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The Representation of Shape in the Context of Visual Object Categorization Tasks

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To investigate the role of human fusiform gyrus in shape processing, we determined the effect of shape degradation on BOLD contrast in this region with fMRI during three tasks requiring subjects to determine either whether two successively presented nonsense shapes had the same global orientation (OR task); whether two successively presented meaningful objects belonged to the same basic level category (CAT task); or whether two successively presented objects represented the same exemplar of a category (EX task). On the behavioral level, shape degradation by locally shifting the pixels constituting the lines of stimuli had no effect on performance in the OR task, while it was detrimental to performance in the CAT and EX tasks. In comparison to the OR task, both the CAT and EX tasks were associated with activations in the occipitotemporal and parietal cortex. When shape degradation was applied, activation in the middle fusiform gyrus was reduced in all tasks. The occurrence of this effect in the OR task indicates that it is independent of memory representations. The persistence of the effect in both tasks that showed a behavioral effect of degradation suggests that it does not reflect the amount of shape processing performed on the stimuli, but rather the specificity of the final perceptual representation that can be built from the shape information that is available. Other studies have shown effects of stimulus familiarity and task requirements in the fusiform gyrus, suggesting that there is no need to assume different modules for perceptual representation and representation in memory.

INTRODUCTION

Neuropsychological studies with patients suffering from visual agnosia have indicated that the identification of visual objects involves several processing stages (e.g., Bruyer, 1994; Farah, 1990; Humphreys and Riddoch, 1987; Humphreys *et al.*, 1988; 1999). Based on earlier theoretical work by Lissauer (1890) most models make a distinction between the perceptual processing of the presented stimulus and the linkage of the resulting perceptual representation to representations stored in memory. Humphreys and his colleagues differentiated between different processes in both stages (see Fig. 1). Similar to computational models of visual perception (e.g., Marr, 1982), they argued that several processes contribute to the final result of perceptual processing, the proximal stimulus representation (PSR), defined as a description of the visual stimulus in a format that allows a direct comparison with memory representations. Several studies have made the distinction between two perceptual processes: the decomposition of objects into parts and the processing of the global form of objects (e.g., Farah, 1991; Marsolek, 1999). The results of both processes are combined into the final PSR of visual objects. In the second stage related to memory, a further distinction is made between three distinct representational systems containing the stored structural representations of the visual form of known objects, semantic representations, and phonological representations.

Neuroimaging studies have tried to localize these different stages. Several studies have compared the viewing of pictures of coherent objects with the viewing of random texture displays or pictures of the same objects that have been scrambled resulting in a loss of the global form of the objects (Grill-Spector *et al.*, 1998; Kanwisher *et al.*, 1997; Malach *et al.*, 1995; Martin *et al.*, 1996). Some studies have found a broad pattern of activated regions in the lateral occipital cortex (Grill-Spector *et al.*, 1998; Malach *et al.*, 1995), whereas the results of other studies pointed to more medial regions in the fusiform gyrus (Kanwisher *et al.*, 1997; Martin *et al.*, 1996). To be able to differentiate between perceptual and memory processes, this comparison has been made both for real objects and for nonsense objects that have no corresponding stored representation. Activity in both the lateral occipital cortex and the fusiform

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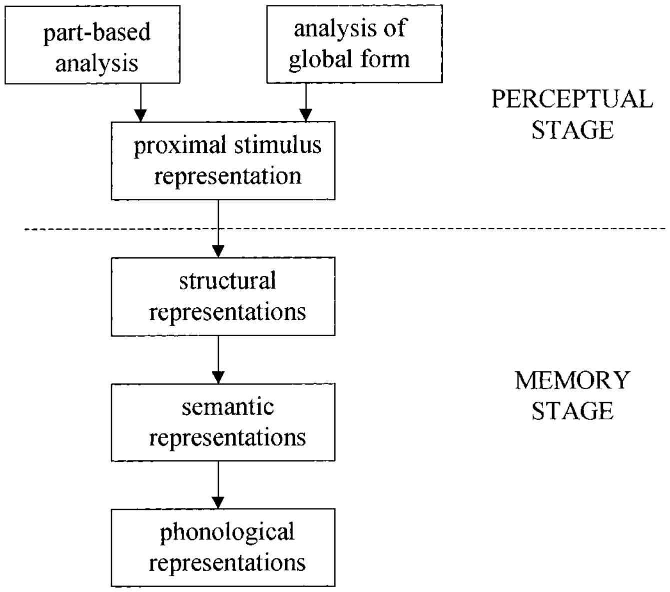

FIG. 1. Neuropsychological model of visual agnosia (based on Humphreys and Riddoch, 1987; Humphreys *et al.*, 1988).

gyrus appeared to be independent of the familiarity of the objects used (Kanwisher *et al.*, 1997; Malach *et al.*, 1995). Whereas this finding suggests that these brain regions are implicated in the perceptual processing of visual form, they do not give any indication toward a finer differentiation between different perceptual processes and stages. Grill-Spector *et al.* (1998) suggested that the lateral occipital cortex would be involved in the processing of object parts whereas the final integration of this part information into a global configuration would be a function of the fusiform gyrus.

Other studies that required subjects to perform a task with the stimuli instead of passive viewing suggest that activity in the fusiform gyrus can also be modulated by task requirements and memory. Martin *et al.* (1996) reported that naming pictures of real objects activated the fusiform region that was also found in the comparison of viewing texture displays and nonsense objects to a larger extent than passively viewing nonsense objects. Moore and Price (1999; see also Humphreys *et al.*, 1999) suggested that this increased activity could reflect the higher identification demands in the naming task. Likewise, Gauthier *et al.* (1997) found that activity in the fusiform and inferotemporal gyri increases when subjects are performing a subordinate categorization task compared with simpler basic-level categorizations. Schacter *et al.* (1995) found regions in the inferotemporal and fusiform gyrus that are more active when subjects are evaluating the structural coherence of possible objects (i.e., objects for which a coherent structural representation can be built) as compared with impossible objects. Whereas this result is compatible with a function of these regions in representing the PSR of a visual object, the same study found that activity in these regions was additionally modulated by the familiarity of objects: studied possible objects yielded more activation as compared with nonstudied possible objects. Finally, other imaging studies indicate that the fusiform gyrus could also be implicated in semantics (for review, see Murtha *et al.*, 1999).

