Brain activity related to integrative processes in visual object recognition: bottom-up integration and the modulatory influence of stored knowledge

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Abstract

We report evidence from a PET activation study that the inferior occipital gyri (likely to include area V2) and the posterior parts of the fusiform and inferior temporal gyri are involved in the integration of visual elements into perceptual wholes (single objects). Of these areas, the fusiform and inferior temporal gyri were more activated by tasks with recognizable stimuli than by tasks with unrecognizable stimuli. We propose that the posterior parts of the fusiform and inferior temporal gyri, compared with the inferior occipital gyri, are involved in higher level integration, due to the involvement of re-entrant activation from stored structural knowledge. Evidence in favor of this interpretation comes from the additional finding that activation of the anterior part of the left fusiform gyrus and a more anterior part of the right inferior temporal gyrus, areas previously associated with access to stored structural knowledge, was found with recognizable stimuli, but not with unrecognizable stimuli. This latter finding also indicates: (i) that subjects may not refrain from (automatically) identifying objects even if they only have to attend to the objects' global shape, and (ii) that perceptual and memorial processes can be dissociated on both functional and anatomical grounds. No evidence was obtained for the involvement of the parietal lobes in the integration of single objects. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Most theories of visual object recognition describe separate stores for the visual and functional attributes of objects and for their names, with object recognition and naming being realized by successive access to these stores (e.g. [24]). While imaging studies have supported such models [17,18] they have not considered in detail the cerebral organization of the processes that operate prior to the activation of stored memories of objects, such as those processes underlying the integration of visual elements into perceptual wholes. The evidence that exists has concerned the local integration of elements into contours, as when illusory contours are formed (see [33,45] for evidence from single cell recording, and [10,30], for evidence from functional imaging). Little is known, though, about the neural processes that support the integration of contours into more wholistic shape representations. In the present study, we used PET to address this question.

Studies of visual agnosia have demonstrated that the processes involved in wholistic integration can break down after bilateral damage to occipito-temporal cortex including the fusiform gyri (see [21] for a review). Interestingly, this breakdown can leave intact the processes that integrate elements into contours [19]. This suggests that wholistic integration can be distinguished from the integration of elements into contours. However, since such patients are rare, it is difficult to evaluate the necessary site of lesion that leads to problems in wholistic integration. This limits any conclusions about the neural organization of the processes involved. We are unaware of any work that uses functional brain imaging to provide converging evidence. One relevant study, conducted by Op de Beeck et al. [32], showed that activation in the anterior fusiform gyri decreased when drawings were degraded by shifting their constituent pixels (relative to when contours were intact). This decrease was found across a range of tasks, including matching the global orientations of the stimuli and categorizing stimuli as belonging to a particular category. Op de Beeck et al. associated this decrease in activation in the fusiform gyri with the development of a less elaborated shape

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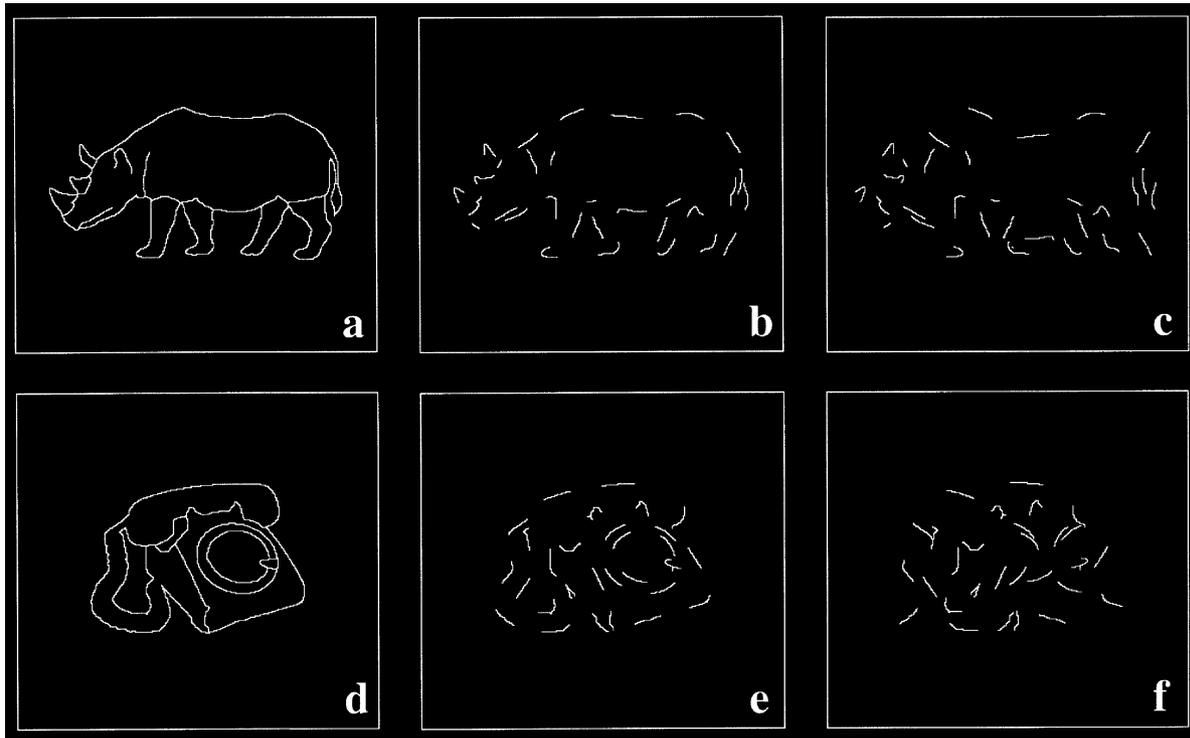*E-mail address:* gerlach@pet.rh.dk (C. Gerlach).

Fig. 1. Examples of the stimuli presented in the task with: (a) outline drawings of natural objects, (b) collinear drawings of natural objects, (c) non-collinear drawings of natural objects, (d) outline drawings of artifacts, (e) collinear drawings of artifacts, and (f) non-collinear drawings of artifacts.

representation. However, this does not show that the fusiform gyri mediate global contour integration processes, but only that activation decreases when integration cues are degraded. The study also did not assess the extent to which activation in the fusiform gyri was contingent on stored knowledge recruited in global orientation matching tasks as well as in tasks requiring explicit stimulus categorization (e.g. [1]).

