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VISUAL TEXTURE SEGMENTATION IN CATS

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The segmentation of visual images on the basis of textural discontinuity was studied in cats using two behavioural paradigms. The first task (Experiment 1) required the animals to detect the presence of a target square of one texture embedded in a background of a second texture. The second task (Experiment 2) required the cats to discriminate between two forms (square and triangle) both of which were defined by texture–texture boundaries. Both detection and discrimination tasks were presented in a transfer paradigm in which the animals first learned a luminance-based form of the same problem. The results indicate that cats are able to segment a visual array on the basis of textural discontinuity in the absence of global luminance differences between figure and ground, and that they are able to use the contour information provided by texture–texture boundaries as a basis for form discrimination.

INTRODUCTION

The task of the visual system is to organize the grey-level images on the two retinae into descriptions of the shapes and positions of object surfaces¹⁷. In non-humans, the perception of shape has usually been studied through discrimination tasks using two-dimensional forms defined by simple luminance boundaries. It is clear, however, that in real visual scenes luminance contrast is not the only cue which could lead to figure–ground segmentation, and that in the human visual system, the three-dimensional shape of objects is determined from changes in motion²⁸, disparity^{12,17} and surface texture²⁴ as well as luminance. Sharp discontinuities in any of these dimensions may indicate a surface boundary, and gradients provide information about the internal structure of the surface. Very few studies have investigated the role of these other forms of ‘contrast’ in non-human species behaviourally, an important

exception being the demonstrations that monkeys^{2,5} and cats¹⁶ can perceive form in random dot stereograms. By relying exclusively on luminance boundaries in the study of ‘form vision’, we are overlooking the complexity of the early stages of visual processing. The present study asks whether textural discontinuity can support figure–ground segmentation and form perception in cats.

Beck¹ has defined a visual texture as a homogeneous array of identical or similar elements which as a whole has such properties as coarseness and brightness. The elements of the textures used in the present study are defined by local luminance transitions; however, isoluminous colour boundaries may also provide the basis for texture, as may elements produced by illusory brightness³⁵. Thus texture should probably be thought of as a higher-order concept which may be applied across visual submodalities to describe a homogeneous surface microstructure. Two tex-

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tures can differ in the identity of their component elements and/or in disposition of those elements on the surface. The textures to be considered in this paper involve non-overlapping elements arranged in regular arrays.

The problem of texture segmentation or detection of boundaries between textures has been studied extensively in human subjects^{1,13,14,15,22,23,27}. In a typical experimental paradigm, two textures are presented contiguously – either side by side or one embedded in the other. Some texture pairs are rapidly discriminable in such a situation, whereas others require prolonged visual search. Julesz^{14,15} and Treisman²⁷ have related this difference to two levels of processing: preattentive and focal attentive. What differentiates preattentively discriminable texture pairs from pairs which are not is still unclear: both global and local differences have been proposed. The local view centres on the idea that there is a relatively small set of feature primitives which the visual system can evaluate in rapid parallel search^{14,15}. Textures differing in the density of such elements, which Julesz calls *textons*, show rapid segmentation. More global views concern the statistical properties such as the power spectra of the texture arrays^{13,23}.

In the present study texture pairs which lead to rapid discrimination in human observers were presented to normal cats in two paradigms. Experiment 1 examines the cats' ability to detect a textural discontinuity in a visual array. Experiment 2 demonstrates that cats can perform form discriminations on the basis of the contours implicit at texture–texture boundaries.

EXPERIMENT 1

Method

Subjects

The subjects were 8 cats from 5 litters born in our laboratory. They were housed with their mothers and siblings until weaning and were then housed individually or in pairs in standard laboratory caging. The animals were provided with ad libitum cat chow and water throughout the studies. The only exceptions were the occasional

animals who ate their entire daily ration immediately upon receiving it. For such animals the daily feeding was withheld until after testing.

All 8 cats had had prior experience in visual discrimination learning in the same experimental situation as was used for the texture studies described below. This experience began at about 30 days of age in all cases and included brightness discrimination, 1–3 pattern discrimination problems, and in 4 cases, psychophysical threshold assessment (spatial resolution). While it is probable that the pretraining had non-specific beneficial effects in teaching the animals to use the apparatus and to examine the available visual information, no specific carryover effects (positive or negative) were found from any individual task. At the onset of training on the sequence of problems which comprise this study, the cats were between 3 and 5 months of age.

