Visual Form Discrimination From Texture Cues: A PET Study

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Abstract: With the purpose of localising the cerebral cortical areas participating in the discrimination of visual form generated exclusively by texture cues, we measured changes in regional cerebral blood flow (rCBF) with positron emission tomography (PET) and ¹⁵O-butanol as the tracer. The subjects performed two odd-one-out discrimination tasks: a form-from-texture discrimination task (in which a visual form was defined by differences in texture) and its reference task, the discrimination of texture. During task performance, activated fields were present bilaterally in the primary visual cortex and its immediate extrastriate cortex, the right lateral occipital gyrus, bilaterally in the fusiform and superior temporal gyri and posterior parts of the superior parietal lobules, along the medial bank of the right intraparietal sulcus, and in the right supramarginal gyrus. Other fields were found in the cingulate and prefrontal cortex. The findings demonstrate that the discrimination of visual form as defined by texture engages cortical fields that are widely distributed in the human brain. In the visual cortex, the activated fields are present in both the occipito-temporal and occipito-parietal visual areas. These results suggest that the perception and discrimination of forms in the visual system requires the joint activation of neuronal populations in the visual cortex. *Hum. Brain Mapping 6:115–127, 1998.* © 1998 Wiley-Liss, Inc.

Key words: visual form discrimination; visual texture; PET (positron emission tomography); human visual cortex

INTRODUCTION

The perception and analysis of form is one of the premier aspects of vision. Not surprisingly, countless

physiological experiments in mammals indicate that a substantial part of the visual system is devoted to it. In monkeys numerous studies indicate that cells sensitive to form are located in regions along a “ventral” occipito-temporal visual pathway. It is often claimed that the final global analysis of visual form occurs, in great part, in the inferior temporal cortex (Gross et al., 1972; Perrett et al., 1982; Schwartz et al., 1983; Desimone et al., 1984). It has also been shown that there are form-selective neurons in the macaque inferior temporal cortex that are equally activated by forms generated by either luminance or motion or texture cues (Sáry et al., 1993) and that many of these cells are tuned to particular forms irrespective of precise retinal position and the orientation of the form, i.e. they have physi-

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ological properties akin to form constancy (Gross, 1992; Lueschow, 1994; Kovács et al., 1995). However, claims that there is a single region in the brain exclusively specialised for the perception of category specific forms such as faces have been challenged by lesion studies in monkeys (Heywood and Cowey, 1992). Indeed, PET studies in humans, using various form-related psychophysical paradigms, have shown a large number of cortical regions to be active during the different form tasks (Corbetta et al., 1991; Sergent et al., 1992; Gulyás and Roland, 1994b). This heterogeneity of cortical fields, participating in the processing and analysis of visual form, has also been supported by neuropsychological observations in patients with well defined deficits in visual form perception resulting from anatomically circumscribed lesions in their brain (De Renzi et al., 1994; Tohgi et al., 1994; Sergent and Signoret, 1992a,b).

The fact that different cortical lesions can disrupt the discrimination of different form categories may be related not only to the different behavioural significance of e.g. faces and inanimate objects but to the fact that visual form can be independently generated by a relatively large number of visual cues, including colour, motion, disparity, luminance or texture. As cells in lower level visual cortical areas exhibit different sensitivities to, among others, colour, luminance, motion, disparity or orientation, it would not be surprising if the various visual cortical areas participate to different extent in the elaboration of visual form information when it is generated by different visual signals.

We have previously analysed human cortical areas participating in the generation of the same visual forms from colour, or motion, or disparity, or luminance cues (Gulyás et al., 1994a,b). Following the same logic, here we investigated cortical fields participating in the discrimination of visual form generated solely by texture cues. Accordingly, we measured the regional cerebral blood flow (rCBF) changes with positron emission tomography (PET) in seven normal subjects while they performed a form-from-texture discrimination task and a reference task involving the discrimination of texture itself.

MATERIALS AND METHODS

Subjects

Seven healthy male volunteers (age: 24–38 years) participated. They were fully informed about the objectives, details, and risks of the experiment and gave written consent, in agreement with the Helsinki Declaration and the NIH report on the Protection of

Human Subjects (1989). All the volunteers were naïve about psychophysical experiments. Although they were informed about the main purpose and detailed technical aspects of the experiment weeks before it, they were not given a description of the psychophysical tasks until an hour prior to being tested. The study was approved by the Ethical, Radiation Safety, and Magnetic Resonance Imaging Committees of the Karolinska Hospital. Six subjects were right handed, one was left handed, according to the Edinburgh handedness inventory (Oldfield, 1971). The subjects denied any relevant medical, neurological or psychiatric history and all had normal or corrected-to-normal visual acuity. None of them had any visual deficit. EOG and EEG were continuously monitored, whereas the arterial PaO_2 and PaCO_2 levels were regularly monitored during the experiment.

