here,
 325 left-to-right), and then reset abruptly from white to black. This progression is clearest for the
 326 examples with maximum correlation strength ($c = 1$). In the “streaks” (Fig. 5B), luminances
 327 of adjacent checks (here, horizontal) tend to match, leading to elongated streaks as correlation
 328 strength increases. In all cases, a correlation strength of 0 corresponds to the random texture,
 329 and the maximum correlation strength is 1.

330 The statistics underlying these textures are specified by an extension of the formalism
 331 used above for three-luminance textures (see Table 1 and Supplemental Document). The G
 332 gray levels are designated by $0, 1, \dots, G-1$, where, by convention, we take 0 to indicate a
 333 gray-level of black, and $G-1$ to indicate a gray-level of white. A horizontal second-order
 334 image statistic $\vec{\sigma}_{(1\ s)}$ is specified by a vector $(v_0, v_1, \dots, v_{G-1})$ of length G , each entry v_h
 335 is the probability that $A_1 + sA_2 = h \pmod{G}$. Vertical second-order image statistics $\vec{\sigma}_{\binom{1}{s}}$
 336 are specified analogously. All coordinates are non-negative and must sum to 1, and the
 337 random texture corresponds to a vector $(v_0, v_1, \dots, v_{G-1})$ with all entries equal to $1/G$. Note
 338 that G , the number of gray levels, and c , the texture contrast, are independent. The G gray
 339 levels always include black and white and $G-2$ equally-spaced intermediate values, and
 340 each gray level occurs in $1/G$ of the checks. Independently, c , the texture contrast,
 341 indicates the departure of the spatial arrangement from randomness.

342 A left-to-right gradient texture can be represented in these coordinates as follows. In a left-
 343 to-right gradient, the probability that $A_2 = A_1 + 1$ is increased. This is equivalent to an
 344 increase in the probability that $A_1 - A_2 = -1 \pmod{G}$, i.e., that
 345 $A_1 + (G-1)A_2 = G-1 \pmod{G}$. Thus, the relevant image statistic is $\vec{\sigma}_{(1\ G-1)}$, and its
 346 final $((G-1)$ th) entry captures this increase. Since the bias increases linearly with
 347 correlation strength, the parameterization of this gamut of textures is given by

$$348 \vec{\sigma}_{(1\ G-1)} = (1-c)\left(\frac{1}{G}, \frac{1}{G}, \dots, \frac{1}{G}, \frac{1}{G}\right) + c(0, 0, \dots, 0, 1). \quad (1)$$

349 At maximum correlation strength ($c = 1$), $G - 1$ is the only permissible value of
 350 $A_1 + (G - 1)A_2 \pmod{G}$, so that $A_2 = A_1 + 1 \pmod{G}$ -- yielding a strict gradient with
 351 luminances increasing to the right. At zero correlation strength ($c = 0$), all values are equally
 352 likely, yielding a random texture. These conventions are consistent with that of Experiments 1
 353 and 2, in which $c = 0$ corresponds to a random texture and $c = 1$ corresponds to a
 354 maximally-structured texture at a vertex of the domain.

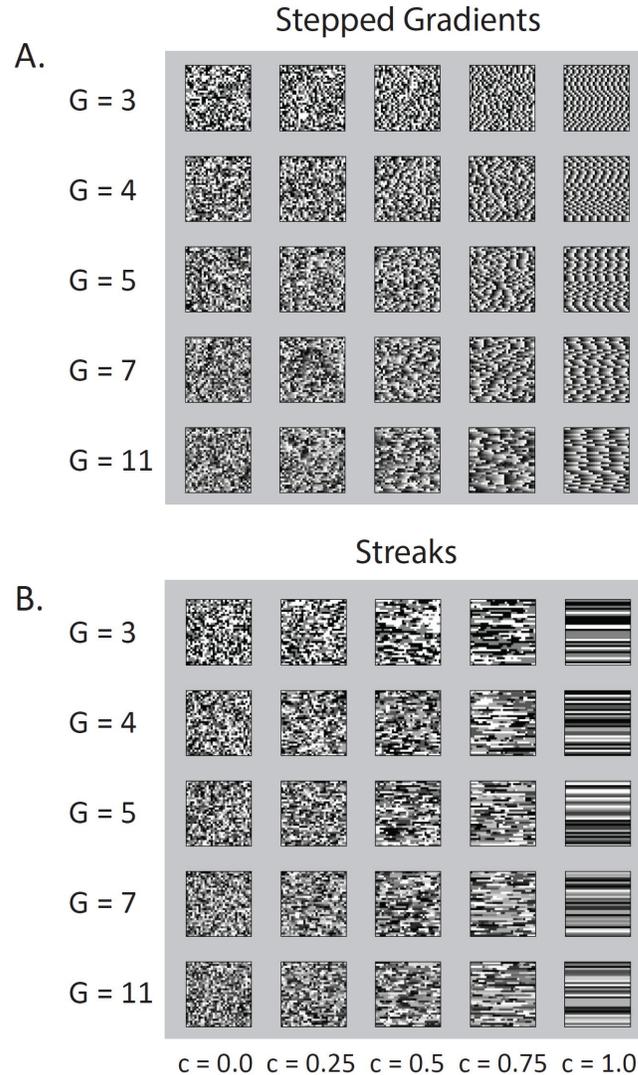


Fig. 5. Examples of textures used in Experiment 3: gradients (A) and streaks (B). Number of gray levels indicated by G . Gradient textures have a directionality -- in the examples shown here, from left to right. In the direction of the gradient, the choice of luminance in each check is biased towards a stepwise increase from black to white, followed by an abrupt decrease to black. This is most evident in the examples with maximal correlation strength (right end of each row, $c = 1$): here, luminances in each row of checks progressively increase from black to white and then reset to black; the phase of each row is random. Streak textures (B) have an orientation -- in the examples shown here, horizontal -- but not a directionality. Along the specified orientation, the choice of luminance in each check is biased to match its neighbor. At maximal correlation strength (right end of each row, $c = 1$), this results in rows of checks whose luminance is constant. In all cases, a correlation strength of 0 corresponds to the random texture.

355 Similarly, a leftward gradient texture is specified by increasing the probability that
 356 $A_2 = A_1 - 1$, i.e., that $A_1 - A_2 = 1 \pmod{G}$. So these textures are parameterized by

357
$$\vec{\sigma}_{(1 \ G-1)} = (1-c)\left(\frac{1}{G}, \frac{1}{G}, \dots, \frac{1}{G}, \frac{1}{G}\right) + c(0, 1, \dots, 0, 0). \quad (2)$$

358 Streaks are created by increasing the probability that $A_2 = A_1$, i.e., that
 359 $A_1 - A_2 = 0 \pmod{G}$. Thus, streaks are parameterized by

360
$$\vec{\sigma}_{(1 \ G-1)} = (1-c)\left(\frac{1}{G}, \frac{1}{G}, \dots, \frac{1}{G}, \frac{1}{G}\right) + c(1, 0, \dots, 0, 0). \quad (3)$$

361 Downward and upward gradients and vertical streaks are parameterized in a similar fashion,
 362 with $\vec{\sigma}_{\begin{pmatrix} 1 \\ G-1 \end{pmatrix}}$ replacing $\vec{\sigma}_{(1 \ G-1)}$.

363 As in Experiments 1 and 2, $c = 0$ corresponds to the random texture and $c = 1$
 364 corresponds to maximal correlation strength – periodic ramps for the gradient texture (eqs. (1)
 365 and (2)), and unbroken lines of constant luminance for the streak texture (eq. (3)).
 366

367 **2.3 Subjects**

368 Studies were conducted in 10 normal subjects (3 male, 7 female), ages 21 to 55. Two of the
 369 subjects (MC and SR) were experienced psychophysical observers. MC, SR, and JB are
 370 authors; LE assisted with the studies; the other observers were naïve to the purposes of the
 371 experiment. All subjects had visual acuities (corrected if necessary) of 20/20 or better.

372 Experiment 1 was conducted in five subjects (MC, SR, NM, WC, ZA) for all first- and
 373 second-order statistics, and for all third- and fourth-order statistics for which thresholds could
 374 be obtained. For Experiment 2, group I was conducted in MC and WC, group II in MC and
 375 ZA, group III in MC and JB, and group IV in MC, WC, ZA, and JB. Experiment 3 was
 376 conducted in six subjects (MC, IL, LE, YCL, EFV, PJ).

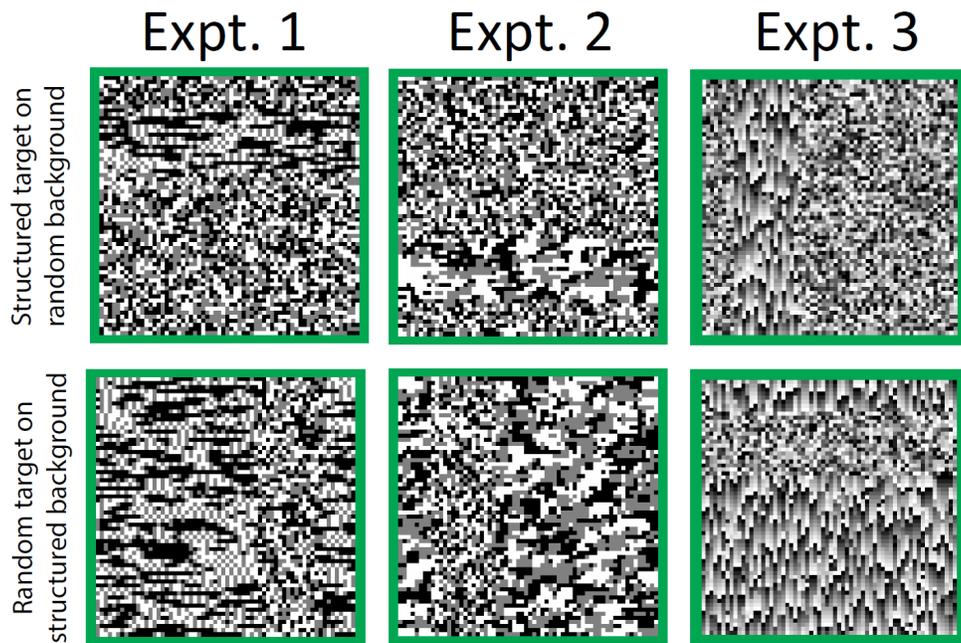
377 This work was carried out in accordance with the Code of Ethics of the World Medical
 378 Association (Declaration of Helsinki), following approval of the Institutional Review Board
 379 of Weill Cornell, and consent of the individual subjects.