In the present study, we looked for the role of the fusiform gyrus in visual object categorization. More specifically, we wanted to address two issues. First, is the fusiform gyrus implicated in the PSR of objects based on integrating the results of multiple perceptual processes? To answer this question, we started at the same point as former studies: Is the effect of image degradation in the fusiform gyrus found with nonsense objects? Instead of passive viewing, we required our subjects to perform a task on which performance was not affected by image degradation. We proceeded by looking at the same effect in tasks performed with line drawings of real objects. However, as revealed by behavioral measures, performance in these tasks was affected by image degradation, requiring the subjects to devote more processing to the degraded images. If the effect of degradation in the fusiform gyrus would appear to be independent of its behavioral effect, then this result would indicate that the effect in the fusiform gyrus is not related to the amount of perceptual processing. Such results would suggest that it reflects the next perceptual processing stage, the final PSR of the presented objects. Indeed, notwithstanding all the effort expended by subjects, this representation would always be less specific for degraded images compared with the PSR that can be built from images that have retained detailed information.

Second, we investigated whether activity in the fusiform gyrus would be modulated by the abstraction level at which subjects categorize objects. In contrast to the study of Gauthier *et al.* (1997), we manipulated this abstraction level without requiring the subjects to do more elaborate memory processing in more specific categorizations. The original formulation of the basic level in categorization (Rosch *et al.*, 1976) emphasized that the priority of this level of abstraction in object recognition could reflect biases in different processing stages. Basic-level categories could be categories that are easy to discriminate visually, that have different semantic associations, and that have phonological labels that are easy to retrieve. We manipulated the abstraction level in a successive picture/picture matching paradigm by asking subjects to solve the same task using different decision criteria, either comparing the basic level of the two exemplars within each trial or deciding whether both exemplars were exactly the same (subordinate level task). As this subordinate level task does not require a profound semantic processing or labeling of the objects (see Discussion), we

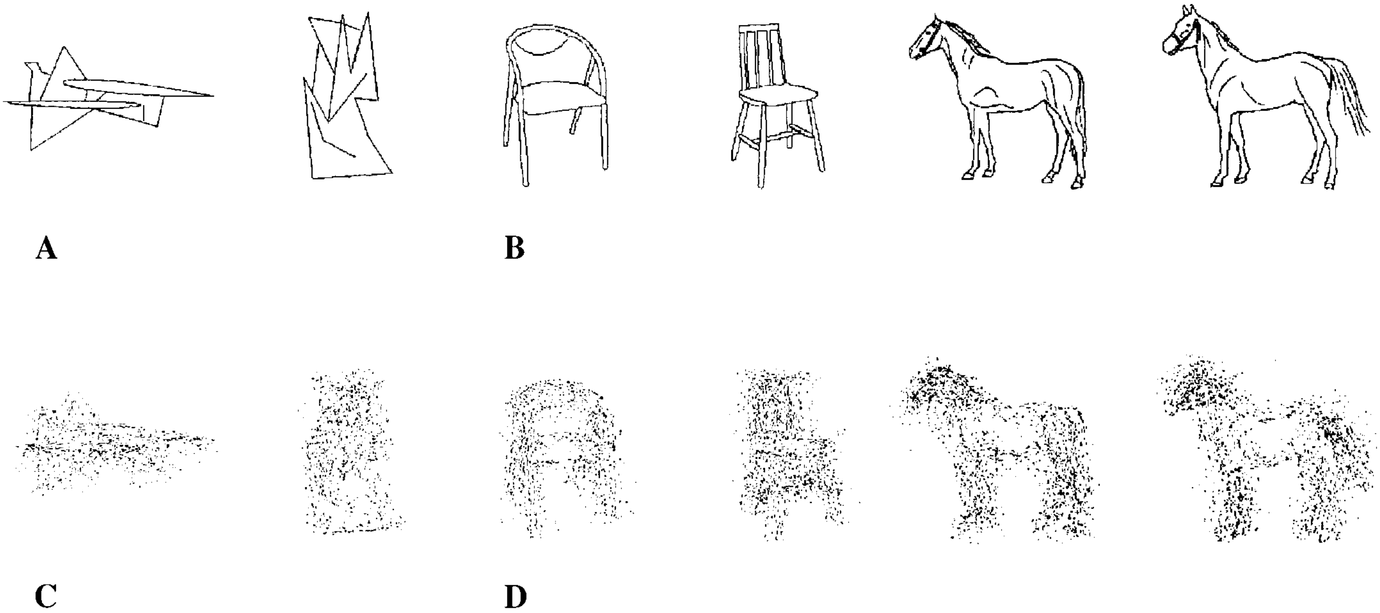

FIG. 2. Some examples of the stimuli used throughout the study: (A) original line drawings from the baseline stimulus set; (B) original line drawings from the experimental stimulus set; (C, D) degraded versions of the stimuli in (A, B), respectively.

focus on the effect of abstraction level on visual processing. If we would still find a modulation of signal intensity in the fusiform gyrus by manipulating abstraction level, then this modulation most likely reflects perceptual mechanisms independent of memory processes.

METHODS

Subjects

Six subjects (four male, two female) participated in this study (mean age, 26 years). Each subject was scanned in two sessions on different days. Data from one male pilot subject are also reported. From this subject, only data from one session are available. All subjects, except one female (M.A), were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal visual acuity. The head of the subjects was immobilized during the scanning sessions using a bite bar. Subjects gave their informed consent for the experiment prior to the first scanning session.

Stimuli

Two kinds of stimuli were used. The baseline stimuli were 72 meaningless line drawings with either a vertical or a horizontal main axis (for examples, see Fig. 2A). The stimulus set in the experimental tasks (for examples, see Fig. 2B) consisted of 120 line drawings of familiar objects and animals (eight exemplars from 15 categories). The 15 categories were: chair, table, cupboard, sofa, automobile, motorcycle, aircraft, rabbit, dog, horse, monkey, butterfly, bird, beetle, and fish. The exemplars and the categories were chosen systematically from the results of a naming study (Op de Beeck and Wagemans, 1999a) by verifying that all exemplars from the 15 categories are named most of the time at the category level (mean for all these stimuli, 92.77% of the answers). The differences between baseline and experimental stimuli in complexity and width in Fig. 2 are representative for the stimulus sets as a whole. In both sets, there were two images of each stimulus: the original and the mirror image.

In half of the trials, the stimuli were degraded with an algorithm that divides the image into small rectangles and permutes these rectangles (see Figs. 2C and 2D). The algorithm was applied once to each stimulus before starting the experiment. Thus, each nondegraded image also had its degraded version.