Experimental design

A problem inherent in animal research is that learning scores reflect both non-specific learning (what the task is about) and specific learning (which is the correct stimulus). In human studies, verbal instructions substantially reduce the first problem. Since we were interested in the degree to which texture segmentation has the automatic quality in cats that it has in humans, we adopted a transfer of training paradigm in which the animals were first taught an analogous luminance-based problem. All stimulus pairs took the form illustrated schematically in Fig. 1. The positive stimulus consisted of a target square centred on a contrasting background. The negative stimulus

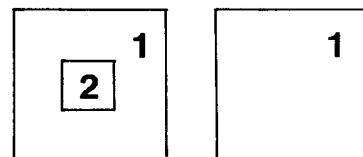


Fig. 1. Schematic representation of the stimuli for Expt. 1. The central target square (2) in the positive stimulus differed in global luminance and/or texture from the background (1). The negative stimulus was homogeneous and matched the background of the positive stimulus. In cases where both target and background were textured, the boundary between them was not marked by a solid contour.

was uniform and matched the background of the positive stimulus along the dimension being examined (brightness, brightness and texture or texture alone, see below). Each stimulus subtended a visual angle of $31^\circ \times 31^\circ$; the target square in the positive stimulus subtended $10^\circ \times 10^\circ$.

Visual textures

Four different visual textures were used. Textures 1–3 (Rings, Dots, Arrows) were made from commercially available transfers (Letraset), Texture 4 (Rectangles) was an ink drafting. Textures 1 and 2 were very closely matched in global luminance, and were used together as a texture pair; Texture 3 (Arrows) was paired with a 90° rotation of the same texture; 90° rotation was also used to produce the Texture 4 pair. The 3 texture pairings are reproduced to scale in Fig. 2.

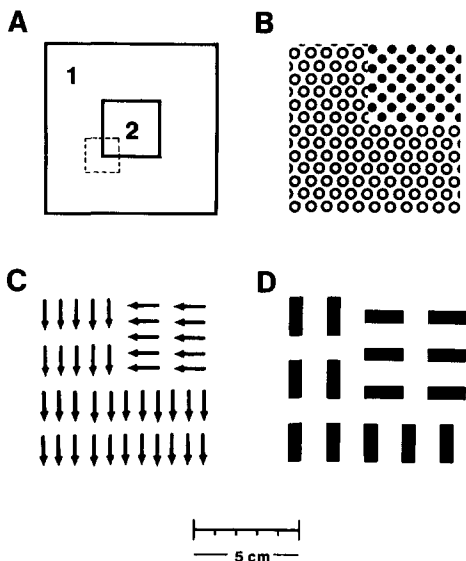


Fig. 2. A: schematic of the positive stimulus, the dotted square marking the area which is represented by the 3 examples of texture–texture borders. B–D: the 3 texture–texture pairings used in Expt. 1. All 3 are reproduced to the same scale as indicated. B: Texture 1 (Rings) and Texture 2 (Dots). C: Texture 3 (Arrows). The elements of the target square are rotated 90° from background elements. D: Texture 4 (Rectangles).

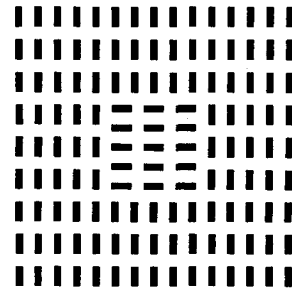


Fig. 3. Reduced reproduction of the positive stimulus for Problem 8 (Texture 4 (90°)/Texture 4). At the viewing distance of 47 cm, the individual elements subtended a visual angle of $2.2^\circ \times 45'$ of arc.

Task sequence

The following sequence of problems was presented to all animals. In each case, the positive stimulus is described. The negative stimulus matched the background of the positive stimulus.