The present investigation assessed the neural substrate of global contour integration processes, and the role played by stored object knowledge, by: (i) using tasks that required the integration of contours into a global shape for judgements of the shape's global form, and (ii) varying whether the shapes could be identified when decomposed into contour fragments (see Fig. 1). Judgement of the global form derived from separated local fragments demands that local contours be integrated, so that the overall global form can be perceived. This should take place with both full line drawings and with drawings with fragmented contours, and it may occur irrespective of whether the shapes can be recognized from the fragmented contours. By testing for brain regions significantly activated for all stimulus types, relative to a baseline condition in which stimuli contained only a single contour, we can ascertain which regions support global contour integration. Which regions are activated when stored knowledge of objects is recruited can be assessed by comparing activation when the stimuli are identifiable (with full line drawings and fragmented forms with collinear contours)

with activation when stimuli cannot be identified (with fragmented forms with non-collinear contours).

The task, of making global shape judgements to objects, has been used in prior behavioral studies by Boucart and Humphreys, with both normal and agnostic individuals [1,2]. They have shown that, even though the task requires only that a physical judgement is made to the stimuli, normal subjects access stored knowledge. For instance, judgements are made faster to pairs of semantically related objects than to pairs of unrelated objects, but only when the local fragments in the shapes are collinear [1]. Thus, the task is sensitive to grouping by collinearity and to stored knowledge accessed once grouping by collinearity has taken place. This makes it suitable for studying both grouping of features and access to stored knowledge about objects.

In Section 3.1, we describe results from a first analysis, focused on the regions common to contour integration across identifiable and non-identifiable stimuli alike. In Section 3.2, we describe results from a second analysis that contrasts activation associated with identifiable and non-identifiable stimuli. The separate analyses enable us to distinguish the neural areas involved in bottom-up integration of contours into wholistic shapes from those areas where activation is modulated by stored object knowledge.

One further factor examined in the study was the category of the stimulus. Several functional imaging studies have now reported on different patterns of neural activation associated with the processing of artifacts, on the one hand, and natural

objects on the other (see [23,31,35] for recent reviews). Category effects have also been observed at different levels in the object recognition system, using tasks that stress access to stored visual knowledge [17] or stored semantic knowledge [18]. Here, we assessed whether category effects could be found when the task stressed wholistic integration—a putative pre-semantic process. To do this, stimuli within a block of trials either comprised artifacts (primarily clothing, tools, vehicles and kitchen utensils) or natural objects (animals, fruits and vegetables).

2. Method

2.1. Subjects

Ten right-handed healthy volunteers (four female, six male) ranging in age from 22 to 27 years (mean, 24.5) participated. Informed written consent was obtained according to the Declaration of Helsinki II, and the study was approved by the local ethics committee of Copenhagen (J. no. (KF) 01-194/97).

2.2. PET scanning

PET scans were obtained with an 18-ring GE-Advance scanner (General Electric Medical Systems, Milwaukee, WI, USA) operating in 3D acquisition mode, producing 35 image slices with an interslice distance of 4.25 mm. The total axial field of view was 15.2 cm with an approximate in-plane resolution of 5 mm. The technical specifications have been described elsewhere [7].

Each subject received 14 intravenous bolus injections of 340 MBq (9.2 mCi) of $H_2^{15}O$ with an interscan interval of 8–10 min The isotope was administered in an antecubital intravenous catheter over 20 s by an automatic injection device followed by 10 ml of physiological saline for flushing. Head movements were limited by head-holders constructed by thermally molded foam.

Before the activation sessions a 10 min transmission scan was performed for attenuation correction. Images were reconstructed using a 4.0 mm Hanning filter transaxially and an 8.5 mm Ramp filter axially. The resulting distribution images of time integrated counts were used as indirect measurements of the regional neural activity [11].

2.3. MRI scanning

Structural MRI scanning was performed with a 1.5 T Vision scanner (Siemens, Erlangen, Germany) using a 3D magnetization prepared rapid acquisition gradient echo sequence (TR/TE/TI = 11/4/100 ms, flip angle 15°). The images were acquired in the sagittal plane with an in-plane resolution of 0.98 mm, and a slice thickness of 1.0 mm. The number of planes were 170 and the in-plane matrix dimensions were 256 × 256.

2.4. Image analysis

For all subjects, the complete PET brain volume was sampled. Image analysis was performed using Statistical Parametric Mapping software (SPM-96, Wellcome Department of Cognitive Neurology, London, UK) [12]. All intra-subject images were aligned on a voxel-by-voxel basis using a 3D automated six parameters rigid body transformation and the anatomical MRI scans were co-registered to the individual averages of the 14 aligned PET scans. The average PET scans were subsequently transformed into the standard stereotactic atlas of Talairach and Tournoux [42] using the PET MNI template defined by the Montreal Neurological Institute [14]. The stereotactically normalized images consisted of 68 planes of 2 mm × 2 mm × 2 mm voxels. Before statistical analysis, images were filtered with a 16 mm isotropic Gaussian filter to increase the signal-to-noise ratio and to accommodate residual variability in morphological and topographical anatomy that was not accounted for by the stereotactic normalization process [13]. Differences in global activity were removed by proportional normalization of global brain counts to a value of 50.

Tests of the null hypothesis, which rejects regionally specific condition activation effects, were performed comparing conditions on a voxel-by-voxel basis. The resulting set of voxel values constituted a statistical parametric map of the *t*-statistic, SPM{*t*}. A transformation of values from the SPM{*t*} into the unit Gaussian distribution using a probability integral transform allowed changes to be reported in *Z*-scores (SPM{*Z*}). Significantly, activated areas were determined based on the change in a single voxel at a threshold of $P < 0.05$ ($Z > 4.4$) after correction for multiple non-independent comparisons. The voxel significance threshold was estimated according to Friston et al. [15,16] using the theory of Gaussian fields. The resulting foci were then characterized in terms of peak *Z*-scores above this level.

2.5. Cognitive tasks

The experiment consisted of seven different tasks repeated twice comprising a total of 14 conditions. In all tasks, the subjects had to indicate whether the global form of the displayed stimuli could best be characterized as round or oval. If the stimulus could best be characterized as round the subjects were instructed to press the 'round'-key (using their index finger) on a serial response box placed in front of their right-hand. If the stimulus could best be characterized as oval, subjects were instructed to press the 'oval'-key (using their middle finger). In tasks where the stimuli consisted of recognizable objects the subjects were requested to base their judgement on the actual line drawing rather than the object it depicted.

The tasks differed from each other in the kind of stimuli displayed so that the judgement was based on either: (a) outline drawings of circles and ovals, (b) outline drawings of natural objects, (c) outline drawings of artifacts, (d)

fragmented versions of the outline drawings of natural objects in which the fragments were collinear, (e) fragmented versions of the outline drawings of artifacts in which the fragments were collinear, (f) versions of the fragmented collinear drawings of natural objects in which the fragments were non-collinear, and (g) versions of the fragmented collinear drawings of artifacts in which the fragments were non-collinear (see Fig. 1). In the following, these tasks will be referred to as: (i) baseline, (ii) outline natural, (iii) outline artifact, (iv) collinear natural, (v) collinear artifact, (vi) non-collinear natural, and (vii) non-collinear artifact. Since the baseline task contained only stimuli with a single contour, it required minimal integration to form the global shape judgement. This was confirmed by the behavioral data.