380 **2.4 Segmentation task**

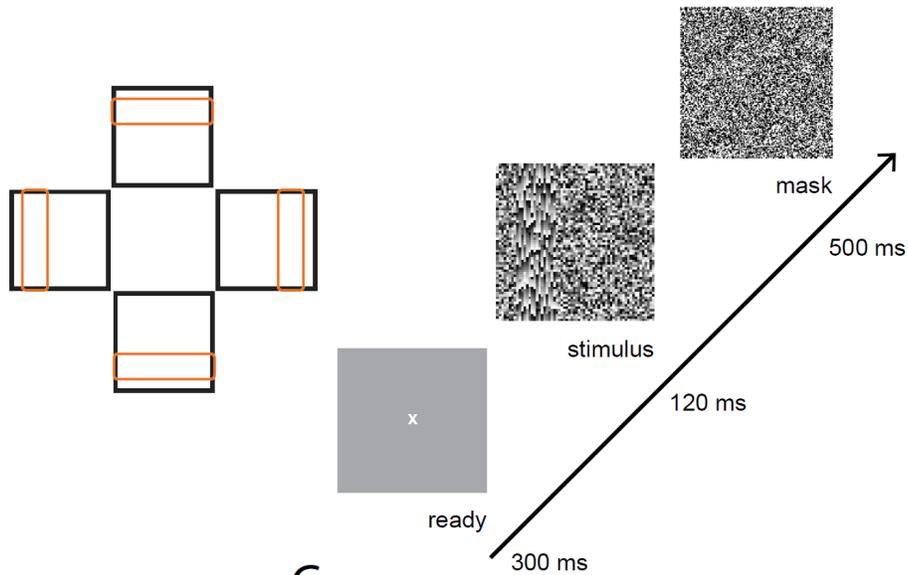
381 For the three experiments, segmentation thresholds were measured in a four-alternative task
 382 adapted from the one developed by Chubb et al., [17] and identical to what was used in
 383 related previous studies[13, 27, 28]. We describe it below for the reader’s convenience, along
 384 with the initial analysis steps.

385 All stimuli consisted of 64×64 arrays of checks; each contained an embedded 16×64
 386 rectangular target whose outer edge was 8 checks from one of the four sides of the array.
 387 Target and background regions were filled either with a structured texture drawn from one of
 388 the domains described above, or a contrasting texture. The contrasting texture was fully
 389 random, i.e., each check was independently colored with one of G equally-spaced luminance
 390 values from black to white, each with probability $1/G$ ($G = 3$ in Experiments 1 and 2;
 391 $G \in \{3, 4, 5, 7, 11\}$ in Experiment 3). To ensure that the subject performed the task by
 392 identifying a texture boundary, rather than a texture gradient [31], half of the trials had a
 393 structured target on a random background and half had a random target on a structured
 394 background. Examples of both kinds of stimuli (structured target on random background,
 395 random target on structured background) are shown in Fig. 6A, and the four alternative target
 396 positions are shown in Fig. 6B.

397 As previous work showed no consistent threshold difference between these conditions, we
 398 pooled data across this randomization. We also found no consistent difference between



A.



B.

C.

Fig. 6. A: Stimulus examples for the three experiments. Stimulus parameters: Experiment 1, from domain of Fig. 2A, with $\vec{\sigma}_{(1)} = [0.75, 0.25, 0]$ (texture contrast $c = 0.66$); Experiment 2, from domain of Fig. 4C, $\vec{\sigma}_{(2)} = [0.6218 \ 0.1891 \ 0.1891]$ and $\vec{\sigma}_{(1)} = [0.5 \ 0.25 \ 0.25]$ (texture contrast $c = 0.5$); Experiment 3, from Fig. 5A, with $G = 11$ gray levels and texture contrast $c = 0.8$. All of these texture contrasts are suprathreshold. B: The four alternative target positions. C: Trial timeline.

399

thresholds for horizontal vs. vertical stimuli in Experiment 3, and therefore pooled across

400 these conditions. Note also that, while this task has a “global” component in the sense that
401 evidence can be pooled across the entire stimulus, this global aspect is constant across all
402 stimuli; the limiting factor is the information contained in local correlations, which is
403 stimulus-dependent.

404 In Experiment 1, each test session explored a triangular domain specified by a texture-
405 statistic genus; examples of these domains are shown in Fig. 1 (first-order), Fig. 2 (second-
406 order), and Fig. 3 (third- and fourth-order). Second-, third-, and fourth-order domains were
407 sampled along 12 rays (Fig. S1A,B); the first-order domain was sampled along 24 rays (Fig.
408 S1C) in separate sessions of 12 rays each. Three texture contrasts were chosen along each ray
409 to span the range from near-chance performance to near-perfect performance in pilot
410 experiments, or, if performance did not achieve near-perfect performance, at texture contrasts
411 (c) of $1/3$, $2/3$, and 1. A single test session contained 8 examples of stimuli specified by
412 all three texture contrasts on the 12 rays; these 8 examples included each of the four target
413 positions, and in both target-structured and background-structured conditions, yielding
414 $3 \times 12 \times 4 \times 2 = 288$ unique trials, presented in random order. We collected responses to 15
415 such 288-trial blocks from each subject, yielding 120 judgments for each of the three contrast
416 levels on each ray. For third- and fourth-order statistics, results from two subjects (MC, SR)
417 showed that sensitivity was largely restricted to a subset of three rays; in these domains, the
418 other subjects (NM, WC, ZA) were tested with only these three rays. In these cases, blocks
419 contained 32 examples of each contrast level on each ray and 4 such blocks were obtained,
420 yielding 128 judgments for each contrast level on each ray.

421 Experiment 2 was organized similarly, with each test session devoted to a domain
422 specified by a pair of second-order texture statistics; examples are shown in Fig. 4 and the
423 sampling strategy is given in Table S1 and Fig. S2.

424 In Experiment 3, each test session consisted of stimuli with a fixed number of gray levels
425 (3, 4, 5, 7, or 11), and included both gradient stimuli (eqs. (1) and (2)) and streak stimuli (eq
426 (3)). To cover the range of performance, five texture contrasts were used:
427 $c \in \{0.2, 0.3, 0.45, 0.6, 0.8\}$ for the gradient stimuli, and $2/3$ of these values for the streak
428 stimuli. There were 6 kinds of stimuli: gradients in each of the four cardinal directions
429 contrasted with the random texture, and streaks in horizontal and vertical orientations
430 contrasted with the random texture. As in Experiments 1 and 2, targets appeared in each of
431 four possible positions, and the textures used to render the target and background were
432 swapped in half of the trials. Thus, there were $5 \times 6 \times 4 \times 2 = 240$ unique trials, presented in
433 random order. We collected responses to 12 such blocks from each subject, yielding 96
434 judgments for each of the five contrast levels and the six kinds of stimuli.

435 We collected data from six subjects (MC, IL, LE, YCL, EFV, PJ) for 3, 5, and 11 gray
436 levels and in four of these (MC, YCL, EFV, and PJ) for 4 and 7 gray levels.

437 2.5 Procedure

438 The procedure for the three experiments was similar to that of previous studies [13, 27, 28]
439 and is summarized here. A Cambridge Research ViSaGe system, running custom Delphi
440 software produced the stimuli and collected responses. Stimuli were displayed on an LCD
441 monitor (mean luminance of 23 cd/m^2 , refresh rate 60 Hz), beginning 300 ms after the subject
442 pressed a “ready” button. Stimuli had a duration of 120 ms, and were followed by a 500-ms
443 mask consisting of checks that were half the size of the stimulus checks, randomly filled with
444 the luminance levels used in the experiment (see Fig. 6C for the timeline). The display size
445 was $15 \times 15 \text{ deg}$ (64×64 checks, 14.8 min each, each check consisting of 10×10 monitor
446 pixels); viewing was binocular at 100 cm, and contrast was 1. Note that the checks were
447 sufficiently large so that, even at the edges of the display, they were plainly visible[32], and
448 previous work with black-and-white textures showed that thresholds are approximately scale-
449 invariant at and below this check size [13]. ViSaGe software and its photometer was used to

450 linearize the monitor’s output via a look-up table, which was recalibrated prior to each
451 experimental session. Thus, the luminance levels used ranged from 0 cd/m² (black checks) to
452 46 cd/m² (white checks). The gray checks in Experiments 1 and 2 were 23 cd/m²; the gray
453 checks in Experiment 3 had luminance levels equally spaced between 0 and 46 cd/m² – for
454 example, for $G = 5$, the luminance levels were 0, 11.5, 23, 34.5, and 46 cd/m².

455 Subjects were informed that on every trial, a target would be present, and was equally
456 likely to be in any of four positions (top, right, bottom, left), which they were to indicate by
457 pressing the corresponding button on a four-button response box. They were asked to fixate
458 centrally and not attempt to scan the stimulus. Trials were self-paced, triggered by a separate
459 button-press. Inexperienced subjects received practice of approximately two hours to become
460 accustomed to the brief stimulus presentation time and to practice maintaining central fixation
461 without scanning. During practice, but not during data collection, subjects received auditory
462 feedback for incorrect responses.