- (1) Black Square on White.
- (2) Black Square on Texture 1 (Rings).
- (3) Texture 2 Square (Dots) on Texture 1 (Rings) (Fig. 2B).
- (4) Black Square on Texture 2 (Dots).
- (5) Texture 1 Square on Texture 2 (figure-ground reversal of problem 3).
- (6) Texture 3 (Arrows). The orientation of the arrows forming the central square differed from that of the background arrows by 90° (Fig. 2C). This was the only task not preceded by a black-on-texture task with the same texture. This was done to assess direct transfer across very different texture elements.

- (7) Black Square on Texture 4 (Rectangles).
- (8) Texture 4 (Rectangles). A central square of vertically elongated rectangles on a background of horizontally elongated rectangles (Figs. 2D, 3).

Problems 7 and 8 (Texture 4) were included because of concern that the elements in textures 1–3 were quite small and rather complex. These problems were not presented immediately after problem 6; in fact, they were introduced after completion of Expt. 2. However, since they have the same format as the other problems in Expt. 1, they are included here for the sake of brevity.

Apparatus and test procedure

All testing was carried out using a modified form of the jumping stand adapted for cats by Mitchell et al.¹⁸. The stimuli were high-contrast black-and-white photographs (25 cm²) mounted on white 33 cm² mounting boards and covered with transparent plastic. The stimuli exactly covered the trapdoors on the jumping stand, and were illuminated as evenly as was possible by a combination of fluorescent ceiling lighting and an incandescent source placed at the cat's level to prevent shadows cast by the cat and jumping platform. Overall illumination was high, averaging approximately 300 cd/m².

The cat viewed the two stimuli from a height of 47 cm, and indicated its choice by jumping onto one of them. Successful responses were rewarded with a small piece of highly preferred food (beef baby food). Positive social reinforcement was also freely given. Errors were followed by a loud noise and a sharp 'no' from the experimenter.

The cats were trained in 40-trial daily sessions until they reached a performance criterion of 27 correct responses in 30 consecutive trials on each of the eight problems described above in turn. The positions of the positive and negative stimuli were alternated according to a pseudorandom sequence. Control tests of various sorts were inserted between problems. These are documented separately below.

Control procedures

The following control procedures were carried out between the test stages. In each case, 10 trials of the control task were presented, with reinforcement given for responses to the stimulus containing the target square. Scores of 9 or 10/10 were considered evidence of transfer. In some instances additional training was given on transfer tasks which were not passed in the first 10 trials.

(1) *Positional variation*. The positive stimulus was replaced with one in which the target square was offset from the centre. By rotating the stimulus card from trial to trial, the target square was made to appear in each of the four quadrants of the stimulus. This test was included after

problems 1, 3 and 5 in order to make certain that the cats were detecting discontinuity, and not some local feature specific to stimulus card that had been used in training.

(2) *Positional rotation*. Following solution of task 6 (arrows) the positive and negative stimuli were rotated through 90°. This reversed the orientations of target and background features which might be expected to cause interference if the task had been learned on the basis of target element identity.

(3) *Height change*. Since the elements of textures 1 and 2 were quite small, we were concerned that the cats might not be resolving the individual elements. While every effort was made to match the mean luminance of target and background, matching two patterns with different element layouts inevitably results in some minor edge effects which may be manifest as local luminance differences. For this reason, most of the cats were given transfer tests at two additional heights on problems 3 and/or 5. The heights chosen were 15 and 60 cm. If the animals were relying on global luminance differences, performance should remain intact as height increases but could break down at the shorter distances where local cues might mask more global ones. If textural cues were the basis of the discrimination, performance should remain high as height is decreased but might decline with increased height as resolution threshold is approached.

Results

Luminance task

The learning scores for the 8 tasks are presented in Table I as Trials to Criterion and Errors to Criterion scores. There was considerable variability in the rate at which the initial black square detection task was acquired (range 4–195 trials). This may have been due in part to the prior training the animals had received, but more likely to individual differences in motivation or ability since the same differences show up consistently across all tasks. After reaching criterion on task 1, all animals were given 10 trials with the square in different off-centred positions (see Table II); 6 of

TABLE I

Learning scores for the 8 cats on each of the 8 detection problems

Trials to criterion are indicated in the upper row for each problem; errors to criterion are shown in brackets beneath. The trials to criterion scores comprise all trials up to but not including the 30 criterion trials. NT indicates Not Tested on that problem. Problems are identified by target square/background and negative stimulus (e.g. Black (square on)/White (background)).