The stimuli (black line drawings on a light gray background) were presented on a partly translucent screen with a video projector. The part of the screen that was translucent measured 14° × 11° (the maximum extent of a stimulus).

Experimental Design

Subjects were requested to match two stimuli either (1) for orientation of the main axis (this question, the OR task, was asked only with the baseline stimuli); (2) for their category (CAT task); or (3) for being exactly the same exemplar from the same category (EX task). The second and third questions were asked only with the familiar stimuli. The task formulation was exactly the same for degraded and nondegraded stimuli. One trial always consisted of a presentation of the first

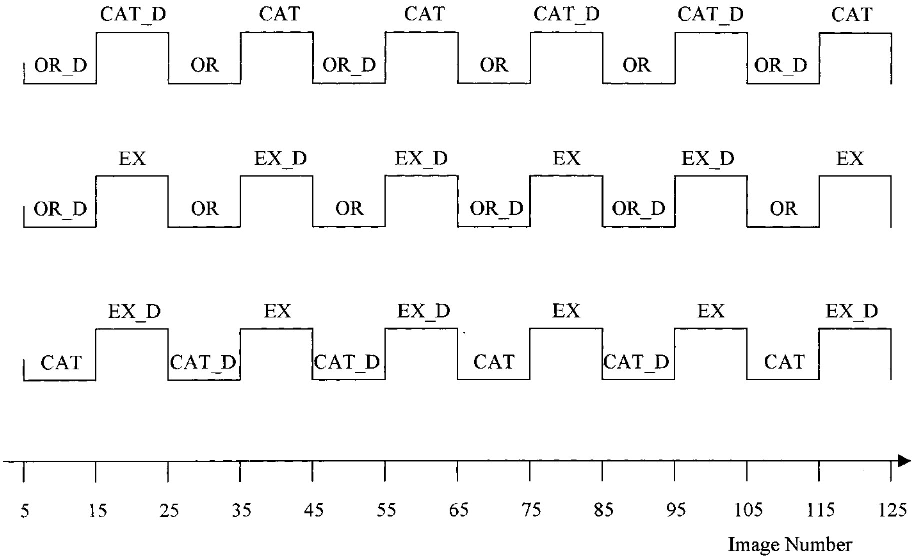

FIG. 3. Representation of three concrete time series as used in the study. OR, CAT, and EX refer to six trials (one epoch) of the baseline task, the category task, and the exemplar task, respectively. Epochs with degraded images are indicated with the suffix _D.

stimulus (1260 ms), an interstimulus interval (1310-ms blank screen with fixation cross), a presentation of the second stimulus (1260 ms), and an intertrial interval (1000-ms blank screen and 1000-ms blank screen with a fixation cross). Subjects could already answer during the presentation of the second stimulus.

In the OR task, two variables, match or not and degradation or not, were crossed. In the CAT task and the EX task, we also manipulated two variables. First, there were three trial types: (i) both stimuli in a trial were the same exemplar (match trials in both tasks), (ii) both stimuli were different exemplars from the same category (match trials only in the CAT task), or (iii) each stimulus was from a different category (nonmatch trials in both tasks). Second, the stimuli were presented in degraded or nondegraded form. In a trial, the images of both stimuli were in the same orientation (most diagnostic part of the image in either the left or the right visual field; the images in Fig. 2 are left images).

Each subject was scanned in two sessions on two different days. Each session consisted of nine time series. All three tasks were never performed in one time series, but three types of time series were constructed by pairing two tasks: OR/CAT, OR/EX, and CAT/EX (see Fig. 3). Both tasks within each time series were alternated in epochs of 35 s (this duration is equal to 6 trials or 10 scans). In three successive time series, each task was presented in two time series and paired with both other tasks. For a particular subject, the order of tasks within and between time series in the three first time series was preserved throughout the other six time series in a session. Both variables (which alternation of tasks was presented first and with which task a time series began) were reversed in the second session for the same subject.

During one time series, 72 trials were presented (36 of each task). In 36 trials of the OR task, all baseline stimuli were presented once. For this task, all stimulus presentations and pairings were randomized between different time series. In 36 trials of the CAT task or the EX task, only half of the stimuli were presented (four from each category). During the second presentation of either the CAT or the EX task throughout time series 1 to 3, we presented the other four exemplars from each category (the same holds for time series 4–6 and 7–9). As a consequence, each exemplar of the experimental stimulus set was presented in three trials in each experimental task in one session.

We randomized the presentation order of most variables, except two: Both the task variable (OR, CAT, or EX) and the degradation variable (degradation or not) were manipulated across epochs. These two variables were entered into the fMRI design. As mentioned above, only two tasks were paired in a concrete time series, resulting in four possible conditions in each time series. The task variable simply alternated. Per group of 24 trials (1–24; 25–48, . . .), each crossing of task and degradation was presented. Moreover, only 12 successive trials could have the same value on the variable degradation (see Fig. 3 for one possible order of the conditions).

Before entering the scanner, the subjects looked at all the exemplars from the experimental stimulus set and read their corresponding subordinate names (familiarization phase). Next, they performed three blocks of 72 trials to ensure that they had understood how to solve each task. In the scanner, the subjects held a response button in each hand. For half of the subjects, a match answer was given with the right hand, for the other half with the left hand.

Image Acquisition

Imaging was performed using a Siemens Vision 1.5-T scanner and a standard quadrature headcoil. Anatomical images were acquired with a T_1-weighted MPRAGE sequence (resulting in a 256 × 256 × 128 matrix with 1 × 1 × 1.25-mm resolution). A functional time series consisted of an echo planar gradient echo sequence of 125 scans (TR = 3500 ms, TE = 40 ms, FOV = 200 mm, 64 × 64 matrix, 32 interleaved transverse slices with slice thickness 4 mm and gap 0.5 mm). The first five scans were not included in the data set. The first stimulus was presented after the fifth scan. The instruction for changing the task was given orally to the subjects through a headphone at the beginning of each epoch of 10 scans. In one experimental session, nine functional time series were recorded. In total, subjects were in the scanner for 2–2.5 h during each session.

Analysis of Behavioral Data

For three of the six subjects, one of the two response buttons did not work appropriately in all time series (no answer was being recorded for a number of trials). All the time series in which the answer of some trials was lost due to this problem (15 of 108 time series) were excluded from the behavioral analyses. Reaction times and performance were analyzed separately using a three-way repeated-measures design with the variables session, task, and degradation.