463 2.6 Analysis

464 For each stimulus type (i.e., for each ray in the texture domains of Experiments 1 and 2, and
465 for each kind of gradient or streak in Experiment 3), we determined the texture contrast
466 threshold for segregation, via a procedure similar to that used in previous studies [13, 26, 27],
467 as summarized here. First, for each set of responses to a given stimulus type, we found the
468 maximum-likelihood fit of a Weibull function to the observed fraction correct (FC):

$$469 \quad FC(c) = \frac{1}{4} + \frac{3}{4} \left(1 - 2^{-(c/a_r)^{b_r}} \right). \quad (4)$$

470 As above, c is the texture contrast, defined as the distance to the fully random texture (the
471 centroid), normalized by the distance from the vertex to the centroid. a_r is the fitted threshold
472 (i.e., the value of c at which FC=0.625, halfway between chance (0.25), and perfect (1.0)),
473 and b_r is the Weibull shape parameter. As previously reported [13, 27], the shape parameter
474 b_r typically had similar values across rays, with overlapping confidence limits that usually
475 included the range 2.2 to 2.7. Since our focus is on determining the thresholds, we then refit
476 the data from each experiment by a set of Weibull functions that shared a common shape
477 parameter b , while allowing the threshold parameter a_r to vary freely across rays. This
478 procedure reduced the number of free parameters without altering the quality of the fit to
479 Weibull functions. 95% confidence intervals were determined via 1000-sample bootstraps.
480 Note that this procedure could yield an estimated threshold $a_r > 1$, i.e., beyond the boundary
481 of the texture domain, if performance was above chance but never reached a FC of 0.625.

482 Sensitivity was defined as 1/threshold, with corresponding confidence intervals. Across-
483 subject averages of sensitivities or thresholds are computed as the geometric means, and
484 statistics are computed on the logarithms of the raw values. All calculations were carried out
485 with in-house MATLAB (MathWorks, Natick, MA) software, which was also used to
486 synthesize the stimuli described above.

487

488 3. Model

489 Here we describe a computational model for discrimination thresholds for textures that
490 contain multiple gray levels and spatial correlations (Fig. 7). As a starting point, we used two
491 complementary sets of psychophysical studies: studies of textures with multiple gray levels
492 but without spatial correlation (“IID textures”), and studies with spatial correlation but only
493 black and white checks. These studies were carried out with different paradigms, in separate
494 labs, and with separate subjects. The model described here is fully constrained by these

495 studies and makes explicit predictions for discrimination thresholds for textures that include
 496 multiple gray levels and spatial correlations.

497 In overview, the model (Fig. 7) is as follows. The first stage of the model accounts for
 498 sensitivity to IID textures by recasting the mechanisms proposed by the studies of Chubb and
 499 colleagues [14, 16, 17, 33] as stochastic thresholds, rather than gray-level sensitivities. This
 500 stage yields a set of internal representations, one for each of the original Chubb mechanisms.
 501 The second stage of the model then processes the local correlations within these internal
 502 representations. The computations used to do this are the same as those deduced in our
 503 previous studies [13, 18, 27, 28] that focused on black-and-white textures.

504 We note that, while we describe the model’s computations in terms of the texture
 505 coordinates introduced above, the model operates directly on the visual input. Thus, it makes
 506 predictions that are independent of the coordinates used to parameterize the textures, it treats
 507 all orders of correlation together, and it is not restricted to the textures that lie within the space
 508 we consider.
 509

510 3.1 First stage: sensitivity to gray-level distribution

511 Chubb and colleagues [14, 17, 33] showed that discrimination of IID textures could be
 512 accounted for by three “dimensions:” one dimension approximating the mean luminance, a
 513 second dimension approximating variance, and a third dimension signaling the fraction of
 514 very dark checks (“blackshot”). Coordinates along dimension m were linear functions of the
 515 histogram distribution:

$$516 \quad c_m = \sum_i D_m(x_i)g(x_i), \quad (5)$$

517 where the sum ranges over the gray levels in the texture, $g(x)$ is the frequency with which
 518 gray level x occurs, and $D_m(x)$ is the extent to which a gray level x contributes to
 519 mechanism m . IID textures that shared the same coordinates (c_1, c_2, c_3) were
 520 indistinguishable, even if their gray-level distributions were disparate. Using an asymmetric
 521 search task, they later [16] showed that these three dimensions derived from the activations of
 522 four underlying mechanisms, which were also linear functions of the histogram distribution:

$$523 \quad a_m = \sum_i F_m(x_i)g(x_i), \quad (6)$$

524 These four mechanisms are necessarily linearly dependent, since they are constrained to
 525 yield the three dimensions of eq. (5) above. For textures with nine equally-spaced gray values
 526 $\{0, 1/8, \dots, 7/8, 1\}$, [16] determined consensus values of the linear functions of $F_m(x_i)$
 527 across three subjects, along with the relative weightings with which each subject used these
 528 mechanisms. These data were kindly provided by C. Chubb and are given in Table S2. The
 529 correspondence to the nomenclature of [16] is as follows: F_1 and F_2 correspond to the two
 530 complementary quasilinear mechanisms (their $F_{*,3}$ and $F_{*,4}$); F_3 corresponds to the
 531 blackshot-like mechanism (their $F_{*,1}$), and F_4 corresponds to the mechanism sensitive to
 532 midrange grays (their $F_{*,2}$).

533 To apply these data to general gray-level distributions, we interpolated these values via a
 534 cubic spline. Thus, for a texture in which $g(x)\Delta x$ is the fraction of checks with gray levels
 535 between x and $x + \Delta x$, the “activation” produced in mechanism m ($m \in \{1, 2, 3, 4\}$) is
 536 given by

537
$$a_m = \int_0^1 F_m(x)g(x)dx. \quad (7)$$

A Model Framework

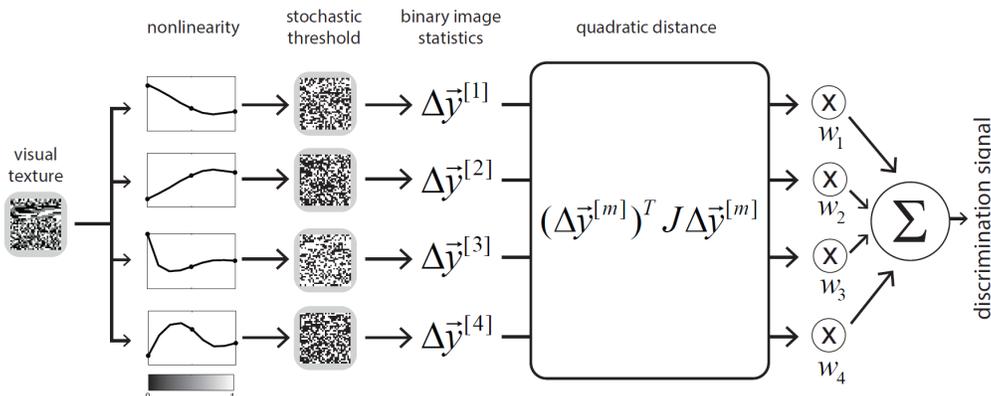


Fig. 7. A model for discrimination of textures with multiple gray levels and spatial correlations, illustrating how it acts on the visual stimuli used here. The four curves labeled “nonlinearity” show the mechanisms F_m^{prob} (eq. (8)). For further details, see text.

538 In our model, we recast each Silva and Chubb mechanism m as a probabilistic
 539 conversion to an internal representation I_m of the original texture. Specifically, we interpret
 540 $F_m(x)$ as a nonlinear function of the gray level, whose value at each location in the texture
 541 determines the probability that the original check is internally represented in the “high” state
 542 (designated 1), vs. the “low” state (designated 0). The probability that a check of gray-level
 543 x is converted to 1 by mechanism m is given by

544
$$F_m^{prob}(x) = \frac{1}{2} \left(1 + \frac{F_m(x)}{\max_{m,x} |F|} \right). \quad (8)$$

545 This remaps the zero-centered $F_m(x)$ ’s to quantities $F_m^{prob}(x)$ that range from 0 to 1, as
 546 shown by the nonlinearities in Fig. 7. We postulate that this stochastic conversion from gray-
 547 level to a binary representation is independent at each check and across the mechanisms.

548 In this re-interpretation, the spatial average $\langle I_m \rangle$ of the internal representation of a
 549 texture with luminance distribution $g(x)$ corresponds to the activation produced by the
 550 mechanism in the original formulation, other than a fixed offset and proportionality constant:

$$\begin{aligned}
\langle I_m \rangle &= \langle F_m^{prob}(x) \rangle = \int_0^1 F_m^{prob}(x) g(x) dx = \frac{1}{2} \int_0^1 \left(1 + \frac{F_m(x)}{\max_{m,x} |F|} \right) g(x) dx \\
&= \frac{1}{2} + \frac{1}{2 \max_{m,x} |F|} \int_0^1 F_m(x) g(x) dx = \frac{1}{2} \left(1 + \frac{a_m}{\max_{m,x} |F|} \right)
\end{aligned} \tag{9}$$

where we have used eq. (7) and $\int_0^1 g(x) dx = 1$, since it is a probability distribution. This

means that two textures are indistinguishable in the original Chubb model if, for each mechanism, their internal representations in the present model have identical average values.

3.2 Second stage: sensitivity to spatial structure

The influence of the spatial organization of these internal representations is addressed by the second stage of the model. Specifically, we posit that texture discrimination is based on comparing the local statistics of these internal representations, and that the local statistics are compared according to the model [13] for black-and-white textures. That model posited that discrimination of a locally-correlated black-and-white texture from a random texture could be accounted for by 10 local image statistics. These quantities, which correspond to the local

image statistics introduced above for $G = 2$ ($\gamma, \beta_-, \beta_+, \beta_\setminus, \beta_\wedge, \theta_\perp, \theta_\lrcorner, \theta_\top, \theta_\ulcorner, \alpha$)

are here collectively denoted by the column vector $\vec{y} = (y_1, y_2, \dots, y_{10})$ to facilitate a compact notation. Sensitivity to these image statistics and their combinations was specified

by a 10×10 symmetric matrix Q , with the threshold for discrimination from a random texture given by an ellipsoid,

$$\vec{y}^T Q \vec{y} = \sum_{i,j=1}^{10} Q_{ij} y_i y_j = S \tag{10}$$

Q is constrained not only by cross-diagonal symmetry ($Q_{ij} = Q_{ji}$), but also by the empirical finding that thresholds are unchanged after 90° -deg rotations of a texture, and after mirroring a texture in the cardinal axes. This leaves a total of 20 free parameters for Q . [13] determined these parameters (for $S = 1$) in 4 subjects (one of whom, MC, was a subject in the present studies) and validated them with out-of-sample predictions for black-and-white textures. Here, we use the average (arithmetic mean) across subjects (Table S2).