In all tasks, the subjects were encouraged to respond as fast and as accurately as possible. Before the actual experiments started the subjects performed a practice version of each task while in the scanner. Stimuli used in these practice versions were not used in the actual experiments.

2.6. Design

Thirty-two stimuli were presented in each task. All stimuli were presented in white on a black background on a PC-monitor hanging 75 cm in front of the subjects. The circle presented in the baseline task had a diameter of 6.5 cm (4.96°), whereas the oval had a width of 7 cm (5.34°) and a height of 3 cm (2.29°). The width and the height of the line drawings (both outlines and fragmented) presented in the other tasks ranged from 2.5 to 7.5 cm (1.9–5.72°). Each stimulus was displayed for 200 ms, with an inter-stimulus interval of 1300 ms, making each task last 48 s. All tasks were initiated approximately 18 s prior to isotope arrival to the brain and continued during the first 30 s of acquisition corresponding to the delivery of radiotracer to the brain. From this point of task offset, the subjects viewed a blank screen for the next 60 s, yielding a total acquisition time of 90 s. By reducing isotope washout and improving counting statistics, this protocol optimizes the signal-to-noise ratio from activated regions [3,26,40]. The delay from injection to isotope delivery to the brain and the estimate of the duration of the critical uptake phase were based on each individual's first scanning. However, correct timing was monitored throughout the scanning sessions and corrections in task onset were made if a change occurred.

In all tasks, 16 round and 16 oval forms were presented. The order of the round and oval forms was randomized. The order of tasks was randomized across subjects.

2.7. Stimuli

The outline drawings were taken from the standardized set of Snodgrass and Vanderwart [41]. A total of 64 pictures was selected (32 natural objects and 32 artifacts). The particular selection was based on the criterion that the pictures had to be as unambiguously round or oval as possible. Accordingly,

16 of the natural objects were round whereas the rest were oval. The same was true of the artifacts.

The collinear fragmented versions of the outline drawings were made by segmenting every outline drawing into fragments of approximately 30 contiguous pixels (the line width of the digitized outline drawings was one pixel) and then removing every second fragment so that approximately half of the contour was deleted. Accordingly, the remaining fragments were aligned on the virtual contour of the source image.

The non-collinear fragmented drawings were made by mirror-reversing the individual fragments in the collinear fragmented drawings with the only constraint being that the fragments should not overlap. Thus, in cases where two fragments would overlap following mirror-reversal one of the fragments was moved slightly. Accordingly, the fragments in the non-collinear version were still centered on the virtual contour of the outline drawings, but no longer in alignment. This operation rendered the non-collinear drawings unrecognizable. The unrecognizable nature of the non-collinear drawings was verified by 10 independent judges who were unable to name any of the non-collinear drawings when presented for 200 ms.

3. Results

3.1. The locus of wholistic integration

The aim of this section was to identify the neural substrates of wholistic integration. To do this, we had to exclude potential activation effects arising from: (a) activation of end-stopped cells (presumably all tasks involving fragmented stimuli would be more likely to cause such activation than tasks with outline drawings), and (b) access to structural or semantic knowledge (presumably all conditions involving recognizable stimuli would cause such activation, i.e. tasks with collinear and with outline drawings). This was achieved in two steps. In the first step, we made a general contrast between all tasks involving pictorial stimuli (outline natural, outline artifacts, collinear natural, collinear artifact, non-collinear natural, and non-collinear artifact combined) and the baseline task. In the next step, we ensured that the areas associated with this general contrast were common for all individual contrasts (outline natural versus baseline, outline artifacts versus baseline, collinear natural versus baseline, collinear artifact versus baseline, non-collinear natural versus baseline, and non-collinear artifact versus baseline). This was done by using SPMs masking option, where we masked the general contrast with the individual contrasts listed earlier. The threshold for the masks was set at $Z > 4.4$. This procedure ensures that areas associated with the general contrast were activated in each individual contrast, and thus, significantly activated regardless of whether the stimuli were fragmented, outlines, recognizable or unrecognizable.
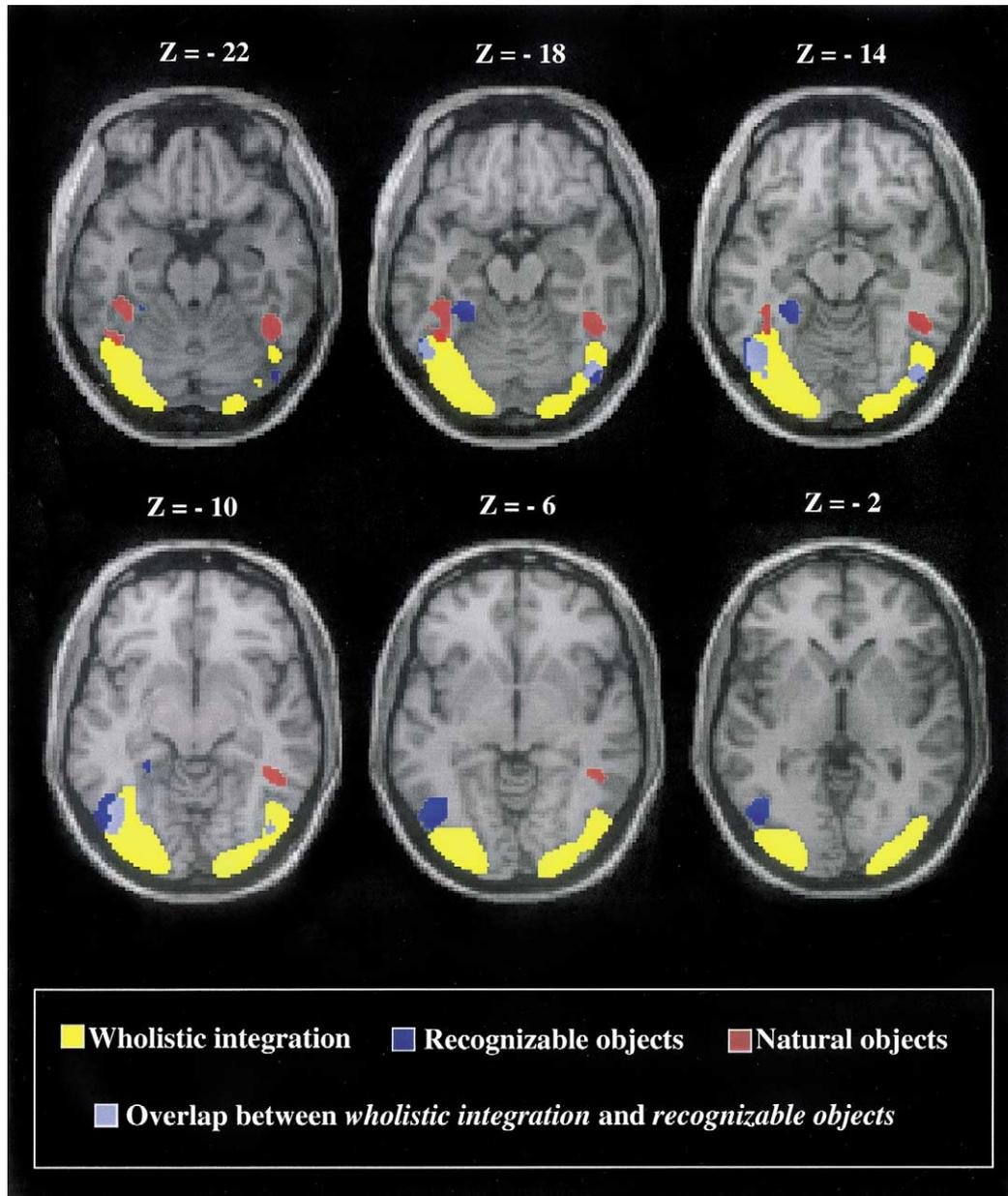
Fig. 2. Six horizontal sections showing the areas associated with: wholistic integration = yellow, recognizable vs. unrecognizable objects = dark blue, natural objects vs. artifacts = red, the overlap between wholistic integration and recognizable objects = light blue. The activated areas are superimposed on a template anatomical MRI scan in co-registration with the Talairach atlas. The SPM{Z}'s were thresholded at a level of $P < 0.001$ uncorrected ($Z > 3.09$). In each slice, the left cerebral hemisphere is displayed to the left.