Analysis of Imaging Data

Correction for head motion, smoothing, and spatial normalization to the MNI template and construction of statistical parametric maps were performed using SPM 96 software (Functional Imaging Laboratory, Queen Square, London, UK). In the basic analysis, all time series with alternation of the same tasks were analyzed together, resulting in three separate explorative analyses (OR/CAT, OR/EX, CAT/EX), each comprising six time series in an individual subject with four conditions (task × degradation or not). Regions were selected for activation height and spatial extent and were considered to be activated significantly if the resulting corrected P value was <0.05. In discussing small foci, we do sometimes refer to individual voxels with an activation height with a corrected P value <0.05. Initially, this basic analysis was performed for each subject individually using voxels of 2 × 2 × 2 mm. Additionally, we performed the same analysis with a lower resolution (3 × 3 × 3 mm) on the pooled group data (not including the pilot subject) using a fixed-effect model.

For investigating the effect of degradation in the fusiform gyrus, we performed a region of interest analysis. Four regions of interest in the fusiform gyrus (a posterior focus and an anterior focus in each hemisphere) were defined on the group data in the contrast CAT_T − OR_T. To obtain two perfectly segregated clusters, the uncorrected P value was lowered to 10^{-7}. We used the method of Worsley *et al.* (1996) for determining the P value after correction for multiple comparisons within each region of interest, to assess the presence of significantly activated voxels in the comparison of degraded and nondegraded images. The critical z values (i.e., the z values corresponding to a corrected P value of 0.05) ranged from 2.85 to 3.00.

To determine the general effect of degradation across all tasks in individual subjects, we analyzed all 18 runs together as one single time series. Because we consider only the results from the subtraction of degraded stimulus conditions from nondegraded stimulus conditions (No_D − D), every term in the subtraction did contain the same number of scans from each time series.

RESULTS

Behavioral Data

Reaction times. The mean reaction time was 726 ms. Only the interaction between task and degradation was significant, $F(2, 10) = 8.64$, $P < 0.01$. As can be seen from Fig. 4A, degradation yielded slower reaction times, but only in the experimental conditions. Indeed, the main effect of degradation across all tasks just failed to reach significance, $F(1,5) = 5.85$, $P > 0.05$. The main effects of session and task were negligible ($F < 1$). Also not significant were the interaction between session and task, $F(2,10) = 2.01$, $P > 0.15$ and the three-way interaction, $F(2,10) = 1.14$, $P > 0.3$.

Performance. Overall, the mean proportion of correct answers was 0.91. Only the main effect of task was significant, $F(1,5) = 9.67$, $P < 0.005$. Pairwise a posteriori contrasts (Tukey procedure) revealed that the category task was solved significantly better than the exemplar task, with the performance on the baseline task being intermediate (not significantly different from the other two tasks). The main effect of degradation failed to reach significance, $F(1,5) = 5.61$, $P > 0.05$. The interaction between task and degradation was also not significant, $F(1,5) = 2.54$, $P > 0.1$. Overall, degradation tended to impair performance on all three tasks, with this effect being smallest on the baseline task (Fig. 4B). All other effects did not approach significance ($F < 1$).

Imaging Data

Matching objects at the basic level. We determined the regions that were activated by categorizing objects

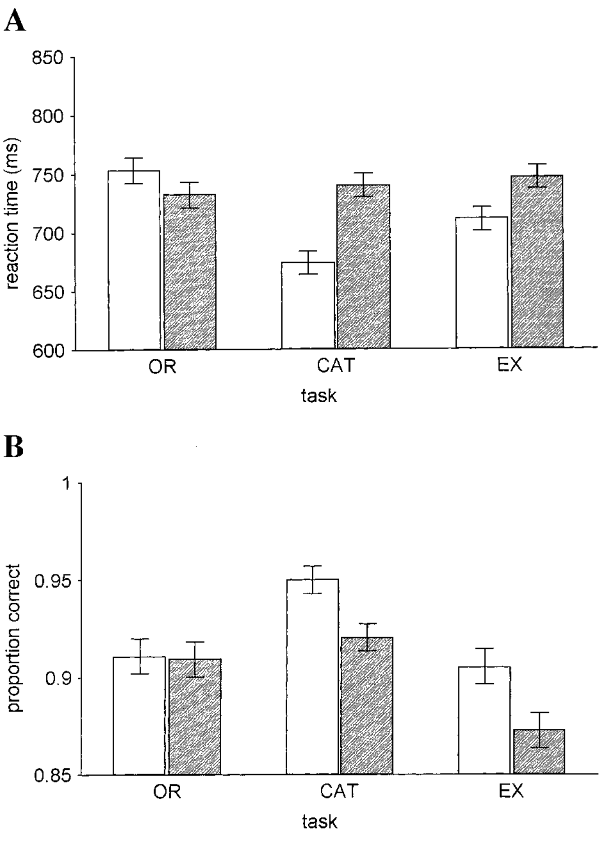

FIG. 4. Mean reaction time (A) and proportion correct answers (B) for each task with nondegraded and degraded stimuli (white and gray bars, respectively). Error bars indicate standard errors of the mean.

at the basic level (see Fig. 5A) by subtracting the OR condition from the CAT condition (for both the epochs with normal and degraded images). This compound contrast is referred to as CAT_T − OR_T (with CAT_T = CAT + CAT_D). By using the OR task as baseline condition, we subtracted the activity related to general task requirements of a sequential picture/picture-matching paradigm. As a result, we isolated activity related to processes that are specific for matching familiar object images at the basic level compared with matching the orientation of nonsense object images. Along the posterior–anterior axis, the group data clearly show two bilateral foci of activation in the fusiform gyrus (Brodmann area 19 (BA 19) and BA 37, respectively; see Fig. 5D). In the remainder of the paper, the anatomical loci of these foci are referred to as the posterior fusiform gyrus and the anterior fusiform gyrus, respectively. In addition, smaller foci were found in striate and extrastriate cortex (including the lingual gyrus). Significant bilateral activation appeared also in the intraparietal sulcus. If the compound subtraction was restricted to either the normal stimuli or the degraded stimuli, both simple subtractions CAT − OR and CAT_D − OR_D yielded the same pattern of activations. The only difference was found in the intraparietal sulcus bilaterally, which was only activated in CAT_D − OR_D, but this effect did not result in a significant interaction in (CAT_D − OR_D) − (CAT − OR).

The data of individual subjects are shown in Table 1. The activations from the group analysis in occipitotemporal and parietal cortex appeared regularly in single subjects, although these foci were not always significant or completely symmetrical in both hemispheres.