To incorporate this process into a model for discrimination of gray-level textures in a way that ensures consistency with findings for black-and-white textures, we need to consider how the characteristics of the mechanisms in the first stage influence the local image statistics $\vec{y}^{[m]}$ of its internal representation. We first consider how a mechanism transforms the probabilities of gray-level configurations into probabilities of binary configurations, and then the transformation from binary configurations into local image statistics.

The key observation is that, although each of the Silva-Chubb mechanisms depends nonlinearly on gray level, they act linearly on the probabilities of local configurations. That is,

a 2×2 region of the stimulus texture with gray-level values $\begin{pmatrix} x_1 & x_2 \\ x_3 & x_4 \end{pmatrix}$ (with x_i in the

range $[0,1]$) will be converted by mechanism m to one of the 16 possible binary

584 representations $\begin{pmatrix} b_1 & b_2 \\ b_3 & b_4 \end{pmatrix}$ ($b_i = 0$ or 1). The probability that this block will be converted to
585 $\begin{pmatrix} b_1 & b_2 \\ b_3 & b_4 \end{pmatrix}$ via mechanism m is equal to the joint probability that each of the x_i is
586 converted to the corresponding internal representation b_i . Since we posit that these
587 conversions are independent,

$$588 \quad p^{[m]} \begin{pmatrix} b_1 & b_2 \\ b_3 & b_4 \end{pmatrix} = F_m(x_1, b_1) F_m(x_2, b_2) F_m(x_3, b_3) F_m(x_4, b_4), \text{ where} \quad (11)$$

$$F_m(x, b) = \begin{cases} 1 - F_m^{prob}(x), & b = 0 \\ F_m^{prob}(x), & b = 1 \end{cases}$$

589 The probability of each binary block type in the internal representation is the sum of
590 contributions from each of gray-level configurations in the original texture:

$$591 \quad p^{[m]} \begin{pmatrix} b_1 & b_2 \\ b_3 & b_4 \end{pmatrix} = \sum_{\vec{x}} F_m(x_1, b_1) F_m(x_2, b_2) F_m(x_3, b_3) F_m(x_4, b_4) p \begin{pmatrix} x_1 & x_2 \\ x_3 & x_4 \end{pmatrix}, \quad (12)$$

592 where the sum is over all G^4 gray-level configurations $\vec{x} = \begin{pmatrix} x_1 & x_2 \\ x_3 & x_4 \end{pmatrix}$. This can be written

593 more compactly as

$$594 \quad \vec{p}^{[m]} = L_G^{[m]} \vec{p}, \quad (13)$$

595 where \vec{p} is a column vector of the probabilities of the G^4 gray-level configurations indexed
596 by \vec{x} , $\vec{p}^{[m]}$ is a column vector of the $2^4 = 16$ binary block probabilities in the internal
597 representation m , and $L_G^{[m]}$ is a $G^4 \times 16$ matrix specified by the multiplier in (12). Note
598 that although $L_G^{[m]}$ is a large matrix, it is entirely specified by the Silva-Chubb model and the
599 set of gray levels, via our probabilistic interpretation.

600 We next consider how $\vec{p}^{[m]}$, the block probabilities of the internal representation, are
601 captured by the binary image statistics $\vec{y}^{[m]}$. Each image statistic is a linear combination of
602 block probabilities -- for example, β_1 , is the difference between the fraction of 2×1 blocks
603 in which the checks match, and the fraction in which they mismatch. Thus, the transformation
604 from block probabilities to image statistics is linear:

$$605 \quad \vec{y}^{[m]} = Y \vec{p}^{[m]}, \quad (14)$$

606 where Y is a 10×16 matrix determined solely by the definition of the image statistics (for
607 details, see [18]), and is given in Table S4. Combining eqs. (13) and (14) yields the
608 transformation from \vec{p} , the block probabilities in the original texture, to $\vec{y}^{[m]}$, the image
609 statistics of the binary representation produced by mechanism m :

$$610 \quad \vec{y}^{[m]} = Y L_G^{[m]} \vec{p}. \quad (15)$$

611 According to our model, the threshold to distinguish two textures, characterized by \vec{p} and
612 \vec{p}' respectively, is based on a comparison of the image statistics of their binary

613 representations, $\bar{y}^{[m]}$ and $\bar{y}'^{[m]}$. For distinguishing between a structured black-and-white
 614 texture with statistics \bar{y} and a random one ($\bar{y}' = 0$), we previously found [13] that thresholds
 615 were accounted for by a quadratic function of \bar{y} (eq. (10)). For comparison of two structured
 616 textures, we previously found [28] that, in the three coordinate planes tested, thresholds
 617 depended primarily on the difference $\bar{y} - \bar{y}'$, and not on the reference texture \bar{y}' . That is,
 618 the texture discrimination signal for two black-and-white textures given is given by:

$$619 \quad S = (\bar{y} - \bar{y}')^T Q (\bar{y} - \bar{y}'). \quad (16)$$

620 Here, we postulate that these findings also apply at the level of the internal binary
 621 representations, i.e., that each internal binary representation generates a signal based on a
 622 quadratic function of the difference in image statistics $\Delta\bar{y}^{[m]} = \bar{y}^{[m]} - \bar{y}'^{[m]}$. The overall
 623 texture discrimination signal S is then a sum of contributions from each of the mechanisms:

$$624 \quad S = \sum_m w_m (\Delta\bar{y}^{[m]})^T J \Delta\bar{y}^{[m]}, \quad (17)$$

625 where the weights w_m are taken to be the weights from the Silva-Chubb model (Table S2).

626 The matrix J describes how the image statistics are used within each mechanism. We
 627 determine it by the requirement that eq. (17) is consistent with previous studies of black-and-
 628 white textures, i.e., eq. (16). Note that this requirement means that J will not be the same as
 629 the matrix Q , since Q acted on the statistics of a black-and-white texture, while J acts on
 630 the statistics of the internal representation of a texture, after it has been transformed by each
 631 mechanism m . The calculation of J is detailed in the Supplemental Document
 632 (“Specification of the model’s quadratic form”), and the resulting matrix is given in Table S3.

633 3.3 Model summary

634 In brief, the proposed model (Fig. 7) specifies a difference signal S that governs the
 635 discrimination of two gray-level textures. The model has two stages. In the first stage, several
 636 independent mechanisms generate distinct internal representations of each texture, by
 637 applying a stochastic threshold that depends nonlinearly on the gray level (eqs. (7) to (9)).
 638 This stage of the model ensures that for textures without spatial correlation (“IID textures”),
 639 the model reproduces the three-dimensional domain (luminance, contrast, blackshot) of
 640 discriminable IID textures identified by Chubb and coworkers [14, 16, 17, 33]. Consistency is
 641 guaranteed because the first stage uses the same mechanisms as the Chubb et al. model, so
 642 IID textures that are indistinguishable according to the Chubb et al. model produce
 643 indistinguishable internal representations in the present model.

644 The second stage of the model confers sensitivity to spatial structure by comparing the
 645 local statistics of these binary representations. The specifics of that comparison (eq. (17)) are
 646 determined by the requirement that for black-and-white textures, the findings of [13] are
 647 recovered.

648 Other than the arbitrary value of S (eq. (17)) at which discrimination occurs, the model’s
 649 parameters are determined by complementary previous studies: discrimination of textures
 650 with multiple gray levels but no spatial correlation, and textures with only black and white
 651 checks, with local spatial correlations in two dimensions. Note that for all textures, the
 652 dependence of the discrimination signal on texture contrast is quadratic, but the
 653 proportionality contrast depends on the kinds of correlations that are present in the texture, via
 654 the model specification. These texture-dependent proportionality constants determine the
 655 predicted relative sensitivities.

656 3.4 Making model predictions

657 To determine model predictions for the current experiments, we simulate the images
658 generated by the stimulation generation procedure and determine the texture contrast for
659 which the discrimination signal S reaches a threshold value. Since the specific experimental
660 paradigm (check size, stimulus size, target size, viewing time, etc.) used here is the same as
661 that of [13, 18, 27, 28] the model predicts the experimentally-measured discrimination
662 threshold to be the value of the texture contrast for which $S = 1$. This computational
663 procedure was modified for rays in which the predicted threshold was high, since the stimulus
664 generation procedure is limited in the range of texture contrasts that can be attained. In those
665 directions, we determine the texture contrast at which $S = 1/16$ rather than $S = 1$. Then,
666 recognizing the quadratic dependence of discrimination signal on texture contrast, we convert
667 this texture contrast into a predicted threshold by multiplying it by $1/\sqrt{S} = \sqrt{16} = 4$.

668 We also made predictions from alternate models that had the same structure as Fig. 7, but
669 posited a different set of first-stage mechanisms. One such model had just one first-stage
670 mechanism, with a threshold at mid-gray: it mapped all darker-than-mean checks to 0, all
671 lighter-than-mean checks to 1, and randomly assigned mid-gray checks to 0 or 1. Other
672 models were reduced from the model of Fig. 7 by omitting one or more of the Silva-Chubb
673 mechanisms from the first stage. Since mechanisms F_1 and F_2 are equal and opposite – and
674 this complementarity was an essential feature of the findings of [16], these reduced models
675 always included either both of these mechanisms, or neither. In all cases, these alternate
676 models were implemented by repeating the above calculations with the modified set of
677 mechanisms, including a re-calculation of the matrix J in eq. (17) so that the resulting
678 model’s predictions remain consistent with our findings for black-and-white textures [13].

679 To provide an omnibus measure of model predictions, we computed the fraction of the
680 variance of the psychophysical thresholds that was unexplained by the model predictions,
681 calculated by comparing the sum of the squares of the difference in measured and predicted
682 thresholds, to the sum of the squares of the predicted thresholds, without scaling. For this
683 purpose, psychophysical thresholds were averaged across individuals via the geometric mean,
684 as in previous studies[13]. For some conditions, the model predicted an infinite threshold (i.e.,
685 the criterion of $S = 1/16$ in eq. (17) was never reached at any texture contrast). For those
686 conditions, we used the largest finite threshold that the model predicted in any other
687 condition. To obtain a comparable measure of intersubject reliability, we computed the
688 fraction of the variance of each subject’s thresholds that was not explained by each other
689 subject, across conditions in common, and report the median value of these variance fractions
690 across all subject pairs. These computations were carried out separately for Experiments 1
691 (first- and second-order statistics only), 2, and 3.