Brain scanning procedures

Each subject wore an individually moulded plastic helmet (Greitz et al., 1980; Bergström et al., 1981) which held the head in identical position during the MR and PET scanning procedures. First, a high resolution nuclear magnetic resonance (NMR) scan (GE Signa scanner, 1.5 Tesla) was acquired for each brain (pulse sequence, a spoiled gradient echo Spoiled-GRASS 3D-sequence; TE = 5 msec, TR = 21 msec; flip angle, 50 deg; NEX, 1; FoV, 25.6 cm × 25.6 cm; voxels, 1 mm × 1 mm × 1 mm). The MR images were used to guide the head positioning in the PET scanner. The MR and PET slices were placed in register and the MR images were used to standardise individual brains, as well as to localise anatomical structures underlying functional changes in the individual brains (see below).

The method of measuring rCBF with PET has been described in detail (Roland et al., 1993), therefore only a short description is needed here. In brief, the PET measurements were made in wobbling mode on a Scanditronix 2048-15B positron camera with 4.5 mm in-plane resolution and 6.5 mm inter-slice distance (Litton et al., 1990; Evans et al., 1991). The effective image resolution in the final statistical images was 3.8 mm along the x axis and 4.5 mm along the y axis (Roland et al., 1993). The camera produced 15 trans-axial slices of the brain. ^{15}O -butanol was used as the tracer (Berridge et al., 1990, 1991), which was given in a bolus injection in the right cubital vein (65 ± 5 mCi dissolved in 7 ml solution of physiological saline [90% of volume] and ethanol [10% of volume]) before each test. Four injections, corresponding to the four tasks presented in a random order, were administered in

each subject. In the emission scans, data were obtained for a total of 100 sec in 20 sequential scans, each lasting for 5 sec, but only the first 80 sec was used for the actual computation of the rCBF. Data acquisition and stimulus presentation started simultaneously.

Under local anaesthesia, the left brachial artery was cannulated and the arterial radiotracer concentration was continuously and automatically monitored during the PET measurements (Eriksson et al., 1988). The sampling velocity was 2.5 ml/min. The time shift between the arterial radiotracer concentration and the global uptake curve from the positron camera was calculated. The arterial PaO_2 and PaCO_2 concentrations were measured regularly (30 sec prior to and 180 sec after the tracer injection). Differences in rCBF between PET measurements of test and reference tasks due to differences in PaCO_2 were corrected to the level of the reference condition (Olesen et al., 1971; Roland et al., 1987). Because of the precise head fixation, in each experiment only one transmission scan was required in the same image planes as those of the emission scans, and it was used to correct for attenuation in each emission scan. The reconstruction filter in both the transmission and emission scans was a 4 mm Hanning-filter (Roland et al., 1993). Images of rCBF (ml per min per 100 g brain tissue) were calculated (Koppe et al., 1985; Roland et al., 1987).

Electrophysiological measurements

The electro-encephalogram (EEG) was recorded with a Siemens Mingograph at an amplification of $\times 100$. Needle electrodes were placed in the scalp at five standard positions: F3, F4, P3, P4, and Cz. In addition, one ground electrode was fixed above the left clavicle. The recordings were analysed off-line for the proportion of different frequency domains during the PET measurements.

To record the electro-oculogram (EOG), two monitoring channels of the same instrument were used. Two silver electrodes were put above the lateral and inferior edges of the orbit on both sides. As determined in earlier tests, the recordings measure the frequency, amplitude, and movement trajectory of saccadic eye movements equal to or larger than 2 deg in amplitude. Fine eye movements smaller than 2 deg in amplitude could not be monitored precisely with the present method.

Visual stimulation

The stimulus displays were presented on a 20 in. colour monitor (Microvitec 2038) with a screen resolu-

tion of 768×576 and at a viewing distance of 125 cm (1 deg = 2.2 cm). The screen subtended 18 deg $\times$ 16 deg. On each trial the display consisted of a horizontal row of three stimuli, separated by 3 deg, and the subject was required to indicate with his right hand the odd-one-out, which could appear at either end of the row, by pressing one of two buttons. There was no time pressure and the subject was encouraged to peruse the display. A new trial immediately followed a response. The difficulty of the discrimination was either increased or decreased following three consecutive correct responses or a single error, respectively. Thresholds (between 75 and 80% of correct responses) predetermined for each task in pilot experiments with each subject ensured that PET measurements were made while the subject was tracking his threshold. These pilot experiments took place right before the actual PET experiment started, while the subjects were already in the scanner. Each subject performed a form-discrimination task (form from texture) and its reference task (texture discrimination). For image analysis, the images revealed by reference tasks were subtracted from the appropriate form-discrimination task.