Matching objects at the exemplar level. The subtraction of the same baseline task from the exemplar task in the OR/EX analysis (EX_T − OR_T) revealed group activations in the same regions, although generally these activations were stronger and more extended (Fig. 5B). In addition, BA 8 and BA 45 were activated. If this compound subtraction was restricted to either normal or degraded stimuli, both simple subtractions EX − OR and EX_D − OR_D revealed the same foci of activation, with generally higher z values and more extended activations (especially in the lingual gyrus) in EX_D − OR_D. Again, these activations from the group analysis appeared regularly in single subjects (Table 2).

Additionally, we compared the category and the exemplar condition directly in the CAT/EX analysis (Fig. 5C). At the group level, this comparison revealed small foci of bilateral activation in the intraparietal sulcus in EX_T − CAT_T. No group activation was found in the fusiform gyrus. The results of individual subjects were diffuse (Table 1). Three subjects showed a significant difference between both experimental tasks in the fusiform gyrus, but the direction of this difference was not consistent (more activation in the EX task in two subjects, but the reverse effect in the third subject).

Degraded Shape Information

The effect of degradation in the four foci in the fusiform gyrus as found in the contrast CAT_T − OR_T was assessed in the three separate group analyses by performing a region of interest (ROI) analysis. Before proceeding to this ROI analysis, we have confirmed in an exploratory analysis involving all voxels that no other brain regions showed a significant effect of degradation similar to or larger than the effects observed in the fusiform gyrus. Only the anterior fusiform gyrus showed less activity in the degraded stimulus conditions compared with nondegraded stimulus conditions. The main results of the ROI analyses in which we determined the significance of the smaller activation levels associated with degraded stimuli are summarized in Table 2. It is clear that the strongest effects appear in the anterior fusiform gyrus. This difference between posterior and anterior foci was apparent in all three tasks. Significant effects (less activation with degraded stimuli) appeared two times in the posterior

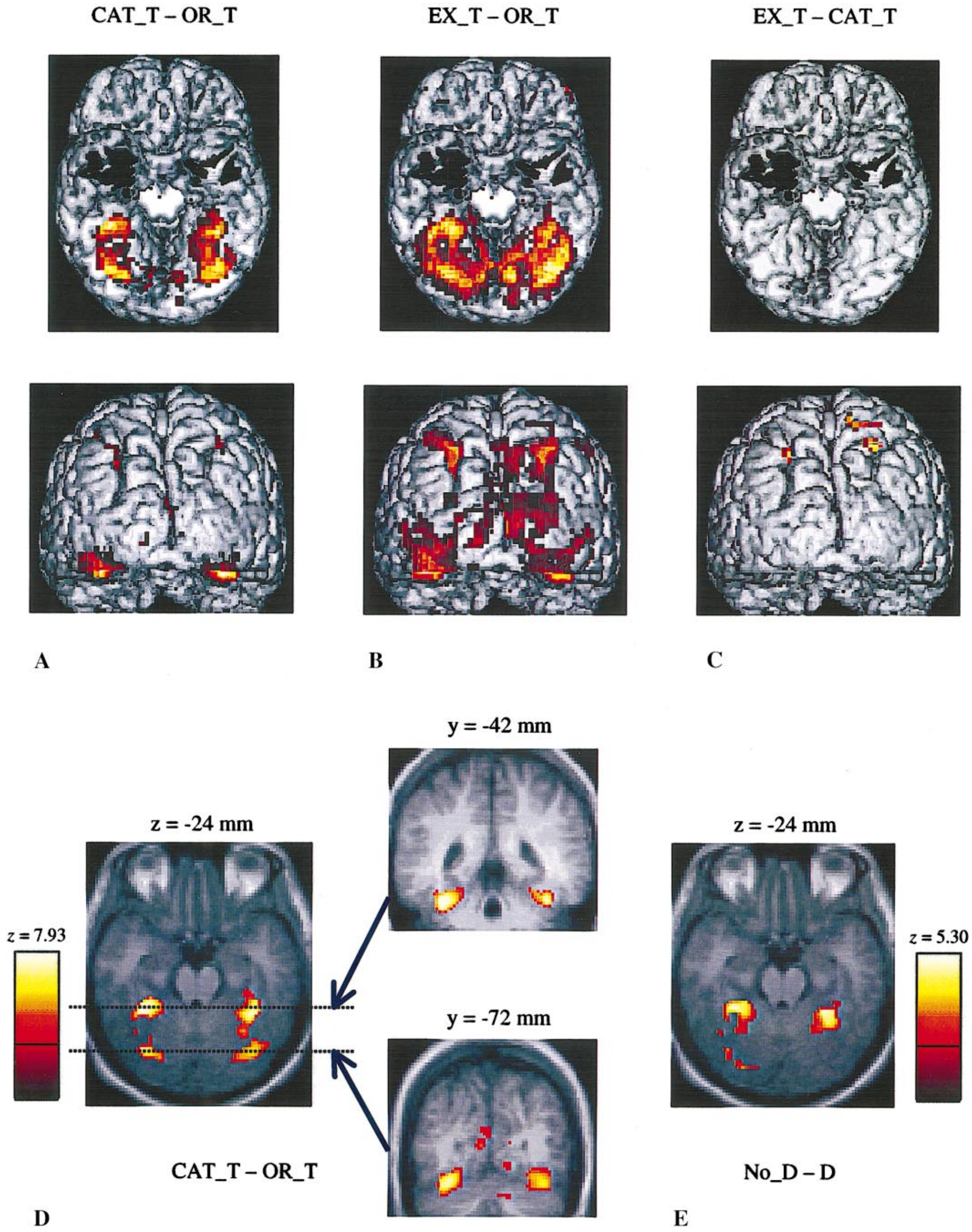
CAT_T – OR_T
EX_T – OR_T
EX_T – CAT_T
A
B
C
y = -42 mm
z = -24 mm
z = 7.93
y = -72 mm
CAT_T – OR_T
D
z = -24 mm
z = 5.30
No_D – D
E

TABLE 1

Talairach Coordinates of the Significant Task Effects in the Group Analyses and in Individual Subjects