3.1.1. Results

3.1.1.1. PET-results: areas activated by wholistic integration processes.
The general contrast between tasks with pictorial stimuli and the baseline task revealed extensive bilateral activation of the ventral parts of the occipital cortex and the extreme posterior and ventral parts of the temporal lobes. The main peak activations were found in the inferior occipital gyri (Brodmann area (BA) 18) from where the activation extended upwards into the middle occipital gyri (BA 19) and forwards into the posterior parts of the fusiform (BA

37) and inferior temporal gyri (BA 37) (Fig. 2: yellow and light blue areas, and Table 1).

3.1.1.2. Behavioral results.
In what follows all behavioral results are based on responses to stimuli presented in the critical scan window (i.e. the last 30 s of each task). Error rates were computed as deviations from the rating given by the experimenters (see Table 2 for the mean error rates). Because the error rates were acceptable and did suggest that the subjects were doing what they were asked to, we based all analyses of the behavioral data on both correct and

Table 1
Areas associated with wholistic integration[a]

Region	Coordinates (x, y, z)			BA	Z-score
Inferior occipital gyrus (L)	−28	−94	−8	**18**	**8.15**
Fusiform gyrus (L)	−46	−66	−18	37	7.93
Inferior occipital gyrus (R)	22	−98	−16	**18**	**7.87**
Inferior temporal gyrus (R)	46	−68	−14	37	7.86
Inferior occipital gyrus (R)	28	−94	−4	18	7.69

[a] Coordinates are in millimeters in the MNI version of the Talairach atlas [42], relative to the anterior commissure. L = left, R = right. Regions written in boldface designate the main peak activation within an area whereas other regions designate associated peaks. Threshold was set at $P < 0.05$ corrected for multiple comparisons ($Z > 4.4$).

Table 2
The mean error rates (in %) across subjects and range of errors within subjects (in %) in the seven different tasks

	Error rate	Range
Baseline	1.5	0–10
Non-collinear artifacts	13.2	0–25
Non-collinear natural objects	17.0	5–35
Collinear artifacts	8.9	0–20
Collinear natural objects	19.0	5–50
Outline artifacts	14.5	0–30
Outline natural objects	21.0	10–40

incorrect reaction times (RT). This was done because the PET data are integrated across trials regardless of whether subjects performed correctly or not and because the error rates are necessarily approximations to a consensus (in any case, analyses based on only correct RTs did not alter the results to be reported in the following sections in any significant way).

The RTs for each of the seven tasks were subjected to a one-way analysis of variance (ANOVA). This analysis revealed a significant main effect of task [$F(6, 131) = 7.41$, $P < 0.001$] (two observations were lost because of a hardware malfunction). Post-hoc analysis (Dunnett's pairwise multiple comparison t-test) revealed that the baseline task was performed significantly faster than each of the other tasks ($P < 0.01$). The mean RTs and S.D.s for the seven tasks are given in Table 3.

3.1.2. Discussion

RTs were significantly faster and error rates lower in the baseline task compared with all other tasks suggesting that

Table 3
The mean RT and S.D. (in milliseconds) for each of the seven tasks

	RT	S.D.
Baseline	416	88
Non-collinear artifacts	571	133
Non-collinear natural objects	670	160
Collinear artifacts	615	147
Collinear natural objects	668	157
Outline artifacts	611	158
Outline natural objects	652	161

this task was easier than the other tasks. This is consistent with the need for contour integration being minimized in the baseline condition.

Relative to the baseline, all other stimuli caused bilateral activation of the ventral parts of the occipital lobes and the extreme posterior parts of the temporal lobes, with the main peaks of the activations lying in the right and left inferior occipital gyri. Based on anatomical [4] and imaging [39] evidence, these peak activations are likely to arise in area V2 with activation extending into areas lateral to area V4 as defined by McKeefry and Zeki [29]. The activations of the inferior occipital gyri are very similar indeed to the activations reported by Ffycthe and Zeki [10] during the perception of illusory contours suggesting that the inferior occipital gyri (likely to include area V2) not only combines elements into contours [33,45], but also integrates contours more wholistically. However, the posterior parts of the fusiform and inferior temporal gyri also seem to be involved in wholistic integration. This finding of activation anterior to the inferior occipital gyri during wholistic integration is in accord with recent imaging studies which have also found activation of the ventral occipito-temporal cortex during perception of illusory contours [30] as well as during perception of segregated vs. uniform textures [27].