Form-from-texture and texture -discrimination tasks

The subjects viewed a yellow display presented on the screen with a 10% yellow random pixel texture. The luminance of the pixels was $10 \text{ cd} \cdot \text{m}^{-2}$. For the form-from-texture task three clear quadrilateral forms were generated by using texture defined contours between the forms and their surround (Fig. 1A). The forms were a row of two squares (2.5 deg $\times$ 2.5 deg) and a rectangle, or vice versa, whose vertical positions were each randomly varied to avoid any collinearity of horizontal edges being used as a cue to solve the task. The average density of the texture inside the three forms (foreground) and in the background was identical. The subject was required to detect the odd-one-out and task difficulty was varied in the manner described above by changing the width/height ratio of the rectangle with a resolution of a single pixel. Three correct responses or a single error resulted in a halving or doubling, respectively, of the difference in length of the long and short sides of the rectangles. For the texture-discrimination task, the display was identical to that described above except that three squares were presented, two of which were generated with an identical underlying texture (although the spatial distributions of their elements was not identical) whereas the third square had a different texture (Fig. 1B). The subject again was asked to indicate the odd-one-out.

Figure 1.

Examples of relatively easily discriminated stimulus patterns used in the FORM FROM TEXTURE (top) and TEXTURE DISCRIMINATION tasks (bottom). In each case the odd-one-out is on the left.

Whether discriminating form (from texture) or texture alone, the underlying texture changed from trial to trial.

Stimulus energies during the four tasks were assessed by using Roland and Mortensen's theory and formula (Roland and Mortensen, 1987), describing the energy of a stimulus as follows:

$$E = \int_{t_1}^{t_2} |f(t)|^2 dt, \quad (1)$$

where $f(t)$ is a set of orthogonal vector functions describing the stimulus in space and time. The above described stimulus sets-up resulted in identical stimulus energies in the four tasks ($1 \text{ cd/m}^2/\text{sec}$).

As the present experiment formed a part of an experimental series, earlier parts of which have been

described in other publications (Gulyás et al., 1994a,b), special care was taken to have unified processing strategies during task performance throughout all experimental conditions. In this respect, we have evaluated the hypothesis that one of the present tasks (form) might be solved by global processing whereas the other (texture) might be solved by local processing. In fact, texture could not be discriminated locally because on each trial a different local arrangement of pixels was used to create the texture and the two examples of the same texture on each trial were also constructed from different arrangements of pixels. In other words there were local differences between all three forms in the present texture-tasks and only the global texture difference could be used to find the odd one out, similarly to the other task conditions of the whole experimental series.

Data processing and analysis

All individual MR and rCBF images were processed with the computerised Human Brain Atlas (HBA) (Roland et al., 1994; Roland and Zilles, 1994). First the individual MR images of the brain were transformed to the standard anatomical format of the HBA. As the PET images do not provide precise anatomical information of the individual brains, but the corresponding MR and PET images were put in register, the standardisation parameters of the corresponding MR images were used in standardising the individual PET images. By using the HBA procedures, standardised individual rCBF images and, by means of pixel by pixel subtractions, ΔrCBF ($\Delta\text{rCBF}_{\text{FORM FROM TEXTURE}} - \text{TEXTURE DISCRIMINATION}$) images were created, which were then averaged across the whole subject population to provide averaged subtraction ($\Delta\text{rCBF}_{\text{AVE}}$) images, as well as corresponding descriptive t images ($\Delta\text{rCBF}_{\text{AVE}}/\text{SEM}$). The voxel size was $1 \times 1 \times 1 \text{ mm}$. The accuracy and precision of the HBA has already been validated (Roland et al., 1994). The variances in sulcal anatomy for major sulci, including the calcarine sulcus (Table 1), were evaluated for the seven participating subjects. The SEMs of the x positions of the calcarine sulcus along the y axis vary between 0.31 and 1.95 mm (mouth) whereas the corresponding z positions vary between 0.60 and 2.60 mm (fundus), i.e. far below the effective image resolution of the PET scanner. Horizontal slices of the averaged standardised MR image (averaged across the population of the seven subjects) (Fig. 2) give an indication of the precision of anatomical standardisation with the help of the HBA.

The anatomically standardised images were analysed for local field activations occurring in the brain

Figure 2.