	CAT_T − OR_T	EX_T − OR_T	EX_T − CAT_T	CAT_T − EX_T
Group	sc(±38,−44,−25) FGA sc(±35,−69,−19) FGP sc(±9,−84,0) BA 17/LGP sc(±30,−60,44) IPS	sc(±36,−44,−22) FGA sc(±35,−69,−19) FGP sc(±6,−79,0) BA 17/LGP sc(±39,−54,44) IPS sc(±5,26,47) BA 8 sc(±48,56,3) BA 45	sc(±25,−68,48) IPS	—
S.T.	sc(−28,−74,−12) FGP sc(−38,−44,−22) FGA sc(−10,−96,−2) BA 17/LGP sc(54,−68,−6) IT	sc(−36,−68,−16) FG/LG sc(44,−56,−16) FG/IT sc(48,54,0) BA 45 sc(±14,−92,−5) LGP/BA 17 sc(56,10,22) BA 44 sc(34,−68,46) IPS sc(−2,24,48) BA 8M	—	sc(26,−42,−26) FGA sc(16,4,42) ACG
B.W.	sc(±39,−44,−22) FGA sc(±37,−71,−14) FGP sv(−26,−68,46) IPS	sc(±35,−47,−16) FGA sc(±37,−71,−18) FGP/IT sc(±25,−62,44) IPS sc(±10,92,8) BA17/LGP sc(−14,24,52) BA 8M sc(38,2,42) BA 6 sc(30,62,−2) BA 10	sc(±26,−67,49) IPS/SPG sc(±55,−61,−5) IT sc(±34,−44,−24) FGA	—
J.W.	sc(±36,−45,−24) FGA sc(±57,26,38) BA 9/8	sc(±23,−68,58) IPS/SPG sc(±38,−47,−24) FGA sc(−46,62,0) BA 10 sc(±57,25,37) BA 9/8	—	—
A.E.	sc(−36,−70,−24) FG sc(36,−46,−24) FGA sc(38,−74,−22) FGP sc(−52,−64,−20) IT	sc(−36,−72,−24) FG/IT sc(36,−46,−26) FGA sc(36,−74,−24) FGP sc(±6,−81,−2) BA 17/LGP sc(±32,−53,43) IPS sc(−2,26,54) BA 8M sv(14,−74,−30) cerebellum	—	—
M.A.	sc(−24,−78,−22) FGP sv(28,−58,−18) FG	sv(−40,−34,−26) FGA	sc(30,26,38) BA 8M	—
G.T.	sc(32,−76,−18) FGP sv(−22,−38,−22) FA sv(0,−88,0) BA 17	—	—	—
J.V.[a]	sc(36,44,−16) BA 10 sv(40,−62,52) IPS sv(30,−86,18) SOG	sc(±43,−42,−28) FGA sc(32,−78,−24) FGP sc(±28,−58,56) IPS	sc(±41,−39,−28) FGA sc(±23,−58,62) IPS sv(56,−66,−12) IT	—

Note. Only the Talairach coordinates (Talairach and Tournoux, 1988) of the most significant voxel of each differentiated focus are given. If we refer to bilateral foci (symbol ±), then only the mean of the two absolute coordinates is given. Larger regions are indicated by "sc," whereas regions that failed to reach significance if spatial extent was taken into account are indicated by "sv." Foci are mentioned in order of decreasing significance level. ACG, anterior cingulate gyrus; BA, Brodmann area; BA8M, medial part of BA8; FG, fusiform gyrus; FGP, posterior fusiform gyrus; FGA, anterior fusiform gyrus; IPS, intraparietal sulcus; IT, inferotemporal gyrus; LG, lingual gyrus; LGP, posterior lingual gyrus; SOG, superior occipital gyrus; SPG, superior parietal gyrus.

[a] From this subject, we have only data from one session.

fusiform gyrus, but in both cases this posterior effect was clearly smaller than the more anterior effect. In addition, in one analysis (the OR/EX analysis), this posterior effect (in the left hemisphere) seemed to be part of a distributed focus extending more dorsolaterally.

Degradation of shape information resulted in less activation in the anterior fusiform gyrus in all tasks.

FIG. 5. Activation foci from the group analyses. The left side of the brain is always at the left side of the figures. (A–C) Rendering of the main effect of task plotted on the normalized anatomy of one subject with (A) CAT_T − OR_T, (B) EX_T − OR_T, and (C) EX_T − CAT_T. Maximum z values were 7.93, 8.23, and 4.83, respectively. The top row represents an inferior view of the brain, whereas the bottom row shows a posterior view (without the cerebellum). (D, E) Group results are plotted on the mean normalized anatomy of the six subjects. (D) both foci in the fusiform gyrus in the contrast (CAT_T − OR_T) in an axial plane (left image) and in two coronal planes. (E) The focus in the anterior fusiform gyrus in the contrast (No_D − D) in the CAT/EX analysis.

TABLE 2

Probability (Corrected for Multiple Comparisons) of the Effect of Degradation (Less Activation with Degraded Stimuli) in Each of the Four Regions of Interest for Each Task and Analysis

Analysis:	OR/CAT			OR/EX			CAT/EX		
Task:	OR	CAT	OR and CAT	OR	EX	OR and EX	CAT	EX	CAT and EX
AFGR[a]	0.035*	0.049*	0.01**	0.0075**	0.30	0.016*	0.022*	0.0034**	0.0001**
AFGL	0.018*	0.43	0.002**	0.0001**	0.095	0.0001**	0.023*	0.0032**	0.0001**
PFGR	1	1	0.12	0.96	1	0.094	0.059	0.017*	0.0048**
PFGL	1	0.29	0.40	0.0072**	0.45	0.0013**	0.0212*	1	0.046*

[a] AFGR, right anterior fusiform gyrus; AFGL, left anterior fusiform gyrus; PFGR, right posterior fusiform gyrus; PFGL, left posterior fusiform gyrus.

* $P < 0.05$; ** $P < 0.01$; $P = 1$ means that no voxel in the region of interest had a z value high enough to yield a corrected P value of less than 1.

Although the effect in the CAT and EX tasks was found only in the CAT/EX analysis and not that strongly in the OR/CAT and OR/EX analyses, we did not find interactions between task and degradation in these ROI analyses. First, the effect was found in the OR task with nonsense shapes, showing that it is not restricted to meaningful stimuli. Second, the effect was still found in both experimental tasks. In these tasks, the degraded shape information is important for task performance, as suggested by the result from the behavioral data that degraded images of real objects require more elaborate processing to be matched at the category and exemplar levels compared with nondegraded images of the same objects. While the task requirements prevent that degradation of the stimuli results in less processing being dedicated to these stimuli, the effect of degradation in the anterior fusiform gyrus was still present. This result contradicts the hypothesis that the effect would reflect the amount of processing done on the stimuli.