It should be noted that if the activations reported earlier were due to differences in visual complexity between the stimuli used in the baseline task and the stimuli used in the other tasks (e.g. differences related to the amount of contour present in the stimuli), rather than to wholistic integration processes, we should have expected to find activation of area V1 also. That no such activation was observed makes it unlikely that the difference in activation between the baseline task and the other tasks should reflect such confounding factors. This assumption is also supported by inspection of the mean adjusted regional cerebral blood flow (rCBF) values associated with the seven tasks which are given in Fig. 3. In no area associated with the contrast between the baseline task and the tasks with pictorial stimuli does there seem to be any consistent effect of outline drawings (which have a rich contour) versus collinear drawings (which have a less rich contour). This would have been expected should these areas reflect differential activation due to differences in visual complexity. The failure to find such differences highlights that there is no simple relationship between the amount of physical energy carried by the stimulus and the degree of activation observed. This observation is similar to that of Ffycthe and Zeki [10] who reported that activation was more potent for illusory contours than real contours.

However, before concluding that the activations associated with the comparison between the baseline task and the tasks with pictorial stimuli do indeed reflect integrative processes we need to consider yet an alternative explanation. Thus, it could be argued that these activations may reflect how difficult it is to decide whether the stimuli are round or oval rather than how difficult it is to integrate the stimuli into perceptual wholes on which judgements can be based.
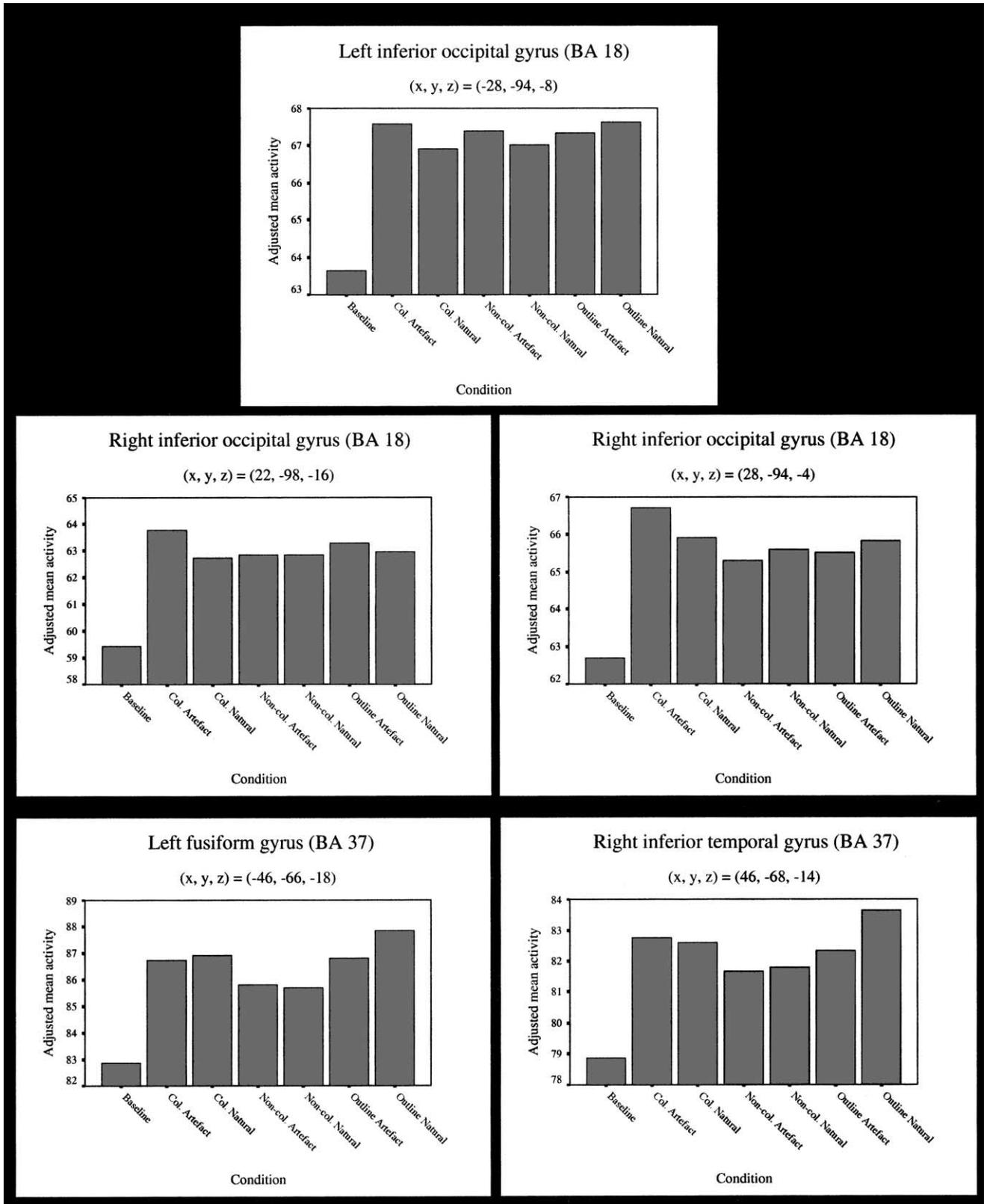
Fig. 3. Plots of the mean adjusted rCBF value for the seven conditions in each of the five regions associated with peak-activations in the contrast between the baseline tasks and the tasks with pictorial stimuli. There are three points to note from this figure: (i) there appears to be no consistent relationship between the mean rCBF values and the mean RTs (given in Table 3) for the tasks with pictorial stimuli suggesting that these activations do not reflect task difficulty per se, (ii) there is no consistent difference between tasks with outline drawings and tasks with collinear forms suggesting that these activations are unlikely to reflect differences in visual complexity related to the amount of contour present in the stimuli, and (iii) differences between tasks with recognizable and tasks unrecognizable stimuli only emerge in regions anterior to the inferior occipital gyri.

If this account is correct, we would expect to find a positive relationship between the rCBF and RT in these areas, also for the tasks with pictorial stimuli. That is, we would expect the rCBF in these areas to be strongest in the tasks which took longest to perform. Although inspection of the mean adjusted rCBF levels in these areas across tasks with pictorial stimuli, which are given in Fig. 3, does not reveal such a relationship, we tested this possibility explicitly by performing a correlation analysis on the mean RTs and the mean adjusted rCBF values across subjects for the six tasks with pictorial stimuli (12 conditions). This was done for each of the five peak-activations associated with the contrast between the baseline task and the tasks with pictorial stimuli. In none of the areas associated with this contrast did we find a significant correlation between rCBF and RT (Pearson r, $N = 12$, $P > 0.25$). This suggests that although RT differences are also likely to reflect how difficult it is to make the global shape judgements in the particular tasks, such differences do not seem to modulate the activations observed. In fact, the behavioral data and the physiological data combined are most easily accounted for by a dichotomous variable that divides tasks into two groups, those with complex contours (tasks with pictorial stimuli) and those with simple contours (the baseline task). Accordingly, we submit that the activations associated with the contrast between the baseline task and the tasks with pictorial stimuli reflect wholistic integration, with this process being relatively easy for stimuli in the baseline task which have simple contours and more difficult for pictorial stimuli which have more complex contours.