Averaged standardised MR images of the seven subjects participating in the present study. HBA convention, A: $z = 0$ mm (plane of the AC-PC line); B: $z = +10$ mm.

as clusters of voxels having high signal-to-noise ratio. The statistical analysis of the cluster detection was described extensively in a recent report (Roland et al., 1993), therefore only a brief description is needed here. From the individual $\Delta rCBF$ images, mean $\Delta rCBF$ images ($\Delta rCBF_{AVE} = \Sigma \Delta rCBF / \text{number of subjects}$) as well as variance images and descriptive Student's t images ($\Delta rCBF_{AVE} / \sqrt{\text{variance}} / \sqrt{\text{number of subjects}}$) were calculated. Subsequently, clusters of voxels with high t values were identified as true activations. The probability of finding one or more false positive cluster in the whole brain was ≤ 0.1 .

The activated significant clusters (henceforth called fields of activation) were localised in relation to the sulci and gyri of the HBA standard brain and in relation to the reformatted mean MRI of the seven subjects. In the case of the striate cortex (V1) and the first extrastriate visual area (V2), the present findings were localised with respect to the average extent of areas V1 and V2, determined in the HBA using quantitative neuroanatomical criteria in post-mortem human brains (Vidnyánszky et al., 1996). The relationship between the stereotactic coordinates of our HBA and the Talairach and Tournoux (1988) atlas is very close, as was evaluated in an earlier study (Roland et al., 1994). The mean $rCBF$ change (ml/100 g/min) and

the mean volume of $rCBF$ change (mm^3) were calculated by voxel by voxel analysis of regions in the mean subtraction CBF images, which had been identified from corresponding regions of significant change in cluster images.

As the data of the present experiment and data from our earlier studies were in standard HBA format, overlaps between activated fields found in the present experimental series and those found in our earlier experiments on discrimination of forms generated by other features than texture (Gulyás et al., 1994a,b) could be analysed by superimposing HBA formatted cluster images of significantly activated fields from the various experiments.

RESULTS

Physiological responses during stimulation

Physiological variables measured during the tasks, including the mean degree of α -blockade in the EEG, the eye movement frequencies, the arterial PaO_2 and PaCO_2 levels, and the global CBF values are displayed in Table 1. The tasks were accompanied by about the same percentage of α -blockade in all leads in the EEG

TABLE I. Standard error of means (SEM) of the position of the calcarine sulcus (in mm)

Coronal position (y coordinate, mm)	Left side				Right side			
	Mouth		Fundus		Mouth		Fundus	
	x	z	x	z	x	z	x	z
-60	0.31	1.14	1.44	0.65	0.48	2.90	1.95	0.93
-65	0.43	1.16	1.00	0.91	0.50	1.36	0.87	1.23
-70	0.49	1.30	1.24	1.01	0.37	1.93	0.98	1.72
-75	0.33	2.02	1.01	1.14	0.34	2.32	0.75	1.76
-80	0.33	2.07	0.53	1.54	0.33	2.60	0.60	1.73
-85	0.44	1.95	1.20	2.04	0.48	2.55	0.94	1.27
-90	0.33	1.83	0.62	1.98	0.91	1.48	1.37	1.73

and similar eye movements. Amplitude analysis of the EOG signals indicated that the distribution of saccadic and pursuit eye movements was not different between the two tasks for any subject. Similarly, there was no significant difference between the tasks with respect to PaCO₂ and PaO₂ levels, nor any significant difference in the gCBF values between the tasks. Performance levels were closely matched to each other, and there was no significant difference between them (paired *t*-test, two-tailed). On the other hand, there was a marked difference between response latencies, resulting in higher response frequency during the form-from-texture task (paired *t*-test, two-tailed, $P = 0.048$) (Table 2).

rCBF measurements and localisation of activity

Using the criteria described in Materials and Methods, regions of activity were determined in the brain for the “form from texture – texture discrimination” subtraction. The delineated regions, their location in the standard stereotactic HBA space, their volume, the

mean *t*-value and rCBF changes within the volumes (in absolute values of blood flow as well as in percentage of changes with respect to the reference state) are presented in Table 3.