692 4. Results

693 4.1 Experiment 1

694 We used a four-alternative segmentation task (Fig. 6) to determine sensitivity to image
695 statistics in textures that contained three gray levels and spatial correlations. Each set of
696 measurements focused on the correlations within a particular spatial template– e.g., a pair of
697 horizontally-adjacent checks – and within this family of correlations, on a specific type
698 (“genus”) of correlations. As detailed in Methods, the genus is defined by constraining the
699 distribution of a specific linear combination of luminance values of the checks in the template,
700 where luminance is denoted by 0 for black, 1 for gray, 2 for white, and the linear combination
701 is computed mod 3. So, for example, for the family of correlations between a pair of
702 horizontally-adjacent checks, the genus specified by $\vec{\sigma}_{(1\ 1)}$ constrains the sum $A + B$ of

703 adjacent luminance values, while the genus specified by $\vec{\sigma}_{(1\ 2)}$ constrains the sum $A+2B$.
 704 Since these sums are computed mod 3, they can have the values 0, 1, or 2, and the

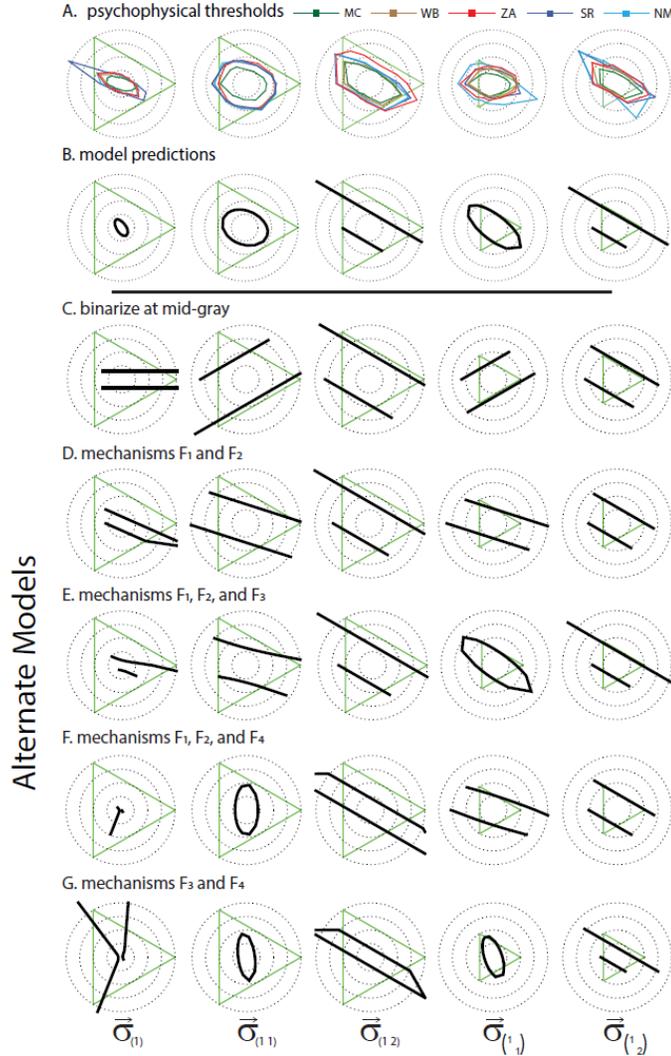


Fig. 8. Psychophysical thresholds (A) and model predictions (B-G) for Experiment 1, first- and second-order statistics. Each triangular domain corresponds to a first-order statistic $\vec{\sigma}_{(1)}$ (Fig.1), a second-order statistic

$\vec{\sigma}_{(1\ s)}$ involving horizontally-adjacent checks (Fig. 2), or a second-order statistic $\vec{\sigma}_{\binom{1}{s}}$ involving checks that

share a corner. Upper row: individual subjects' data. The origin corresponds to a random texture; green triangle corresponds to the boundary of the domain, whose vertices are at $(1,0,0)$, $(0,1,0)$, and $(0,0,1)$. Rings indicate textures of equal correlation strength, with a correlation strength of 1 at the vertices of each domain. Thresholds outside the domain correspond to conditions in which performance was above chance, but did not reach the criterion fraction correct within the stimulus domain. Note that the domains for $\vec{\sigma}_{\binom{1}{s}}$ are plotted on a different scale. For

thresholds <1 , uncertainties (2SEM) for individual subject thresholds are typically $<10\%$ of the measured thresholds, and are not shown. Model predictions are shown for the full model (B) and for alternate models consisting of a single channel that binarizes at mid-gray(C) or subsets of the Silva-Chubb mechanisms (D-G). For model predictions, isodiscrimination contours are disconnected if predicted thresholds at intermediate directions are >4 .

705 probabilities of these three values describes a triangular domain (see Fig. 2). Similarly, the
706 first-order domain $\vec{\sigma}_{(1)}$ (Fig. 1) is parameterized by the distribution of single-check gray
707 levels, and the third- and fourth-order domains (for example, $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$, Fig. 3) are
708 parameterized by the distribution of linear combinations of gray levels in 3 and 4 neighboring
709 checks, respectively. In each domain, the centroid is the random texture; the measured
710 thresholds indicate, in multiple directions within each domain, the distance from randomness
711 that is necessary for the statistical structure of the texture to be visually apparent.
712 Fig. 8A shows the measured thresholds for the first- and second-order domains in five
713 subjects. Thresholds are lowest for the first-order statistics, and, within the second-order
714 statistics, lower for the statistics that describe correlations among horizontally-adjacent checks
715 ($\vec{\sigma}_{(1 \ s)}$) than for the statistics that describe correlations among checks that share a corner,
716 $\vec{\sigma}_{\begin{pmatrix} 1 & \\ & s \end{pmatrix}}$. This pattern holds in all subjects. Additionally, the isodiscrimination contours are
717 approximately elliptical and symmetric about the origin, other than for directions in which
718 thresholds are high and therefore not precisely measurable. Thresholds for correlations among
719 vertically-adjacent checks $\vec{\sigma}_{\begin{pmatrix} 1 \\ s \end{pmatrix}}$ were not systematically determined, as pilot experiments (as
720 well as our previous studies with black-and-white textures [13]) showed that they were very
721 similar to the corresponding thresholds for horizontally-adjacent checks.
722 As detailed in Methods, we constructed a model (Fig. 7) for discrimination of spatially-
723 correlated gray-level textures, based on two previously-obtained complementary datasets: (i)
724 studies of discrimination of gray-level textures with no spatial correlation [14, 16, 17, 33], and
725 (ii) studies of discrimination of spatially-correlated black-and-white textures [13, 18, 27, 28].
726 In brief, the model had two stages: a first stage that analyzed luminance distributions via
727 multiple parallel mechanisms, and produced an internal binary representation along each
728 channel, and a second stage that was sensitive to spatial correlations present within each of
729 these internal representations. The model had no free parameters, as it was fully constrained
730 by the requirement that it accounted for these two previous complementary datasets.
731 Fig. 8B shows the thresholds predicted by this model. The model approximates the
732 absolute thresholds found experimentally, and fully accounts for the ordering of thresholds
733 among the correlation types. It also accounts for the elliptical shapes of the isodiscrimination
734 contours where thresholds can be reliably determined. However, the model is clearly
735 imperfect. It predicts a greater sensitivity for first-order statistics than we observed, and the
736 axes of the ellipses are inaccurately predicted for $\vec{\sigma}_{(1)}$, $\vec{\sigma}_{(1 \ 1)}$, and $\vec{\sigma}_{\begin{pmatrix} 1 & \\ & 1 \end{pmatrix}}$. Note, however,
737 that all model parameters were determined from independent experiments involving textures
738 with either no spatial correlations [16] or experiments involving black-and-white textures [13,
739 18], and a nearly non-overlapping set of subjects.
740 We next examined the extent to which the multichannel nature of the model is critical to
741 achieve a good correspondence to the experimental observations. We considered a simplified,
742 one-channel model in which the first-stage mechanism was a threshold, sending darker-than-
743 mean checks to 0 and lighter-than-mean checks to 1, and randomly assigned mid-gray checks.
744 We also considered multichannel models in which one or more of the Silva-Chubb
745 mechanisms were deleted. For the latter models, we either retained both F_1 and F_2 , or
746 deleted both – as their complementary, linearly-dependent nature was an important feature of
747 the Silva-Chubb analysis [16]. In all cases, the model’s second stage was adjusted to ensure

748 that it produced thresholds for black-and-white textures that corresponded to previous
749 psychophysical measurements [13, 18].
750 The last five rows of Fig. 8 show that overall, the predictions of these alternate models
751 differ substantially from the measured thresholds. While the alternate models make similar
752 predictions for $\bar{\sigma}_{(1\ 2)}$, and $\bar{\sigma}_{\begin{pmatrix} 1 \\ 2 \end{pmatrix}}$ (third and fifth columns), their predictions for the first-
753 order statistic and the other second-order statistics differ widely from the psychophysical
754 measurements. The model with binarization at mid-gray (Fig. 8C) and the model with
755 luminance-like mechanism pair F_1 and F_2 (Fig. 8D) predict very high thresholds in some
756 directions in the domains of $\bar{\sigma}_{(1)}$, $\bar{\sigma}_{(1\ 1)}$, and $\bar{\sigma}_{\begin{pmatrix} 1 \\ 1 \end{pmatrix}}$, in contrast to the psychophysical
757 measurements and the predictions of the full model (Fig. 7). The other reduced models (Fig.
758 8E-G) do not predict unreasonably high thresholds for $\bar{\sigma}_{(1\ 1)}$ and $\bar{\sigma}_{\begin{pmatrix} 1 \\ 1 \end{pmatrix}}$, but nevertheless
759 fail dramatically for $\bar{\sigma}_{(1)}$, and, in some cases (Fig. 8F,8G), for $\bar{\sigma}_{(1\ 1)}$ and $\bar{\sigma}_{\begin{pmatrix} 1 \\ 1 \end{pmatrix}}$ as well.
760 Note that the rather strange predicted isodiscrimination contours for $\bar{\sigma}_{(1)}$ result not only from
761 omitting mechanisms, but also from constraining the model's second stage to account for
762 thresholds to spatially-correlated black-and-white textures.
763