3.2. Areas modulated by stored knowledge

In this section, we investigated whether activation associated with wholistic contour integration was influenced by stored knowledge of objects. This was done by identifying areas more activated by recognizable stimuli (with collinear forms and outline drawings) than areas activated by unrecognizable stimuli (with non-collinear forms). Because the non-collinear stimuli were unrecognizable, activation associated with this comparison should reveal: (a) areas involved in access to either structural or semantic knowledge, or (b) areas involved in integration that are also modulated by either structural or semantic knowledge accessed by the identifiable forms. This analysis was performed in two steps. In the first step, we made two contrasts; one between tasks with recognizable natural objects (outlines and collinear forms) and non-collinear natural objects and one between tasks with recognizable artifacts (outlines and collinear forms) and non-collinear artifacts. In the next step, we looked for areas that were common for both contrasts and in which the rCBF did not differ significantly between the two contrasts, that is areas that were activated by both recognizable natural objects and recognizable artifacts relative to non-collinear natural objects and non-collinear artifacts. This was done using conjunction analysis [34]. To further ensure that each of these contrasts contributed to the conjunction, we

Table 4
Areas activated during the presentation of recognizable stimuli relative to presentation of unrecognizable stimuli[a]

Region	Coordinates (x, y, z)			BA	Z-score
Inferior temporal gyrus (L)	**−48**	**−66**	**−12**	**37**	**5.69**
Middle occipital gyrus (L)	−38	−80	16	19	5.19
Fusiform gyrus (L)	**−34**	**−40**	**−18**	**37**	**5.67**
Inferior temporal gyrus (R)	**44**	**−76**	**−16**	**37**	**4.48**

[a] See footnote to Table 1 for details.

excluded all voxels from the analysis that were not significant in each contrast at a threshold of $P < 0.005$ (uncorrected for multiple comparisons), using the masking option in SPM. Accordingly, activations associated with the conjunction analysis should reveal areas activated more by tasks with recognizable stimuli than by tasks with unrecognizable stimuli regardless of category (natural objects versus artifacts).

3.2.1. Results

3.2.1.1. PET results: areas more activated by recognizable stimuli than by unrecognizable stimuli. The processing of recognizable stimuli relative to the processing of unrecognizable stimuli regardless of category was associated primarily with activations in the left occipital and temporal lobe. The main peak activations in the left hemisphere were found in the posterior part of the left inferior temporal gyrus (BA 37), where activation extended backwards and upwards into the left middle occipital gyrus (BA 19), and the anterior part of the left fusiform gyrus (BA 37). A peak activation was also found in the posterior part of the right inferior temporal gyrus (BA 37) (Fig. 2: dark and light blue areas, and Table 4).

It should be noted that even though the activation associated with the processing of recognizable stimuli was predominantly left sided, activation of the anterior part of the right fusiform gyrus (BA 37), corresponding to the following coordinates in MNI Talairach space $(x, y, z) = (34, -36, -18)$ and with a Z-score of 3.75, was in fact observed. However, this activation was only found when the threshold for the masks was lowered to $P < 0.05$ uncorrected. This suggests that although the processing of recognizable objects caused more activation in the anterior parts of the fusiform gyri (BA 37) than the processing of unrecognizable objects, this difference in activation was more pronounced in the left hemisphere.

3.2.1.2. Behavioral results. The RTs from the tasks with outline drawings and the tasks with collinear drawings were collapsed into one group and then compared with the RTs from the tasks with non-collinear drawings. This analysis did not reveal any significant difference between the two groups ($t_{116} = -0.49$, $P = 0.62$). The mean RT and S.D.

(in brackets) for tasks with recognizable stimuli and tasks with unrecognizable stimuli were 636 (155) and 621 (154), respectively.

3.2.2. Discussion

Compared with unrecognizable stimuli recognizable stimuli caused increased rCBF mainly in the left occipital and temporal lobe. As mentioned earlier, these activations could reflect areas involved in the storage of either structural or semantic knowledge or areas involved in integration which are also modulated by access to structural or semantic knowledge. Comparing the results of this analysis with the results from the analysis performed in Section 3.1 some overlap is apparent. Thus, the posterior parts of the fusiform and inferior temporal gyri (BA 37) as well as the left middle occipital gyrus [1] (BA 19) were also found to be activated during wholistic integration unconfounded by structural or semantic processing (cf. Section 3.1 and Fig. 2: light blue areas). Accordingly, these areas seem both to be related to wholistic integration and to be modulated by stored knowledge of objects. However, the activation of the anterior part of the left fusiform gyrus (BA 37) was not found during wholistic integration unconfounded by structural or semantic processing [2,3] (Fig. 2: dark blue areas). From this, we can conclude that the activation reflects access to object knowledge rather than processes related to wholistic integration per se. The most likely account of this activation is that it reflects the matching of visual forms to memory, akin to accessing the structural description system in models of object recognition [24]. Support in favor of this suggestion comes from PET-studies which have found activation of the left anterior fusiform gyrus during (pre-semantic) structural processing (e.g. [17,37]) as well as from studies which have found reduced activation of this area during perception of degraded stimuli [20,32]. Thus, in the study of Gerlach et al. [17], the left fusiform gyrus was found activated during object de-

cision tasks [4] compared with a pattern discrimination task. The overlap between the activations found by Gerlach et al. [17] during object decisions and the activation found in the present study during processing of recognizable objects relative to unrecognizable objects is shown in Fig. 4 as light blue areas.

Since the recognizable stimuli produced stronger activation in some areas, we infer that there was contact with stored object knowledge. Previous behavioral studies have shown that this can also influence RT performance, when semantic priming effects between stimuli are examined [1]. Overall RT differences in global shape judgements between recognizable and unrecognizable stimuli, however, may depend on factors such as the spacing between individual contours, which was not controlled across the stimuli. Consequently, we cannot make conclusions from the lack of an overall behavioral difference between the recognizable and unrecognizable items in the present experiment.