Cortical fields activated in form discrimination

Regions activated by the discrimination of visual forms were relatively widespread in the cortex (Table 3). In the occipital lobe they were located in both the right and left cuneus, bilaterally in the fusiform gyri, and in the right lateral occipital gyrus. The activations in the cuneus included both activations inside and outside the primary visual cortex, the borders of which were determined on the basis of cytoarchitectural criteria in post-mortem human brains, using the HBA standard brain anatomical conventions. Temporal lobe activations included fields in the right and left superior temporal gyri. In the parietal lobe, activations were present symmetrically in the posterior superior parietal lobules, as well as in the cortex lining the banks of the right intraparietal sulcus and in the supramarginal gyrus. Frontal lobe activations were widespread and included fields in the left precentral gyrus, the right inferior and middle frontal gyri, the right frontal operculum, and three fields in the left cingulate gyrus. There was one field in the anterior part of the right cingulate gyrus for which the regional blood flow was less in the form-from-texture task and significantly increased in the texture-discrimination task. Finally, there was also activation in the vermis of the cerebellum (Figs. 3, 4, and 5).

Distribution of fields in the brain

In Table 3, fields of different volumes are listed. The probability that these are false positive activations declines steeply with field size. For example, a field of 400 mm³ has a $P < 0.1$ of being false positive, whereas one of 500 mm³ has only a $P < 0.01$ of being false positive (Roland et al., 1993). On the basis of activated fields listed in Table 3, we can calculate their number and the total volume of cortex activated for the form-from-texture discrimination tasks.

Keeping these considerations in mind, we estimated the relative size of the activated cortical fields in terms of cortical grey matter in various parts of the cortex. Assuming an average brain surface (cerebral cortex, 1.680 cm²; cerebellar cortex, 450 cm²) and average

TABLE II. Physiological and response measurements during the tests (mean $\pm$ 1 sd)

	Form from texture	Texture discrimination
gCBF (ml/100 g/min)	49.73 $\pm$ 3.39	48.37 $\pm$ 4.28
PaCO ₂ (kPa)	5.43 $\pm$ 0.26	5.41 $\pm$ 0.38
PaO ₂ (kPa)	13.60 $\pm$ 0.95	13.40 $\pm$ 0.63
O ₂ Saturation (%)	97.6 $\pm$ 0.4	97.8 $\pm$ 0.6
Eye movements (Hz)	0.77 $\pm$ 0.26	0.66 $\pm$ 0.27
α -blockade in the EEG (%)	94.9 $\pm$ 5.0	94.9 $\pm$ 3.9
Response latency (sec)	3.52 $\pm$ 1.22	5.41 $\pm$ 1.66
Performance levels (%)	72.3 $\pm$ 6.0	81.0 $\pm$ 13.8

TABLE III. Cortical fields of activation, “form-from-texture – texture-discrimination” task

Anatomy	HBA coordinates			Size (mm ³)	Δ rCBF (in %)	Seen in Figure 4
	x	y	z			
Cuneus L (areas V1 + V2)	-7	-76	15	525	26.5	(Figure 5!)
Cuneus R (areas V1 + V2)	1	-74	3	615	26.4	
Lateral occipital gyrus R	29	-79	13	782	36.9	G
Fusiform gyrus L	-33	-54	-16	402	30.5	A, E
Fusiform gyrus R	35	-62	-14	489	35.4	A
Superior temporal gyrus R	44	-25	9	581	33.3	H
Superior temporal gyrus L	-51	-27	4	663	33.5	D
Posterior superior parietal lobule R	9	-72	38	528	26.5	C, F
Intraparietal sulcus R	24	-61	41	527	42.8	C, G
Supramarginal gyrus R	35	-57	17	580	50.2	
Middle frontal gyrus R	31	25	33	459	31.6	C, E, H
Frontal operculum R	40	12	8	464	23.1	
Cingulate gyrus, mid part L	-11	-35	44	429	29.9	
Cingulate gyrus, mid part L	-4	-52	27	445	28.2	C
Cingulate gyrus, mid part L	-15	-27	24	540	50.2	
Cingulate gyrus, anterior part R	9	39	5	646	-50.9*	B

* I.e., in this case there was a significant decrease in rCBF between the form-discrimination task and its reference task.

thickness of cortex (cerebral cortex; 2.2 mm; cerebellar cortex, 0.7 mm) (Blinkov and Glezer, 1967), we estimated the volume of the whole cerebral and cerebellar cortex involved in the specific activations in the form-discrimination task (Table 4).

The activated fields were present in the occipital lobe (20.2% of all activations), the temporal lobe (26.2%), the parietal lobe (21.2%), and the prefrontal cortex (32.4%). The total activated field volume in the right hemisphere (60.8%) surpassed that in the

Figure 3.

The loci of the image slices, shown in Figure 4, in the standard HBA brain. AC = anterior commissure, PC = posterior commissure; AC-PC = line/plane intersecting the anterior and posterior commissures, VCA = vertical axis/plane intersecting the anterior commissure.

Figure 4.