764 **Table 2. Quantification of Model Predictions**

765

766 model	767 Experiment 1	768 Experiment 2	769 Experiment 3
770 full (F_1, F_2, F_3, F_4)	0.268	0.138	0.274
771 binarize at mid-gray	1.739	1.565	0.391
772 F_1 and F_2	0.713	0.573	2.840
773 F_1, F_2 , and F_3	2.481	3.441	0.712
774 F_1, F_2 , and F_4	1.769	0.231	0.856
775 F_3 and F_4	1.403	0.240	0.158
776 intersubject variability	0.585	0.130	0.212

777 Model predictions are quantified by the fraction of the variance of the threshold measurements accounted for by the
778 model. For Experiment 1, only first- and second-order statistics are considered. The entry for intersubject variability
779 is the median of the fraction of variance of one subject's data that is accounted for by a second subject. For further
780 details, see Methods.
781

782 Table 2 (second column) quantifies the goodness of fit of the full model and the alternate
783 models considered in Fig. 8, in terms of the fraction of variance unexplained by each model's
784 prediction of the average psychophysical thresholds. The full model leaves 27% of the
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798 variance unexplained; the best alternate model (F_1 and F_2 only) leaves 71% of the variance
 799 unexplained. For the other models, more than 100% of the variance is unexplained (i.e., in
 800 terms of explained variance, the model is worse than a model that simply predicts that all
 801 thresholds are zero). The last row of Table 2 compares these statistics with a measure of
 802 intersubject variability, the median of the fraction of the variance unexplained in one subject's
 803 data, based on a second subject (see Methods). For the full model, the fraction of variance
 804 unexplained is comparable to the intersubject variability; for all the alternate models, the
 805 fraction of variance unexplained is greater than the intersubject variability, often substantially
 806 so.

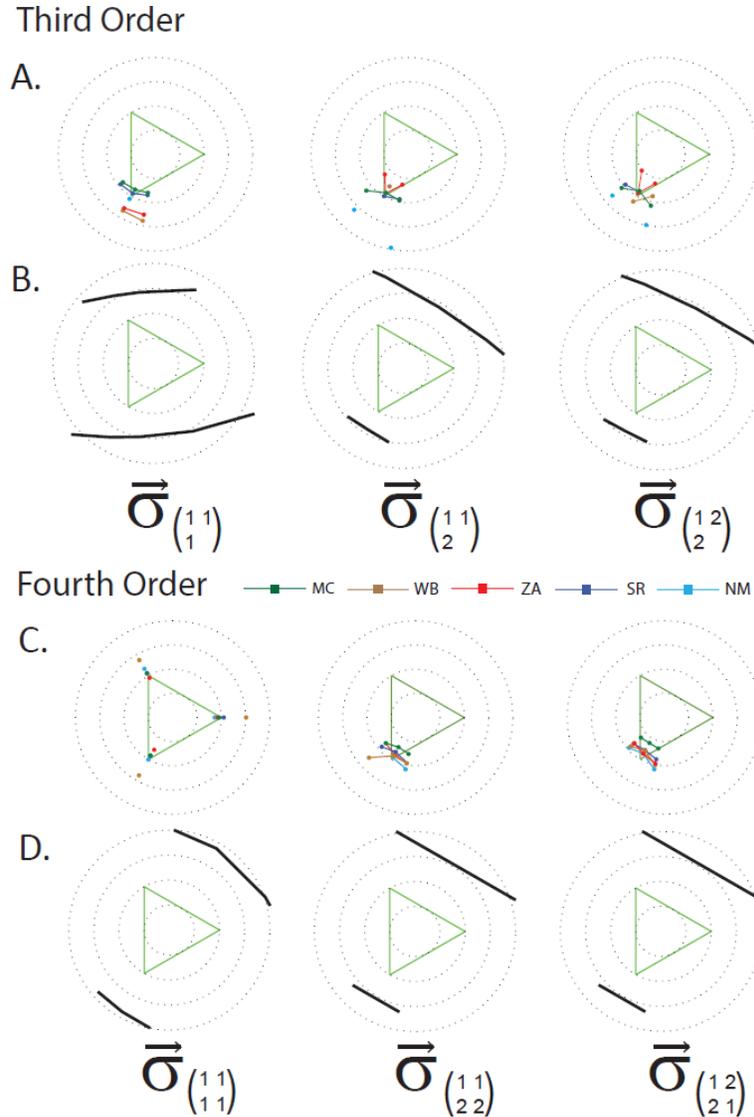


Fig. 9. Psychophysical thresholds and model predictions for Experiment 1 in the triangular domains of selected third- and fourth-order statistics. First and third rows show experimental measurements; second and fourth rows show model predictions. Points are disconnected if intervening directions correspond to chance performance (psychophysical data) or thresholds > 4 (model). For examples of the domains, see Fig. 3: the third-order domain $\vec{\sigma}_{(1)}^{(11)}$ is shown in Fig. 3A; the fourth-order domain $\vec{\sigma}_{(2)}^{(12)}$ is shown in Fig. 3B. Other plotting conventions as in Fig. 8.

807 Thresholds for third- and fourth-order statistics are shown in the first and third rows of
808 Fig. 9. Thresholds were generally much higher than for first- and second-order correlations,
809 and there were many directions in the third- and fourth-order domains in which performance
810 was at chance, even for maximally-correlated textures. The model predicts these higher
811 thresholds, and largely accounts for the directions in which thresholds could be measured. For
812 the third-order domains and the fourth-order domains $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix}}$ and $\vec{\sigma}_{\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}}$, predicted
813 thresholds are closest to the borders of the stimulus domain in the direction of the lower-left
814 vertex, corresponding to configurations in which luminance values sum to zero (mod 3).
815 These are the directions in which subjects' performance was better than chance. However, for
816 the fourth-order domain $\vec{\sigma}_{\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}}$, subjects' performance was better than chance at each vertex,
817 and this does not appear to be accounted for by the model.

818 *4.2 Experiment 2*

819 Experiment 2 examines how different kinds of image statistics combine, focusing on second-
820 order image statistics. Studies were organized into four groups: group I made use of stimuli
821 that combined $\vec{\sigma}_{(1 \ 1)}$ and $\vec{\sigma}_{(1 \ 2)}$; the other groups made use of stimuli that combined a
822 horizontal correlation $\vec{\sigma}_{(1 \ s)}$ with a vertical correlation $\vec{\sigma}_{\begin{pmatrix} 1 \\ s' \end{pmatrix}}$. Each of these genera of

823 correlations includes three species (corresponding to the three vertices of its domain), so
824 pairwise combinations of genera encompassed multiple pairwise combinations of specific
825 image statistics (Table S1).

826 Experimental results are shown in alternate rows in Fig. 10. All combinations of image
827 statistics supported image segmentation, and the pattern of threshold behavior is consistent
828 across subjects, as in Experiment 1 (Fig. 8A). Moreover, thresholds are again nearly
829 symmetric for positive and negative correlation strengths, and isodiscrimination contours
830 were very nearly circular or elliptical. These behaviors were also captured by the model of
831 Fig. 7, including the orientation of the isodiscrimination contours in most cases.

832 Quantitatively (Table 2), the model of Fig. 7 also performs well; the fraction of variance
833 unexplained (14%) is comparable to median intersubject variability (13%). None of the
834 alternate models perform comparably: two (the models with mechanisms F_1 , F_2 , and F_4 ,
835 and the model with mechanisms F_3 and F_4) have reasonable performance (23-24% of
836 variance unexplained); the others perform very poorly.

837 *4.3 Experiment 3*

838 Experiment 3 determines sensitivity to a salient subset of second-order statistics across a
 839 range of gray levels. Specifically, we examined two kinds of correlations between adjacent
 840 checks: correlations that produced gradients (Fig. 5A), and correlations that produced streaks
 841 (Fig. 5B). Note that for a given number of gray levels, the luminance distribution is the same
 842 for the two kinds of stimuli, but the spatial organization differs.

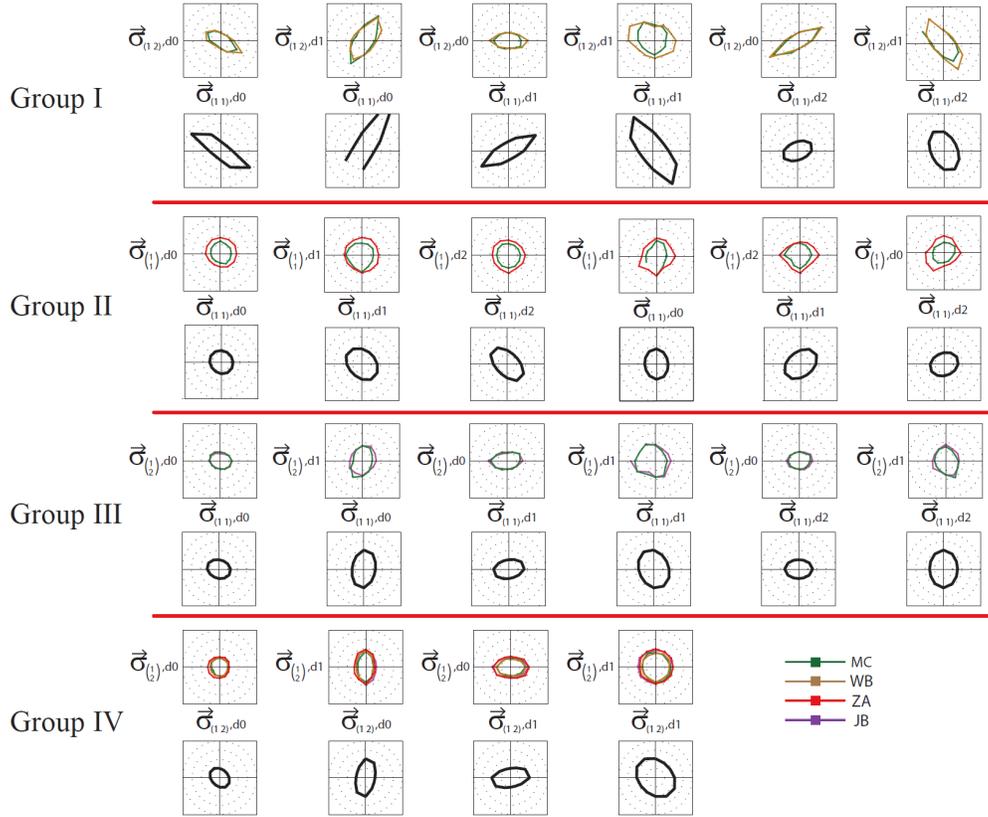


Fig. 10. Psychophysical thresholds and model predictions for Experiment 2, which combines pairs of second-order statistics. Each pair of rows corresponds to an experimental group, delineated in Table S1. The upper row of each group shows experimental measurements; the lower row shows model predictions. The domains in each group combine a second-order statistic drawn from two genera, shown at the beginning of the rows, as delineated in Table S1. Individual domains are labeled according to the correlation species varied along the ordinate and abscissa, each of which is defined by a vertex within the genus' triangular domain (e.g., Fig. 2). Barycentric coordinates of the vertices are indicated by d0 for (1,0,0), d1 for (0,1,0), and d2 for (0,0,1). The first and fifth domains of Group I are shown in Fig. 4AB; the first domain and third domains of Group IV are shown in Fig. 4CD. Other plotting conventions as in Figs. 8 and 9.