Problem	Cat							
	N54	N58	N59	N60	N64	N67	N75	N77
1. Black/White	165 (77)	51 (28)	46 (21)	195 (66)	4 (2)	29 (9)	19 (8)	15 (10)
2. Black/Texture 1	67 (27)	38 (16)	125 (34)	41 (11)	147 (63)	142 (32)	103 (28)	49 (35)
3. Texture 2/Texture 1	52 (17)	0 0	0 0	56 (11)	0 0	6 (2)	0 0	3 (2)
4. Black/Texture 2	40 (11)	0 0	0 0	0 0	0 0	0 0	5 (2)	1 (1)
5. Texture 1/Texture 2	42 (8)	0 0	3 (1)	67 (16)	0 0	9 (3)	24 (5)	5 (1)
6. Texture 3/Texture 3 (90°)	51 (11)	0 0	1 (1)	144 (35)	15 (4)	4 (1)	19 (4)	0 0
7. Black/Texture 4	NT	0 0	32 (6)	NT	0 0	0 0	131 (39)	2 (1)
8. Texture 4/Texture 4 (90°)	NT	16 (4)	24 (5)	NT	0 0	27 (8)	100 (28)	1 (1)

TABLE II

Scores (/10) from transfer tests following texture detection tasks

The numbers in brackets indicate the number of additional 10-trial blocks required to reach criterion performance (9/10). B/W, Black square on White; T1, Texture 1 (Rings); T2, Texture 2 (Dots).

Cat	B/W	Position change		Height change				90° rotation
		T2/T1	T1/T2	T2/T1		T1/T2		Arrows
				15 cm	60 cm	15 cm	60 cm	
N54	10	9	10	10	NT	10	NT	10
N58	9	10	9	NT	NT	NT	NT	9
N59	9	9	7 (1)	9	NT	10	7	7 (1)
N60	10	9	9	6	6	7	5	9
N64	10	9	8 (1)	8	NT	6	9	10
N67	9	9	9	10	5	9	4	8 (1)
N75	7 (3)	10	8 (1)	9	4	9	7	8 (1)
N77	6 (10)	9	9	10	NT	10	6	10

the 8 cats achieved scores of 9 or 10; the remaining two cats were given additional training on this problem until they achieved a run of 9/10 correct.

Transfer from task 1 to task 2 (black square on texture 1) was in no case immediate, even though the second task also contained a strong luminance cue. In fact, there was a tendency for animals which had acquired task 1 quickly to have more difficulty with task 2 than those which had required many trials to master task 1.

Texture segmentation – Dots and Rings

Four of the 8 cats showed perfect transfer from task 2 to the first texture/texture problem (task 3), reaching criterion in the first 30 test trials. Two additional cats made 2 errors each before beginning their run of 90% correct in 30 trials. The final two cats reached criterion in the second test session. On the positional transfer test (Table II), all 8 cats achieved scores of 9 or 10/10 when the position of the target square was varied from trial to trial. Very rapid transfer was also shown to tasks 4 (Black on Texture 2) and 5 (Texture 1 on Texture 2), with a maximum of 67 trials (16 errors) on the latter problem. Again, positional transfer tests (Table II) caused no major problem.

Height controls were carried out after tasks 3 and 5 in some of the cats. In each case, when viewing distance was reduced to 15 cm, 5 of the 7 cats tested were successful (i.e. 9 or 10/10). On the other hand, when viewing height was increased to 60 cm, all cats tested failed with a single exception (N64; see Table II: T2/T1 60 cm and T1/T2 60 cm). Thus it seems that the nature of the task did not change with viewing distances of 47 and 15 cm, but may have at the 60 cm distance. We did not give extended retraining on these tasks because we did not wish to introduce inconsistencies in treatment across animals. Therefore, we can not be certain whether the difficulties at 60 cm were temporary disturbances or represent a real inability to detect the textural discontinuity at this viewing distance.