Significant activations in the 'FORM FROM TEXTURE - TEXTURE DISCRIMINATION' subtraction. The significantly activated cortical fields (yellow and red) are projected onto the standard MR brain image of the HBA. In the horizontal and coronal slices, left in the images corresponds with the right hemisphere, and vice versa (neuroradiological convention). Horizontal slices: A. $z = -12$ mm. B. $z = +4$ mm (this

is the only panel in the series showing decrease!). C. $z = +37$ mm. Sagittal slices: D. $x = -54$ mm. E. $x = -30$ mm. F. $x = +9$ mm. G. $x = +25$ mm. H. $x = +51$ mm. The location of most of the fields, displayed in the figures, are indicated in Table 4.

Figure 5.

Activations (in red) in visual areas V1 (yellow) and V2 (light blue). HBA convention, parasagittal slice, $x = +2$ mm.

left hemisphere (39.2%), and this difference, even more accentuated, was already present in the occipital lobe.

Field overlaps between the present form-discrimination task and other form-discrimination tasks

Field overlaps between the present form-discrimination task and other form-discrimination tasks, investi-

gated in our previous experiments, are listed in Table 5. Field overlaps were identified in the present form-discrimination task and another four tasks (colour, motion, luminance and disparity), but they were largely restricted to three structures: the left and right fusiform gyri (texture vs. motion, luminance, disparity) and the right lateral occipital gyri (texture vs. motion and colour).

TABLE IV. Total volume of activated cortical fields and their distribution in the cortex

	Occipital	Temporal	Parietal	Frontal	Total
A. Volume of cerebral cortical fields activated in form discrimination (in mm ³)					
R	1397	1070	1635	923	5025
L	525	1065	0	1414	3004
Total	1922	2135	1635	2337	8029
B. Relative volume of cerebral cortical fields activated in the tasks (in % of the total activated fields)					
R	17.4	13.3	20.4	11.5	62.6
L	6.5	13.3	0	17.6	37.4
Total	23.9	26.6	20.4	29.1	100
C. Total volume of fields activated in the task (as % of the whole surface), cerebral cortex					
R	1.38				
L	0.83				
Total	2.21				

DISCUSSION

The results of the present study demonstrate that 1) a simple visual form-discrimination task activates widespread functional fields in the human brain and 2) both the occipito-temporal and occipito-parietal visual pathways are engaged by form-discrimination-from-texture cues. These observations, in conjunction with our earlier studies (Gulyás and Roland, 1994a,b; Gulyás et al., 1994a,b; Gulyás and Roland, 1995), demonstrate that the analysis of simple forms generated by single visual cues involves a number of disparate cortical fields in the human brain, although they do not

reveal whether, or the extent to which, the fields are interactive.

The lack of any significant difference between performance levels in the different tasks, as well as the facts that there were no significant differences between EEG frequencies, saccadic eye movements, arterial blood gas levels, or gCBF levels between the tasks indicate that the tasks were effectively matched in all respects except two: 1) the specific task features, which were the subject of the present investigation, and 2) the response latencies, which differed. These observations emphasise the visual feature specificity of the activated fields present in the averaged Δ rCBF images. The fact that the response frequencies were somewhat higher in the form-from-texture task than in the texture-discrimination task can also explain a sub-threshold activation cluster in the precentral gyrus which has not reached the level of significance, but whose center-of-gravity was related to the representation of the right hand region (center-of-gravity in HBA x, y, z coordinates: $-42 -13 49$; clustersize: 367 mm^3 [cfr. threshold size: 400 mm^3]; Δ rCBF: 27%).

The present experiments, along with our earlier studies on the perception of visual form generated by various other individual visual cues (Gulyás et al., 1994a,b), were not designed to reveal the loci of cortical fields responsible for the generation of cue-invariant visual *percepts*. They were, instead, designed to explore the constellation of cortical fields processing and analysing visual form information generated by different visual features. In our earlier and present experiments, a form component was present in both the form tasks

TABLE V. Field overlaps between the "shape-from-texture – texture-discrimination" task and other shape-discrimination tasks

Anatomy	HBA coordinates			Other shape task
	x	y	z	
Fusiform gyrus L	-34	-54	-12	motion ^a
Fusiform gyrus L	-37	-50	-18	disparity ^b
Fusiform gyrus L	-37	-49	-18	luminance ^c
Fusiform gyrus R	32	-59	-19	luminance ^c
Lateral occipital gyrus R	29	-81	11	motion ^a
Lateral occipital gyrus R	26	-82	14	colour ^d

^a "Shape from motion – motion discrimination" task.

^b "Shape from disparity – disparity discrimination" task.

^c "Shape from luminance – luminance discrimination" task.