843 Thresholds were measured in six subjects, using the same procedures as Experiments 1
 844 and 2. One subject, MC (an author) was also a participant in Experiments 1 and 2.
 845 For the gradients (Fig. 11A, left), thresholds were an inverted-U function of the number of
 846 gray levels, with texture-contrast thresholds of approximately $c = 0.5$ for 3 and 11 gray
 847 levels, and a maximal threshold of 0.7-1.0 for 5 gray levels. For the streaks (Fig. 11A, right),
 848 thresholds were 0.2-0.3 for all subjects, and independent of gray level. Thresholds were
 849 independent of the direction of the gradient or the orientation of the streak.
 850 The thresholds predicted by the model are shown in Fig. 11B. The model predicts the
 851 inverted-U shape of the sensitivity function and its peak position, as well as the absolute

852 thresholds at the extremes of the curve, but overestimates the threshold for 5 gray levels. For
 853 streaks, the model predicts the independence of gray levels and also predicts the absolute
 854 thresholds.

855 Fig. 11C shows the predictions of the alternate models in Fig. 8. With regard to the
 856 gradients, several of these models predict unreasonably high thresholds for 3 or 4 gray levels,
 857 far exceeding the psychophysical findings. The one model that does not fail in this fashion
 858 (F_3 and F_4 only) predicts a higher threshold for 7 gray levels rather than 5; all subjects

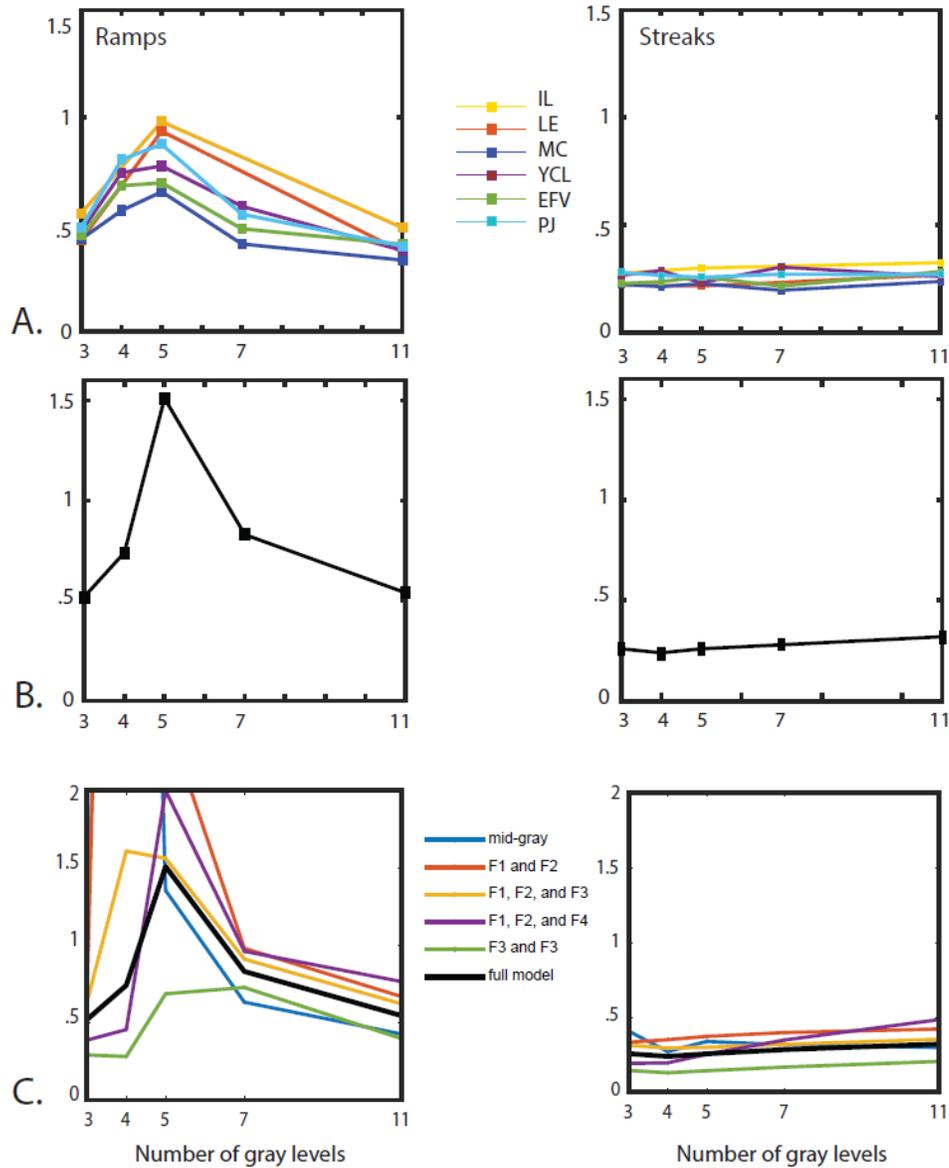


Fig. 11. Psychophysical thresholds and model predictions for Experiment 3, gradients (left) and streaks (right). A: Individual subjects' data. Uncertainties (2SEM) for individual subject thresholds are <0.05 and are not shown. B: Predictions of the model. C: Predictions (color) of alternate models whose first stage consists of a single mechanism with a threshold at mid-gray, or a subset of the Silva-Chubb mechanisms. The predictions of the full model are shown in black. Off-scale points correspond to predicted thresholds > 4 .

859 showed the opposite behavior. With regard to streaks, most of the alternate models correctly
860 predicted the finding that thresholds were approximately independent of the number of gray
861 levels. However, the threshold predicted by the F_3 and F_4 only-model was lower than
862 measured, and the thresholds predicted by the F_1 , F_2 , and F_4 model showed a near-
863 doubling of threshold as the number of gray levels increased from 3 to 11, also inconsistent
864 with the data.

865 In a quantitative analysis (Table 2), the accuracy of model predictions (27% of variance
866 unexplained) is comparable to intersubject variability (21% of variance unexplained). Most of
867 the alternate models do not perform as well. The model with mechanisms F_3 and F_4
868 provides a better fit in this experiment (16% of the variance unexplained), but, as noted
869 above, this model performs very poorly in Experiment 1 (none of the variance explained).
870

871 5. Discussion

872 This study examined sensitivity to visual textures, with the broad goal of understanding how
873 neural computations analyze a high-dimensional sensory space. Visual textures constitute
874 such a space, as their parametric description – local image statistics – includes not only the
875 luminance distribution, but also spatial correlations among pairs of checks, triplets, etc. While
876 human visual sensitivity to image statistics is selective [24], the number of perceptually
877 relevant texture parameters is quite large. The visual system can detect texture differences
878 based on several aspects of the luminance distribution in the absence of spatial correlations,
879 and multiple kinds of spatial correlations, even for textures that only have black and white
880 elements. Moreover, typical textures have spatial correlations *and* are not restricted to two
881 luminance levels; the number of parameters required to describe spatial correlations grows
882 rapidly as the number of luminance levels increase [20]. Here, to understand how such
883 textures are processed, we examine perceptual thresholds for discrimination of several classes
884 of textures that have multiple gray levels and also spatial correlations.

885 Our main findings in Experiments 1 and 2 are that two observations previously made for
886 black-and-white spatially-correlated textures [13] apply in this more general context:
887 thresholds for negative and positive correlations are nearly equal, and signals from different
888 local image statistics combine quadratically. The net result is that isodiscrimination
889 thresholds, parameterized by local image statistics, are approximately elliptical.

890 Our main finding in Experiment 3 is that gray-level distribution and spatial correlations
891 interact: for one kind of spatial correlation (gradients), threshold for discrimination from
892 randomness has a sharp maximum when 5 gray levels are present; for a second kind of spatial
893 correlation (streaks), the threshold is approximately independent of gray levels.

894 While this interaction is perhaps unsurprising, it provides empirical evidence that gray-
895 level distributions and spatial correlations are not merely processed independently. In an
896 attempt to capture how these dimensions interact, we constructed a computational model to
897 account for our findings, based on previous studies of gray-level textures without spatial
898 correlations, and studies in our lab of spatially-correlated black-and-white textures. As the
899 model is fully constrained by those previous studies, it has no free parameters. The model
900 reproduces the qualitative features of our findings --the elliptical shape of the
901 isodiscrimination contours seen in Experiments 1 and 2, and the interaction between the
902 number of gray levels and spatial correlations seen in Experiment 3 – and provides a
903 reasonable quantitative prediction of the thresholds as well.

904 We note, however, that all of the stimuli are constructed with discrete, monochrome
905 checks, so it is an open issue as to whether the approach extends to textures with continuous
906 gradations and/or chromatic content.