Texture segmentation – oriented elements

Task 6 involved very different textures from the previous tasks. The target square was composed of the same texture as the background (rows of

arrows) except that the orientation of the elements was rotated 90°. Nevertheless, although not preceded by a Black on Texture 3 phase, transfer to the Texture 3 problem was very rapid for 6 of the cats; the slowest cat required 144 trials, making 35 errors.

After an intervening period of several weeks, 6 of the cats were tested on tasks 7 and 8. Only one cat (MK75) made more than 10 errors in reaching criterion on either task, indicating that the cat's ability to perform texture segmentation is not restricted to very small elements.

There was clear evidence of between-cat performance variability. The two cats (MK54 and MK60) which had taken longest to learn the initial Black Square on White (task 1) performed consistently more poorly on all subsequent tasks. It should also be noted that on all tasks except task 1, the number of errors to criterion on a given task ranged from 1/3 to 1/5 of the number of trials to criterion for all cats, including MK54 and MK60. This indicates that performance was above chance for much of the training period, even though the cats were not immediately able to maintain 90% performance.

Discussion

The findings of Expt. 1 clearly indicate that cats are able to segment a visual pattern on the basis of discontinuity in texture. The very rapid transfer shown by all animals from luminance to texture tasks (problems 3,5,8 – Table I) and between texture tasks (problem 6) strongly suggests that the cats were using a global segmentation strategy, and not a point-by-point comparison of local stimulus elements under the control of focal attention. This conclusion is supported by the excellent performance shown by the animals when the position of the target square was moved. Had the animals learned a local search strategy directed to the central area of the stimuli, one would have predicted more initial errors on this control task.

The fact that decreasing viewing height had no adverse effects on the texture segmentation tasks involving Textures 1 and 2, whereas increasing viewing height was disruptive, provides a strong argument against non-textural cues such as global

luminance difference providing the basis for the animals' discrimination performance. Global luminance differences, which were minimal as measured by photometry, would be expected to become more noticeable as the individual elements become less distinct, and less noticeable as the elements become more prominent. This would be expected to produce the opposite pattern of results to that reported above. Thus we feel secure in concluding that the texture elements were clearly visible to the animals.

To human observers the link between luminance or textural discontinuity and form in these stimuli is immediately apparent – the target is seen as a square. Since in the texture segmentation cases there are no solid contours between figure and ground, this implies that the visual system constructs implicit or virtual contours along lines of discontinuity detected on the basis of either local comparisons of features, or more global comparisons of dispersion of elements. However, we have no way of determining from the data of Expt. 1 whether the cats perceived the targets as forms with clearly definable contours or were merely responding to change between the centre and periphery of the positive stimulus. Expt. 2 was carried out to determine whether cats could use implicit contours as a basis for form discrimination.

EXPERIMENT 2

Method

Subjects

The same 8 cats were used. However, 3 of them failed to reach criterion on the initial pattern discrimination task (see below) within 500 trials and were therefore not tested further; the remaining 5 cats completed all stages of the experiment.

Stimuli

All stimuli took the general form illustrated in Fig. 4. The positive stimulus was a target square on a contrasting background. The negative stimulus was a target triangle, matched in area, mean luminance, and texture to the square. Lumi-

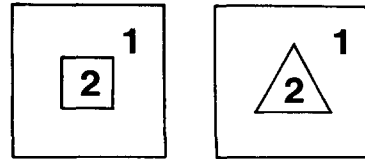


Fig. 4. Schematic representation of the stimuli for Expt. 2. The central target forms (2; square positive, triangle negative) were matched in area and in luminance or texture. The backgrounds (1) of the positive and negative stimuli matched each other and contrasted with the central forms in luminance and/or texture.

nance (Black on White), Luminance + Texture, and Texture + Texture variants were used as in Expt. 1. The textures used were Textures 1 and 2 from Expt. 1; hence, the positive stimuli were the same as in the previous experiment; the only difference was that they were paired with different negative stimuli.

Procedure

Testing was carried out on the jumping stand exactly as in Expt. 1. Three cats were trained to criterion on the following sequence of tasks:

- (1) Black square vs black triangle on white backgrounds.
- (2) Black forms on Texture 1 backgrounds.
- (3) Texture 2 forms on Texture 1 backgrounds.
- (4) Black forms on Texture 2 backgrounds.
- (5) Texture 1 forms on Texture 2 backgrounds.