^d "Shape from colour – colour discrimination" task. All other shape tasks according to Gulyás et al., 1994a,b.

and their reference tasks. However, whereas the subjects had to make the perceptual discrimination along the form dimension in the form tasks, the form was irrelevant in the reference tasks. In turn, a specific visual component (colour, motion, disparity, luminance, or texture, respectively, cfr. Gulyás et al., 1994a,b) was also present in both tasks, and the subjects used it in both the form and reference tasks. We hypothesised therefore that the cortical fields present after the form task – reference task subtractions are specifically related to the processing and analysis of visual form information generated by one input visual cue, in the present case texture. On the other hand, after subtracting the reference task from the form-discrimination task, cortical neuronal populations responsible for the analysis of visual cues present in *both* stimulus conditions should be annulled.

The present results demonstrate that form discrimination based upon texture cues activates even the primary visual cortex, at first sight a surprising finding if one assumes that the primary visual cortex processes elementary visual information present in both stimulus conditions, and this should be cancelled by the subtraction procedure. This was actually the case in our earlier studies using other visual cues to generate form (Gulyás et al., 1994a,b). The present finding of activation in area V1 may be the result of two operations: 1) The form-discrimination task requires more local neuronal operations in area V1 than the reference task, for in order to solve the form-discrimination task, one must use the texture contours present in the stimuli, whereas performance with the reference task does not require the detection and analysis of any texture borders present in the stimulus. In fact, texture contours are an example of illusory contours and there is evidence in primate studies that in some cases illusory contours are already registered in area V1 (Grosz et al., 1993). On the other hand, several other investigators report that only cells in extrastriate areas can register illusory contours (Von der Heydt et al., 1984, 1989; Larsson, Gulyás and Roland, unpublished observations). 2) The possible increased attentional demand in the form task compared to the reference task. As attentional effects can change the distribution of rCBF (Roland, 1981a,b; Corbetta et al., 1991), the significantly increased rCBF pattern in area V1 might reflect an increased focal attentional effect in these areas during the form-discrimination task. However, several parameters obtained during performing the two tasks are against this possibility: a) there was no significant difference in gCBF between the two tasks indicating no global attentional differences; b) no significant differences in the α -blockade or eye move-

ment frequencies either, a further sign for no differences in attentional levels; c) finally, the response latencies were *longer* in the texture discrimination task than in the form-from-texture task, indicating that the texture-discrimination task was more demanding than the form-from-texture task.

However, if 1) and 2) above are correct, it is surprising that in our previous form experiments (form from colour, motion, luminance and disparity; Gulyás et al., 1994a,b) the primary visual cortex was never selectively activated. In fact it was evident in those experiments that V1 was activated in both form and reference tasks.

1) One possible explanation for the activation differences with regard to area V1 between the previous tasks and the present task is that in the previous tasks the activations in the form tasks and their reference tasks were well balanced and therefore eliminated after subtracting the reference task from the respective form task. The present form-from-texture task may, however, require more local neuronal operations in area V1 than its reference task, resulting in more activation. Due to the fact that special care was taken to balance the form task and its reference task with regard to local and global processing (see Materials and Methods), this possibility can be ruled out.

2) Another possibility for explaining the increased primary visual cortex activation in the form-from-texture task may come from the fact that a figure-ground segregation procedure is a strong component of the present form task, whereas it is not an emphasised aspect of the reference task, and the figure-ground segregation processes contribute to the increased activation in area V1. However, this possibility is not supported by a more recent experiment in our laboratory (Larsson et al., 1997) in which figure-ground segregation resulted in no activation in area V1.

3) Finally, yet another possibility is that in the present experiment the higher response frequencies in the form task may also result in differentially more activation in areas V1 and V2 than in its reference task. It is true that in the present experiment the stimulus rates were not identical in the two tasks (as shown by the significant difference in the response latencies). Nevertheless, the stimulus energies (Roland and Mortensen, 1987) under both conditions were identical. For these reasons the activation in the primary visual cortex in the form-from-texture task cannot be explained by mere *quantitative* differences (i.e. differences in stimulus rates resulting in differences in stimulus energies, etc.) between the two tasks but *qualitative* differences (due to stimulus- and/or task-features) between the tasks should be taken into

consideration in order to explain the phenomenon. This would, in turn, indicate that certain neuronal populations in area V1 may specifically be engaged in the processing of form-from-texture stimuli.