3.3. Effects of category on wholistic integration

In this section, we investigated whether natural objects or artifacts caused different patterns of activation across the tasks with outline drawings and collinear drawings. [5] The results from the tasks with outline drawings and the tasks with collinear drawings were subjected to a two-by-two factorial analysis with the factors Task Type (outlines versus collinear drawings) and Category (natural objects versus artifacts) This factorial approach enabled us to evaluate main effects as well as interactions between Task Type and Category. To ensure that main effects were not confounded by interactions, main effects were identified by use of conjunction analysis [34]. Thus, in what follows all main effects were identified by creating an SPM of the sum of two simple contrasts and subsequently eliminating voxels where differences between the two simple contrasts were significant. As an example, the main effect of outline drawings was computed by: (a) contrasting the task with outlines of artifacts with the task with collinear drawings of artifacts, (b) contrasting the task with outlines of natural objects with the task with collinear drawings of natural objects, and (c) finding areas of activation that were common for both contrasts and in which the rCBF did not differ significantly between the two contrasts. To further ensure that each contrast contributed to the conjunction we excluded all voxels from the analysis that were not significant in each simple main effect at a threshold of $P < 0.005$ (uncorrected for multiple comparisons), using the masking option in SPM.

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[1] It should be mentioned that activation of the left middle occipital gyrus, associated with the general contrast aimed at establishing effects of wholistic contour integration, was only revealed when the threshold for the masks was lowered to $Z > 3.09$ ($P < 0.001$ uncorrected for multiple comparisons).

[2] This held true even when the threshold for the masks applied in Section 3.1 was lowered to $Z > 3.09$ ($P < 0.001$ uncorrected for multiple comparisons).

[3] Because the threshold applied for the contrast between tasks with recognizable stimuli and tasks with unrecognizable stimuli may be considered conservative, the possibility remains that differences between recognizable and unrecognizable stimuli may occur in regions other than those indicated in blue (although they may be less pronounced). Thus, one might speculate that differences between recognizable and unrecognizable stimuli would also be detectable in the inferior occipital gyri if the threshold was lowered. That this is probably not the case can be appreciated from Fig. 3 where differences between recognizable and unrecognizable stimuli only emerge in regions anterior to the inferior occipital gyri. Accordingly, the contrast between tasks with recognizable and tasks with unrecognizable stimuli does not seem to 'underestimate' the areas showing differential activation.

[4] In object decision tasks subjects are requested to decide whether pictures represent real objects or non-objects. These tasks are thought to tap structural knowledge primarily [36,38].

[5] Note that the non-collinear stimuli could not be categorized as being derived from natural objects or artifacts.
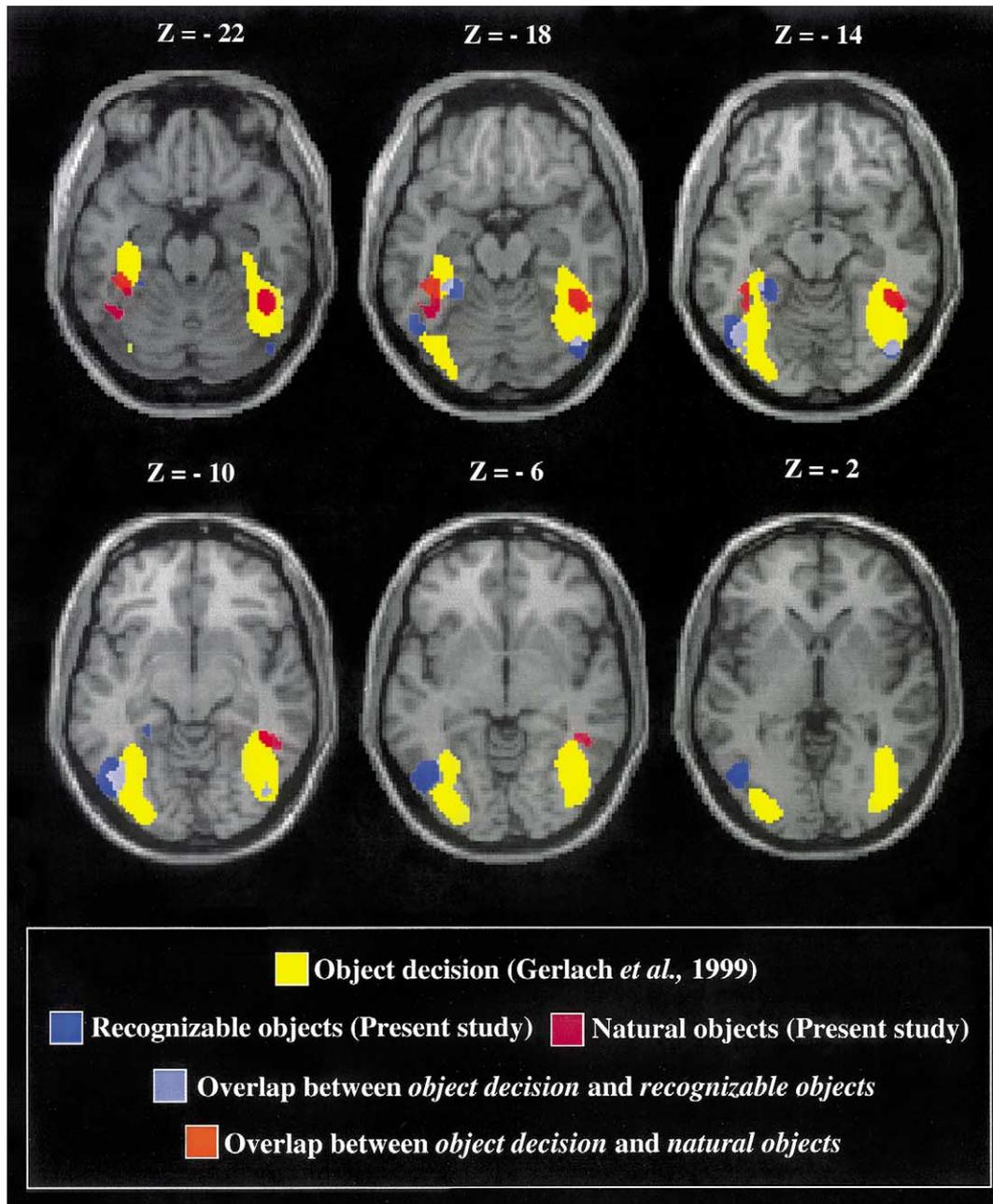
Fig. 4. Six horizontal sections showing the areas associated with: object decision vs. pattern discrimination [17] = yellow, recognizable objects vs. unrecognizable objects = dark blue (present study), natural objects vs. artifacts = red (present study), the overlap between object decision and the processing of recognizable objects = light blue, and the overlap between object decision and natural objects = orange. The activated areas are superimposed on a template anatomical MRI scan in co-registration with the Talairach atlas. The SPM{Z}'s were thresholded at a level of $P < 0.001$ uncorrected ($Z > 3.09$). In each slice, the left cerebral hemisphere is displayed to the left.