For the compound and simple main effects of degradation in the three separate analyses, we did not refer to results from single subjects, because, overall, the effect of degradation was too weak to be robust in individual data. This is not surprising, given the fact that previous studies (e.g., Kanwisher *et al.*, 1997; Malach *et al.*, 1995) found their more prominent activations by constantly presenting stimuli. We presented stimuli only for less than half of the duration of a trial. Moreover, the difference between the two kinds of stimuli are more subtle in our study, which is reflected by the fact that degraded stimuli can still be recognized rather well (see behavioral data). In the additional analysis with all runs from each individual subject, the only consistent activation in No_D − D was also located in the anterior fusiform gyrus (significant in three of six subjects). One subject additionally showed a small effect in the posterior fusiform gyrus. Figure 6 displays the difference in signal between the degraded and nondegraded conditions for this subject, averaged across all voxels in the same ROIs as used previously. Even in this subject, the difference in the posterior fusiform gyrus was clearly smaller than the corresponding difference in the anterior fusiform gyrus.

DISCUSSION

Our study found that matching objects at the basic level was associated with activity in both ventral and dorsal visual cortex. These regions were also activated by the matching of objects at a more specific level. The only region that was specifically activated by this latter task was located within the intraparietal sulcus. Activity in the fusiform gyrus was not modulated in a consistent manner by the abstraction level of the task. In contrast, degrading shape information in the stimuli produced a consistent effect in the fusiform gyrus. This effect was also found with nonsense stimuli and

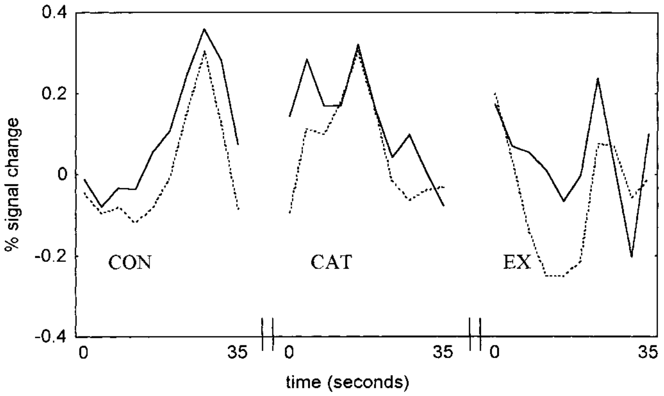

FIG. 6. Differential time courses from one subject denoting the effect of stimulus degradation in the anterior fusiform gyrus (solid lines) and the posterior fusiform gyrus (dashed lines) in the three task conditions (averaged across all voxels from the ROIs in both hemispheres). Each differential time course represents the subtraction of the time course in the degraded conditions from the time course in the nondegraded conditions, averaged across all different epochs of a particular condition.

seemed to be independent of the behavioral effect of such degradation on task performance.

Functional Neuroanatomy of Basic-Level Categorization of Visual Objects

Compared with a matching task with artificial shapes, the categorization of pictures of meaningful objects at the basic level was associated with activity in ventral and dorsal visual cortex. Task requirements related to the general processes implicated in the execution of a sequential matching task were controlled by using this baseline task. However, both conditions are still different in several respects as they differ in stimuli and in the decision criterion. As a result, differences could exist in any of the stages of Fig. 1. First, the baseline stimuli do contain less visual features and are explicitly constructed to have no matching memory representations. So, more extended activations with the familiar stimuli, possibly related to any of the differentiated stages, could be expected, even without any different task requirements. Second, although both decision criteria require subjects to categorize the stimuli (either into orientation categories or into basic-level categories), the way in which stimuli have to be analyzed to solve the tasks could be different. As indicated by several experimental and theoretical studies (e.g., Biederman, 1987; Tversky and Hemenway, 1984), basic-level categories seem differentiated by their part configuration. As a result, matching objects at the basic level will put other demands on the visual processing compared with matching objects for their main orientation, possibly also requiring other patterns of eye movements, which would be a possible explanation for the activity in the intraparietal sulcus[2]. Third, there could be interactions between the nature of the stimuli and task requirements as indicated by recent behavioral research (Schyns, 1998). In the present study, we investigated the effect of task only with familiar stimuli (comparison of basic-level and subordinate-level categorization). The cause of the activations in the comparisons with the baseline task can be derived only indirectly from a comparison with other studies. However, it is the nonspecificity of the contrast that makes it interesting for the definition of the regions of interest in the fusiform gyrus. Since several hypotheses related the activity in this brain region to different processing stages (e.g., Kanwisher *et al.*, 1997; Murtha *et al.*, 1999), a more specific contrast would be too restrictive and could induce a bias favoring one of the hypotheses. For example, if the contrast would result only in activation related to nonvisual processing, then it would become impossible to replicate the result of Kanwisher *et al.* (1997) with unfamiliar stimuli in the defined regions.

While differences could also exist between both conditions in semantic and phonological processing, we did not find any activation in nonvisual regions. In contrast, several other imaging studies of object recognition have found activity mainly in the left hemisphere that seemed to reflect semantic and linguistic processing (e.g., Moore and Price, 1999; Murtha *et al.*, 1999; Price *et al.*, 1996; Sergent *et al.*, 1992). However, we choose our stimuli systematically to be sure that they were initially recognized at the basic level that was relevant for task performance, while some of the other studies required subjects to categorize objects at a superordinate level. Since Jolicoeur *et al.* (1984) found that superordinate categorization is associated with semantic processing, it is not surprising that these studies found more activity related to semantic processing than we did. Our results suggest that the matching of objects at the basic level does not require elaborate semantic and linguistic processing. As a qualification to this conclusion, we have to emphasize that our subjects were performing a picture/picture-matching task. This paradigm will always require less semantic and linguistic processing compared with a picture/name-matching task or an explicit naming task. Future studies are needed to compare basic-level and superordinate categorization within the same paradigm.

Functional Neuroanatomy of Subordinate Level Categorisation

Overall, subordinate-level categorization was associated with an activation of the same network of brain regions compared with basic-level categorization. This suggests that the processing of the familiar stimuli proceeds in a rather fixed manner and is not influenced that much by task requirements.