Significant activations were also present bilaterally in the fusiform gyri and the superior temporal gyri, i.e. the occipito-temporal visual pathway. It is widely accepted that neurons in the inferior temporal cortex of monkeys are selectively excited by often complex visual forms (Schwartz et al., 1983; Gross, 1992, 1994), and indeed, earlier PET studies have also found widespread activations in various temporal lobe locations (Corbetta et al., 1991; Gulyás and Roland, 1991, 1994; Sergent et al., 1992; Haxby et al., 1991; Grady et al., 1994). In our earlier studies, in which we used other visual cues (colour, luminance, disparity, motion) to generate form (Gulyás et al., 1994a,b), there were systematic activations of temporal lobe regions. However, these studies also revealed that parietal lobe neuronal populations are also active in visual form discrimination (Gulyás and Roland, 1994b; Gulyás et al., 1994a,b).

In the present study, too, there was considerable parietal lobe activation in the form-discrimination task, indicating the possible involvement of the occipito-parietal pathway in form discrimination. Other PET studies also support the view that in the human brain both temporal and parietal lobe fields participate in the detection and/or discrimination of forms (Gulyás and Roland, 1991, 1994b; Corbetta et al., 1991; Sergent et al., 1992; Roland and Gulyás, 1995). In fact, parietal lobe activations in visual discrimination processes may also be the result of the neuronal control of eye movements (Andersen, 1989; Gnadt and Mays, 1995). As neither the amplitudes nor the frequencies of eye movements were significantly different between the two tasks, this possibility is not supported even if it cannot entirely be ruled out, as our eye movement monitoring technique did not allow the registering of fine eye movements with an amplitude less than 2 deg. A further possibility is that neurons in the parietal lobe are involved in registering that contours are present and exactly where they are, without being involved in form perception per se. Further studies are required to rule out these options.

Earlier observations in primates led to a functional separation of cortical visual areas into an occipito-temporal and an occipito-parietal visual pathway, the former engaged by object-centered visual analysis (the “what” in the visual system), the latter mainly engaged by spatial visual analysis (the “where” in the visual system) (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). According to this hypoth-

esis, neuronal operations related to identifying and discriminating form are predominantly linked with the occipito-temporal system. Furthermore, abundant single cell recordings in primates supported the view that cells in the occipito-temporal visual pathway exhibit properties essential for analysing form (Gross et al., 1972; Gross, 1994). These observations in primates have been further supported by clinical and neuropsychological studies in patients with anatomical lesions localised in the occipito-temporal lobes who showed an impaired performance in visual form-related recognition or discrimination tasks (Meadows, 1972; Goodale and Milner, 1992).

The hypothesis of sharp functional segregation between the two pathways is no longer tenable in view of the increasing evidence from both primate studies and human observations which indicates a role for the occipito-parietal visual pathway in visual form detection and discrimination. Single cells recordings and ablation studies in parietal lobe indicate that these visual cells participate in neuronal operations related to the detection or discrimination of elementary visual cues, important for the generation of percepts of visual form (Eacott and Gaffan, 1991). These observations were further supported by studies in neurological patients with parietal lobe lesions exhibiting impaired performance in orientation, length, and texture discrimination (Von Cramon and Kerkhoff, 1993) or global form perception (Warrington and Taylor, 1973).

Compared with our previous PET studies on visual form discrimination on the basis of different single visual cues using an odd-one-out paradigm (Gulyás et al., 1994a,b), it is worth noting here that these processes systematically engage both the occipito-temporal and occipito-parietal visual pathways. In all these experiments we have used an odd-one-out paradigm. In other experiments, using other types of experimental paradigm, visual form detection or discrimination processes also engaged both visual cortical pathways (Corbetta et al., 1991; Haxby et al., 1991; Sergent et al., 1992; Gulyás and Roland, 1994b). It is, however, noteworthy that in these studies there were surprisingly few overlaps between cortical fields activated during different types of visual form discrimination (cfr. Table 5). This observation suggests that there is a substantial segregation of regions concerned with generating form from different cues, despite the fact that each condition activates several areas. On the other hand, one of the few regions wherein overlaps were found between the various tasks (cfr. Table 5), the fusiform gyrus, is indeed involved in various form tasks and anatomical deficits in this regions result in

impairments in form recognition, detection, and discrimination (for review, see Damasio et al., 1989).

The present observations, together with former PET studies on visual form perception tasks, support the view that processing and analysis of visual form information in the human brain engages multiple cortical neuronal populations. These neuronal populations are present in the primary visual cortex and in extrastriate visual cortices including visual regions in both the occipito-temporal and occipito-parietal visual pathways, indicating a strong functional “cross-talk” between these major processing pathways. These multiple cortical neuronal populations, engaging both occipito-temporal and occipito-parietal ones, may form a functional network of cortical regions essential for the generation of simpler or higher visual form percepts.

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