The remaining two cats (MK74 and MK75) were not tested until several weeks after the completion of Expt. 1, during which period they participated in unrelated experiments. For these animals the testing sequence was reversed: task 1 was followed by tasks 4, 5, 2, and 3 in that order.

The triangle form used in tasks 2 and 3 differed from that used in tasks 4 and 5 in shape but not in area.

RESULTS

The 5 cats who mastered the initial pattern discrimination task within the allotted 500 trials required a range of from 127 to 443 trials to reach criterion. All 5 animals were then successful in mastering the remaining 4 transfer tasks (see Table III). However, most of the cats evidenced

TABLE III

Learning scores for square/triangle discrimination tasks

Trials to criterion indicated in the first row; errors to criterion in brackets.

Problem	Cats				
	N58	N59	N64	N75*	N77*
1. Black/White	483 (173)	169 (37)	127 (50)	340 (132)	330 (112)
2. Black/Texture 1	83 (21)	89 (21)	327 (96)	10 (3)	120 (32)
3. Texture 2/ Texture 1	184 (76)	127 (36)	120 (40)	30 (11)	55 (16)
4. Black/Texture 2	117 (41)	12 (4)	3 (2)	0 (0)	0 (0)
5. Texture 1/ Texture 2	263 (108)	89 (22)	53 (11)	60 (14)	0 (0)

* N75 and N77 were tested on problems 4 and 5 before problems 2 and 3.
Expt.

greater difficulty with the discrimination tasks than they had with the detection tasks (Expt. 1; see Table I). This is particularly clear on the first transfer from Black-on-Texture to Texture-on-Texture (task 3). Whereas in Expt. 1, 6 of the 8 cats showed excellent transfer, in Expt. 2 three of the 5 cats actually required more trials to learn the Texture-on-Texture problem (i.e. showed negative savings).

Discussion

Given the fact that the positive stimuli in this experiment were identical to those used in Expt. 1, it is somewhat surprising that the cats required as many trials as they did to master the new problems. One interpretation of this finding would be that in Expt. 1, the cats were not attending to the form of the target. In all parts of Expt. 1, recognizing that 'something changes' was sufficient to correctly identify the positive stimulus. In Expt. 2, both positive and negative stimuli met this definition, and hence discontinuity no longer provided a reliable cue. The similarity of the stimuli to those in the first experiment may

have evoked the 'change detection' strategy on each new task. On the other hand, the fact that considerably greater savings were shown in the transition from task 1 to task 2 than from 2 to 3 (the reverse was the case in Expt. 1) suggests that contour extraction from texture-texture boundaries may be a considerably more demanding task than texture boundary detection.

The lack of perfect transfer should not obscure the main finding of this experiment, that cats are able to use the contour information provided by texture/texture boundaries as a basis for form discrimination.

GENERAL DISCUSSION

The present studies were undertaken to determine whether textural discontinuity can be utilized as a cue for image segmentation by the cat. Our findings clearly indicate that visual texture boundaries can be a highly salient stimulus for the cat. Texture segmentation in humans has been described as 'preattentive'^{1,14,15,27}, meaning that it does not require a serial element-by-element comparison. The experimental conditions for defining preattentive vision include discrimination under conditions of very limited exposure time (under 50 ms). Since exposure time could not be controlled in our paradigm, we cannot draw a direct analogy between the performance of our cats and that of human subjects. However, certain features of the cats' performance does suggest a striking similarity. In particular, the extremely rapid transfer shown by the cats between problems was quite different from the prolonged learning usually seen in discrimination tasks. This was particularly striking in the case of transfer from task 5 to task 6 in Expt. 1, where the elements of task 6 were completely novel to the animals, and the dimension along which target and background varied (orientation) was not a local cue in any of the previous tasks. The immediate errorless performance of several of the cats on task 6 argues strongly against a search based on the identity of the elements. The finding that texture-texture boundaries can support form discrimination (Expt. 2) also argues for some sort of automatic parallel process, since retaining in

memory the locations of serially detected boundary points would seem an excessively demanding task.