907 **5.1 The model**

908 The proposed model (Fig. 7) combines elements that process luminance distributions and
909 elements that process spatial pattern in a novel manner. We emphasize that it is a
910 computational model; its components are not intended to have direct physiologic correlates.

911
912 The first stage of the model consists of a set of parallel mechanisms that process luminance
913 distributions. Each mechanism transforms the visual input into a binary representation,
914 assigning each check to 0 or 1 with a probability determined by the gray-level of the stimulus.
915 The characteristics of these mechanisms – i.e., the way that the probability depends on gray
916 levels (F_m , eq. (6)) and their relative strengths (w_m , eq. (17))-- are taken from the studies of
917 Silva and Chubb [16], in which they used a search task to measure discrimination of spatially-
918 uncorrelated gray-level textures. By using the Silva and Chubb mechanisms, our model is
919 guaranteed to reproduce the key findings of Chubb and colleagues [14, 16, 17, 33]: that
920 spatially-uncorrelated gray-scale textures form a three-dimensional perceptual space, and
921 textures that are indistinguishable by these mechanisms are perceptually indistinguishable.

922 The second stage confers the sensitivity to spatial correlations. Each of the internal
923 representations produced by the first stage is analyzed by mechanisms sensitive to patterns in
924 2×2 clusters of checks. The second stage is thus sensitive not only to pairwise correlations,
925 but also to third- and fourth-order correlations among nearest neighbors, as is needed to
926 account for early observations concerning isodipole textures [34]. The way that signals from
927 these local correlations combine (eq. (17)) is fully constrained by the requirement that the
928 model accounts for discrimination thresholds for black-and-white textures, previously
929 measured in our lab [13, 18, 27, 28], as detailed in the Supplemental Document,
930 “Specification of the model’s quadratic form.”

931 Our model can be viewed as a generalization of a “back-pocket” [15] framework: its first
932 stage consists of several independent analyzers and their outputs are combined quadratically.
933 But in contrast to the standard back-pocket model, the outputs of the analyzers are
934 multivariate quantities that contain spatial information, rather than scalars. Correspondingly,
935 the quadratic combination rule is a quadratic form, rather than a simple square law. This
936 generalization allows for interactions between gray-level distributions and spatial pattern.

937 The ability of the model to predict our findings, both qualitatively and quantitatively,
938 depends not only on its overall structure, but also on the specifics of the model’s first stage:
939 the four independently-identified Silva-Chubb mechanisms [16]. When these mechanisms are
940 replaced by a simple threshold, or, when one or more of them are removed, the elliptical
941 isodiscrimination contours of Experiments 1 and 2 are lost, and some thresholds are predicted
942 to be unreasonably large (Fig. 8C-G). These alternate models also are not able to account for
943 the interaction of the gray-level distribution and spatial correlations seen in Experiment 3
944 (Fig. 11). Alternate models also fall short in terms of quantitative prediction of the measured
945 thresholds for first- and second-order statistics and their combinations (Table 2).

946 **5.2 Simplifications and approximations**

947 In keeping with the goal of focusing on the structure of the computations underlying texture
948 processing and avoiding an explosion of parameters, the model makes substantial
949 simplifications regarding the neural circuitry underlying spatial processing. Center-surround
950 organization and orientation-tuned spatial filtering are not explicitly modeled. Instead, the net
951 effect of checks surrounding the central element are lumped together into the stochastic
952 threshold that converts the central check into an internal binary representation. As we don’t
953 model “receptive fields” explicitly, we don’t take into account eccentricity-dependence of
954 receptive field centers and surrounds (and consequent eccentricity-dependent changes in the
955 typical number of checks within a receptive field). Finally, the nearest-neighbor correlations
956 that define the textures necessarily induce longer-range correlations, but these are neglected –

957 the model's sensitivity to spatial structure is determined only by configurations in a 2×2
958 block of checks, independent of eccentricity.

959 These simplifications enable us to constrain the model based on previous studies – though
960 this too entails some assumptions. The first-stage mechanisms are taken from previous studies
961 with spatially-uncorrelated textures [16]. This makes the assumption that these mechanisms
962 are unchanged when spatial correlations are present, and when the specific gray level
963 distributions differ substantially. Further, the second-stage mechanisms we use to model the
964 processing of spatial structure were determined from studies in which structured textures were
965 discriminated from random ones [13]. Here they are applied to internal representations in
966 which the comparison is between two non-random textures. The “translation invariance”
967 needed for this generalization (i.e., that discrimination between textures with coordinates \bar{y}
968 and \bar{z} depends only on $\bar{y} - \bar{z}$) is only approximate [28]. Moreover, these internal
969 representations, though binary, are outside the stimulus set used in [13]: because of the action
970 of the stochastic threshold, they are no longer maximum-entropy.

971 Despite these approximations and simplifications, the agreement of the model with the
972 experimental data is good -- but there are also specific systematic discrepancies that are larger
973 than intersubject variability. Overall, the model underestimates the thresholds for first- and
974 some second-order statistics, and overestimates the threshold for third- and fourth-order
975 statistics. For some first- and second-order statistics, the orientation of the isodiscrimination
976 ellipse is also not accurately predicted.

977 While any of the above approximations and simplifications may contribute to the model's
978 inaccuracies, the overall under-prediction of low- order thresholds and over-prediction of
979 high-order thresholds is expected to be very sensitive to the precise shapes of the operating
980 curves of the first-stage mechanisms. Specifically, if the thresholds were slightly less
981 stochastic – i.e., the curves transitioned more rapidly from 0 to 1 – then the balance would tilt
982 towards the high-order correlations, as these rely on preservation of the image structure in
983 multiple neighboring checks. The precise shapes of the first-stage mechanisms will also
984 influence the orientation of the ellipses, as well the replacement of true surround subtraction
985 by a stochastic threshold, as well as the neglect of correlations at larger spatial scales.

986 While our focus is on a simple conceptual model for visual computations, the model's
987 structure is fully compatible with more elaborate, physiologically-realistic models. Our main
988 building blocks – linear summation and pointwise nonlinearities – are typical building blocks
989 of such models. As mentioned above, the stochastic threshold is an approximation of the
990 influence of the receptive field surround. Moreover, the nonlinearities required to extract
991 third- and fourth-order spatial correlations are known to exist in primate area V2 [35], and
992 emerge naturally in models of recurrent neural networks[36].

993 *5.3 How visual modalities combine*

994 An important way in which the brain copes with the complexity of the visual world is to
995 utilize separate regions or networks specialized for processing of visual modalities, such as
996 orientation, color, shape, motion, and depth. While initial studies emphasized specialization
997 and modularity[2, 37, 38], it is now well-recognized that these modules are not independent,
998 as subsequent studies revealed both physiological and psychophysical evidence for
999 intermixing [8, 9, 39-41].

1000 The model structure we propose presents a common theme for the way in which cross-
1001 modal interactions are structured. In our model, local luminance is processed by a parallel set
1002 of mechanisms, each of which provides an internal representation that is then analyzed by a
1003 second stage, which is sensitive to spatial correlation. Similarly, in Papathomas' [39] study of
1004 chromatic interactions with motion, local chromatic signals provide tags, which is then used
1005 by a standard spatiotemporal analyzer to extract unambiguous motion. Non-Fourier motion
1006 can be viewed in the same way: it can be detected by a cascade in which local flicker or local

1007 unsigned contrast becomes tokens that serve as a starting point for standard motion
1008 analysis[42]. Finally, in studies of structure-from-motion [43], the spatial arrangement of
1009 locally-extracted motion signals constitute an internal representation that is then analyzed for
1010 shape.

1011 Our model is a further elaboration on this theme. In the first stage of our model, multiple
1012 internal representations are abstracted from the luminance image. At the model's second
1013 stage, each of these internal representations undergoes a spatial analysis. Each of these
1014 transformations is both local and nonlinear, but the nonlinearities address different aspects of
1015 the input: luminance distribution and spatial structure. The net result is a computation that
1016 could not be achieved by independent processing within these modalities.
1017

1018 *5.4 Relevance to visual processing of natural scenes*

1019 The computation captured by this model is central to efficient visual processing of natural
1020 scenes. As has been proposed by the efficient coding hypothesis [44], the visual system is
1021 tuned to take advantage of the distinctive statistical characteristics of natural visual inputs.

1022 These characteristics include not only their well-known $1/f^2$ spatial power spectra [45-47],
1023 but also, their luminance and local image statistics [23-25, 48]. Specifically, some kinds of
1024 local image statistics are quite variable across natural scenes, and are therefore highly
1025 informative, while others are relatively more stereotyped and/or predictable, and therefore less
1026 informative. Importantly (and perhaps surprisingly), these previous studies [23-25] have
1027 shown that the informativeness of different kinds of local image statistics in natural scenes is
1028 closely correlated with visual sensitivity to these statistics when they are isolated in our
1029 synthetic textures. Our model shows that the computations that implement efficient coding
1030 can be accomplished in a compact fashion, that is, by combining the outputs of a small
1031 number of local mechanisms (the first stage of the model) with a single quadratic nonlinearity
1032 (the second stage of the model).

1033 Note also that our findings are inconsistent with the notion that visual sensitivity to an
1034 image statistic merely reflects the extent to which the statistic reduces entropy. All texture
1035 domains have a fully random (maximally entropic) texture at the origin, and, for small texture
1036 contrasts, the reduction in entropy depends only on the distance from the origin (Appendix B
1037 of [18]), independent of the domain or the direction of the displacement. The widely varying
1038 sensitivities we observe, and the elliptical rather than circular isodiscrimination contours,
1039 indicate that sensitivity varies widely across image statistics, even though they each reduce
1040 entropy by the same amount. This selectivity is inconsistent with coding entropy reduction
1041 *per se*, but, as mentioned above, corresponds instead to the efficient coding of natural scenes.

1042 Finally, we note that the efficient coding framework is also relevant to understanding
1043 how the chromatic content of natural scenes is processed [49-52]; however, the present
1044 analysis (and that of many others [21, 53-56]) is limited to their achromatic aspects.

1045 **6. Back matter**

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1053 **Data availability.** Data underlying the results presented in this paper are not publicly available at this time but may
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1055 **Supplemental document.** See Supplemental Document for supporting content.

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