In contrast to the results of Gauthier *et al.* (1997), we found no differential activity in the fusiform gyrus or the temporal pole. Moreover, by adding a baseline condition, we now know that the fusiform gyrus is also

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[2] We did not measure eye movements and we did not ask subjects to fixate during stimulus presentations because we wanted to avoid artifacts that may result from requiring subjects to process stimuli in an artificial way. As a result, differences in eye movements could be a potential confound in all contrasts. Several studies have revealed the basic circuitry underlying eye movements and pointed mainly to regions in the parietal cortex and in the frontal cortex (human FEF; see Corbetta, 1998). Some activity in the ventral visual stream could be related to differences in eye movements more indirectly, but this effect would be much smaller than the effect in parietal regions and the frontal eye fields (as is also indicated by studies in monkeys, e.g., Sobotka *et al.*, 1997). As the fusiform activations in the CAT-OR and EX-OR contrasts are accompanied by activation in the parietal cortex (but not with FEF activity), we cannot exclude the possibility that a small part of this fusiform activations would be related indirectly to differences in eye movements. However, our main conclusions are based on the effects of degradation that were not accompanied by any of the activations that are typically related to eye movements. So, we can say that this activation in the fusiform gyrus is independent of eye movements.

activated by basic-level categorization, indicating that any change in activity related to the categorization level would be a relative change (merely a higher activation of a region that was already activated). We noted in the Introduction that a manipulation of the categorization level can be associated with differences in several processing stages. As our manipulation minimized such differences in nonperceptual stages, in contrast to the study of Gauthier *et al.* (1997), it seems to suggest that the activations found in this earlier study were related to these nonperceptual processes. Such relation could be a direct one, with activity in fusiform gyrus and temporal pole reflecting semantic or phonological processes per se, or a more indirect one, with activity in these regions reflecting perceptual processes that are influenced by such nonperceptual processing stages. While the first interpretation is the most likely for activity in the temporal pole, our effect of degradation in the fusiform gyrus suggests that the second interpretation could apply to the activation in the fusiform gyrus in this previous study.

The Proximal Representation of Shape in the Fusiform Gyrus

Comparing the effect of degrading shape information in the different task conditions helps us to determine the stage in object recognition it reflects. It is important to realize that degrading stimuli could have effects on different processing stages. To begin with the first stage in Fig. 1, the effect of degrading shape information on the initial processing of the shape information will depend on task requirements. If the task does not make it necessary to recover some of the lost information, the presentation of less shape information will most likely result in less shape processing. However, if the degraded information is important for task performance, then the degradation will result in more processing being devoted to the stimuli. As we found that the metabolic effect of degradation in the fusiform gyrus was independent of such task requirements, unlike the behavioral effect, it is unlikely that it would reflect the first processing stage.

Second, notwithstanding the task requirements, degrading shape information will always have the same effect on the next stage of visual processing, the construction of a PSR of the presented stimulus. As it will not be possible to recover all information that is destroyed by degrading an image, this representation will always be less elaborate as a consequence of stimulus degradation. The results were consistent with this hypothesis.

Third, hypotheses related to memory stages were contradicted as the effect of degradation was also found with nonsense stimuli without matching representations in visual, semantic, and phonological memory. This reasoning critically depends on the assumption that these nonsense stimuli do not activate memory representations, an assumption that has also been made in previous studies (e.g., Kanwisher *et al.,* 1997; Martin *et al.*, 1996). This assumption has been criticized recently (Murtha *et al.*, 1999) by arguing that it is possible that viewing such objects produces partial activation of stored structures or would induce attempts to match the stimuli against known objects. However, our nonsense stimuli are clearly more meaningless than in these previous studies. We explicitly asked several pilot subjects whether some of these objects reminded them of familiar objects, and they all answered negatively. Moreover, we had more control on attempts to match meaningless stimuli to stored representations by requiring the subjects to perform a particular task instead of passively viewing the objects.

The interpretation of activity in the fusiform gyrus as partly reflecting the proximal stimulus representation is a powerful one in explaining and predicting other data. As long as two conditions differ in the specificity of this representation, we would expect modulation of activity in the fusiform gyrus. Several lines of research (e.g., Gauthier *et al.*, 1997; Moore and Price, 1999) have post hoc relevance for this statement as tasks with higher or more specific identification demands will require a more specific proximal stimulus representation. However, in all these studies it is difficult to know whether the fusiform activity is related to differences in perceptual processes, to a more specific PSR, or to differential activation of visual and semantic memory representations (see Murtha *et al.*, 1999). The fact that we did not find a consistent effect in the fusiform gyrus in the contrast EX_T − CAT_T suggests that categorization at different levels of abstraction is not necessarily linked to differences in PSR specificity with more specific tasks being related to more specific PSRs. Additional behavioral evidence (Op de Beeck and Wagemans, 1999b) has confirmed this hypothesis: the EX task requires other information compared with the CAT task, but not necessarily additional information.

Shape Representation in Visual Perception and Visual Memory

The effect of degrading shape information does not depend on the familiarity of the objects. However, we mentioned in the Introduction that other studies indicate that activity in the fusiform gyrus can be modulated by object familiarity and task requirements. Likewise, the activation of the fusiform gyrus related to basic-level categorization in the present study could partly reflect these processes. Furthermore, the interindividual variability in the effect in the fusiform gyrus in the comparison of basic-level and more specific categorization in our study suggests that differences in the strategies used by individual subjects can have an effect on activation in this region.

Are all these effects merely a consequence of differences in the proximal stimulus representations? They could be, as all these manipulations of stimulus familiarity and task requirements partly affect the PSR. For example, Dolan *et al.* (1997) found that priming with gray-level images can induce activity in the fusiform gyrus in a condition with two-tone versions of these images. Behaviorally, these two-tone images are recognizable only with such priming. The difference in recognizability between the primed and unprimed conditions is associated not only with differential activation of memory representations, but also with a more specific PSR. The fact that this contrast revealed only one activation focus in occipital and temporal cortex suggests that both the perceptual and the memory stages are associated with activity in the same region. Whereas Fig. 1 suggests different modules for the proximal stimulus representation and the stored structural representations, in line with traditional approaches to visual agnosia, neuropsychological data can also be interpreted without making such a strong distinction (Farah, 1990, 1997). As perception and memory are tightly linked behaviorally, whatever being their neuroanatomical relation, it will prove very difficult to differentiate between both possibilities. It would require a study that manipulates stimulus familiarity or memory processes with a rigid control of the PSR.

CONCLUSION

The decrease of neuroimaging signal in the fusiform gyrus as a consequence of degrading shape information in stimuli is found independently of task requirements and the behavioral consequences of such degradation. This result suggests that the fusiform gyrus is involved in the final stimulus presentation that is matched with stored representations. The available evidence does not allow us to conclude that fusiform activity reflects only this final perceptual stage and that it would never reflect differences in memory processes in the absence of related differences in the PSRs.

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