Local and global processing

Having determined that cats are capable of texture segmentation, it remains to be asked on what basis the discriminations are made. Visual textures may differ in the identity of their component elements and/or in the disposition of those elements. Regular textures such as those used here often evidence global organization as well as local characteristics. This global organization may be thought of as Gestalt grouping, or in spatial frequency terms as organization carried by low spatial frequency components of particular orientations. In practice, the former could be mediated by the latter in some but not all instances (see, for example, ref. 17, p. 46). In the present study, texture 3 (arrows) shows strong global organization of this sort, with target and background differing by 90° in global organization as well as in local structure. For Textures 1 and 2, the difference in global organization is much less striking, although in each case the elements do group on the basis of proximity. Whether segmentation is based on differences in global structure or differences at the level of the local elements (Gestalt similarity grouping), or both, cannot be determined from the present data. In general, while many texture pairs giving rise to rapid segmentation can be differentiated in either of these ways, Julesz^{14,15} has pointed to instances which can only be differentiated in terms of local features, and argues that parallel local analysis forms the basis for all preattentive texture segmentation in human subjects. In Textures 3 and 4 the predominant local feature distinguishing the texture pairs is element orientation. The elements in Textures 1 and 2 are locally non-oriented; the major differences between them – overall diameter and solid vs outline structure – may act together to give rise to local contrast differences at certain scales of analysis (receptive field sizes). Local contrast has not received much attention as a cue to texture segmentation, but is probably an important factor.

Hughes¹¹ examined the sensitivity of cats to

local structure and to global organization or grouping separately in tasks involving a two-choice discrimination paradigm. Positive and negative stimuli each contained a single texture, i.e., the tasks were texture discrimination tasks rather than segmentation tasks. In the grouping task, all elements were identical dots. Spacing between dots gave rise to obliquely oriented 'lines', positive and negative stimuli differing by 90° in orientation. Cats showed very rapid transfer from obliquely oriented grids of solid contours to these dotted line grids, suggesting that proximity grouping of this sort has an automatic quality in the cat as it does in man, perhaps through direct activation of low spatial frequency channels (a possibility considered at length by Hughes¹¹). Cats did not show transfer from global orientation to local orientation of randomly arrayed line segments, although they were also able to learn the locally based problem. When local and global structure were pitted against one another (45° segments which grouped to form 135° lines and vice versa), global structure dominated the animals' performance. These findings clearly indicate that cats are able to discriminate on the basis of both local features and global structure; presumably, either type of information could have provided our cats with the basis for the differencing leading to segmentation. However, Hughes' results do not provide us with any insights as to how that differencing is accomplished. In his task, a strong memory component for orientation is required; i.e. in each case, the correct stimulus has a specific orientation (e.g. 45°) which must be remembered and recognized from trial to trial; in the present case neither element identity nor orientation of global structure need be retained; a discontinuity or difference in either one is all the animal had to look for.

Neural correlates

The first neurophysiological work to use textured fields rather than solid line stimuli was that of Hammond and McKay^{9,10}. Their demonstrations concern boundaries defined by the displacement of a bar of random texture across a similarly textured background, and hence are not directly related to textural discontinuity the sense dis-

cussed in the present report. They did, however, demonstrate that cortical complex cells are responsive to the movement of both textured bars and whole field textures across their receptive fields, indicating that extended solid contours are not the only stimuli to which such cells respond.

Recently, Northdruff and Li^{20,21} have reported electrophysiological data which are directly relevant to the issue of texture discrimination as discussed here. Their stimulus patterns were fields of small elongated elements which varied in both orientation and contrast. Orientation differences led to the definition of one central form or global pattern (like the central square in our study), while contrast differences defined a different central form on the basis of a global luminance difference. To a human observer, when the size of the individual elements is decreased below threshold, the second, luminance-based form appears as a light grey shape on a darker gray background. By systematically changing element size, Northdruff and Li were able to determine texture acuity thresholds for individual cells.

Their findings indicate that simple and complex cells show specificity for the orientation of texture elements over a very similar range of element sizes, although the nature of the response differed in the two cell classes. Complex cells showed poorer resolving power for individual elements than did simple cells, but continued to show differential orientation specificity across the same range of texture granularity as simple cells. With very small elements (below the texture threshold), both cell classes responded only to the oriented part of the global luminance border. At intermediate element sizes, simple cells showed a region of 'texture blindness' where neither the individual texture elements nor the luminance border elicited responding. Complex cells, on the other hand, often showed an ambiguous response in this intermediate zone, responding both to element orientation and to global luminance change (although the latter response was not orientation specific in this intermediate range). Thus either or both of these two cortical cell groups may participate in the early stages of analysis leading to texture segmentation.

One important finding of Northdruff and Li's

work^{20,21} is that no cells were found in cat area 17 which responded to the texture–texture boundary defined by change in element orientation. That is, the explicit coding of contour produced by these boundaries does not seem to occur in area 17. Where might such a response be expected? Two possibilities which are not mutually exclusive, suggest themselves. Contour information contributing to the definition of edges in a form recognition process might be sought in extrastriate cortical areas (areas 18, 19, 20, 21 or the lateral suprasylvian cortex). Hughes¹¹, whose work on grouping was discussed above, points to area 20 as possibly involved in grouping on the basis of a deficit seen in one lesioned animal. The recent finding in monkeys that illusory contours of a different kind are coded in area 18 (ref. 29) suggests that an earlier site is possible. In any case, some sort of explicit cortical representation of these boundary contours seems very probable. One must also consider a second possibility, that of a subcortical 'registration' of the textural discontinuity corresponding to the preattentive mechanism of segmentation and its role in guidance of focal attention. This need not be and probably is not an explicit representation of the sort discussed above. The basic idea of global parallel preattentive search is that regional differences in feature density are detected at an early stage and direct focal attention to the region of change^{14,15,27}. In neural terms, this could be reflected in a process like the response enhancement seen in superior colliculus before a saccade^{33,34}. Any or all of corticogeniculate, corticopulvinar and corticocollicular pathways might participate in enhancement of this sort. For example, Crick's recent searchlight hypothesis⁶ would point to a thalamic site for such an attentional effect. The point is that this need not be an explicit representation of orientation (i.e. cortical cell tuned to texture–texture boundary orientation); local minima in intracortical inhibition among cells responding to similar features or textons could occur at such boundaries, and might have the consequence of stronger subcortical output in the region of the border. The individual cortical cells involved, however, would show spatial specificity for the local feature, not

the implicit contour. If such an arrangement existed, one might predict that the integrity of striate cortex and its subcortical projections would be sufficient for performance of the boundary detection task of Expt. 1 but not for the discrimination task of Expt. 2.

In the cat, the discrimination of shapes defined by luminance contours does not depend on the integrity of the striate cortex⁸. Indeed, adult cats show residual form discrimination ability after lesions which include areas 18 and 19 in addition to area 17^{4,25,32}, and if the lesions are made in the neonatal period, apparently normal form perception develops (refs. 7, 19, 30 but see refs. 3 and 8). However, natural visual scenes are much more complex than this simplified experimental world of gratings, circles and triangles, and information about object shape must be derived from a variety of sources (texture, relative motion, shading, disparity etc.)¹⁷. In ongoing studies in our laboratory, we have been using texture segmentation as one measure of the ability of the neonatally damaged visual system to process complex visual arrays. Our preliminary findings³¹ reveal severe deficits in cats whose pattern vision, assessed by more traditional measures, is excellent.

CONCLUSIONS

In relating electrophysiological descriptions of the visual process, obtained in non-human species, to the properties of human vision, a critical link is the assessment of the particular visual function in question in the species in which the electrophysiological analysis has been carried out. Without evidence that cats or monkeys actually use information derived from stereo-matching, textural analysis, relative motion etc., electrophysiological evidence of cells with properties suggestive of such analysis could be interpreted only in a very speculative fashion. The present study makes a beginning at establishing this link in the case of textural analysis by demonstrating that textural boundaries do provide a cue to image segmentation and can be used as a basis for form discrimination in the cat. The

parameters of texture discrimination in this species remain to be explored in future research.

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