3.3.1. Results

3.3.1.1. PET results: areas associated with main effects. The only main effect associated with significant activations was the main effect of natural objects. This held true even when the criterion adopted for defining an activation difference was lowered to $P < 0.001$ uncorrected for multiple comparisons ($Z > 3.09$). The main effect of natural objects was associated with increased rCBF in the anterior part of the

left fusiform gyrus (BA 20) and the right inferior temporal gyrus (BA 37) (see Fig. 2: red areas). The peak activation in the left fusiform gyrus corresponded to the following coordinates in MNI Talairach space $(x, y, z) = (-42, -42, -22)$ and had a Z-score of 4.86. The peak activation in the right inferior temporal gyrus corresponded to the following coordinates in MNI Talairach space $(x, y, z) = (44, -46, -4)$ and had a Z-score of 4.55. This right inferior temporal gyrus activation was more anterior than the one associated with

Table 5
The mean RT and S.D. (in milliseconds) for the tasks with outline drawings and collinear drawings

	RT	S.D.
Collinear artifacts	610	150
Collinear natural objects	669	161
Outline artifacts	615	161
Outline natural objects	652	161

the contrast between tasks with recognizable versus tasks with unrecognizable stimuli.

3.3.1.2. PET results: task and category-specific effects. There were no task- and category-specific effects. This held true even when the criterion adopted for defining an activation difference was lowered to $P < 0.001$ uncorrected for multiple comparisons ($Z > 3.09$).

3.3.1.3. Behavioral results. A two-way ANOVA was carried out. The factors were Task Type with two levels (outline drawings versus collinear drawings) and Category with two levels (artifacts versus natural objects). There was a significant main effect of Category [$F(1, 18) = 15.5$, $P < 0.001$] with slower RTs to natural objects. No other effects were significant (one set of observations was excluded from this analysis because of a hardware malfunction in one condition for one subject). A similar trend was also observed with respect to error rates as these were higher in tasks with natural objects than in tasks with artifacts. This finding suggests that there was no tradeoff between RT and accuracy. The mean RTs and S.D.s are given in Table 5.

3.3.2. Discussion
Although interpretations of null effects are ill-advised, the failure to find any effects of outline drawings (which have a rich contour) or collinear drawings (which have a less rich contour) is compatible with the suggestion raised in Section 3.1.2 that the areas associated with wholistic integration are unlikely to reflect differences in visual complexity.

The main effect of natural objects was associated with activation of the anterior part of the left fusiform gyrus and the right inferior temporal gyrus. Given that these areas have previously been associated with access to stored structural knowledge [17,37] (see also Fig. 4: orange areas), this activation pattern suggests that structural knowledge is activated more during the processing of natural objects than during the processing of artifacts. We return to the significance of this finding in the general discussion. For now, we only note that category effects in the processing of collinear drawings and outline drawings strongly supports the suggestion, raised in Section 3.2, that subjects may not refrain from identifying pictures of objects even though they only have to attend to their global shape.

In the behavioral data, RTs were slower to natural objects than to artifacts. However, it is not clear that this result reflects access to stored knowledge. A comparison of RTs to non-collinear artifacts and non-collinear natural drawings reveals that RTs to non-collinear drawings (derived from natural objects and artifacts) is also slower for the natural kinds [$t_{19} = -6.48$, $P < 0.001$]. Thus, we cannot conclude that wholistic integration processes are affected by category, as opposed to factors such as the complexity and number of contours (which would affect recognizable and unrecognizable stimuli alike). This, however, does not mean that such a difference will not be found in other contexts (e.g. in naming tasks that explicitly stress object recognition).

4. General discussion

4.1. Wholistic integration processes

The wholistic integration of contours, to make global shape judgements, was associated with bilateral activation of the ventral parts of the occipital lobes and the extreme posterior parts of the temporal lobes. This occurred across all stimulus types (outline drawings, collinear and non-collinear forms). The peaks of these activations were located in the inferior occipital gyri, possibly corresponding to area V2, with activation extending into the posterior parts of the fusiform and inferior temporal gyri. Of these areas, the fusiform and inferior temporal gyri (BA 37) were more activated by recognizable stimuli (outline drawings and collinear drawings) than by unrecognizable stimuli (non-collinear drawings). At first, this finding might imply that contours from outline drawings and collinear drawings were harder to integrate than contours from non-collinear drawings. This hypothesis, however, is not supported by the behavioral data where no significant effect of collinearity was obtained. Alternatively, these activations associated with recognizable stimuli may reflect top-down (re-entrant) processing from stored object knowledge. Evidence in favor of this interpretation comes from the finding that the contrast between tasks with recognizable stimuli and tasks with unrecognizable stimuli was also associated with activation of the anterior part of the left fusiform gyrus (BA 37), an area previously associated with access to stored structural knowledge [17,37]. It follows that the posterior parts of the fusiform and inferior temporal gyri (BA 37) become more activated during the wholistic integration of recognizable stimuli, relative to the wholistic integration of unrecognizable stimuli, because recognizable stimuli activate stored structural representations (associated with more anterior parts of the fusiform gyri (BA 37). This activation from stored knowledge may augment bottom-up contour integration.

It is of interest that, in the contrast discussed earlier, activation reflecting access to stored structural knowledge seemed more pronounced in the left than in the right hemisphere. However, strong involvement of also the right hemisphere in structural processing might be obscured because the comparison was performed using a conjunction

analysis. Thus, if regions anterior to the posterior parts of the fusiform and inferior temporal gyri (BA 37) were not activated to the same extent by recognizable natural objects and recognizable artifacts, these areas might not be revealed. Accordingly, given that a more anterior part of the right inferior temporal gyrus was activated more by natural objects than by artifacts regardless of stimulus type (outlines or collinear forms), we suggest that there was in fact contact with stored structural knowledge also in more anterior parts of the right hemisphere (see Section 3.3). In Section 4.2, we address why this activation might be more pronounced for natural objects than for artifacts. For now, we only note that this evidence, for both left and right hemisphere involvement in access to stored knowledge, is consistent with evidence from visual agnosia, where patients typically have bilateral lesions affecting ventral posterior brain regions (e.g. [21]).

Based on the data considered so far it would appear that, although both the inferior occipital gyri (likely to include area V2) and the posterior parts of the fusiform and inferior temporal gyri are involved in wholistic contour integration, this process in the posterior parts of the fusiform and inferior temporal gyri is modulated by stored structural knowledge about objects. In addition, the finding that the anterior part of the left fusiform gyrus and a more anterior part of the right inferior temporal gyrus were not associated with the processing of unrecognizable stimuli, whereas more posterior visual areas were, implies that perceptual and memorial processes can be dissociated on both functional and anatomical grounds. The more posterior areas (the inferior occipital gyri and the posterior parts of the fusiform and inferior temporal gyri) seem to be involved in perceptual processing (wholistic integration of contours) even when stimuli cannot be recognized; in contrast, the anterior part of the left fusiform gyrus and the more anterior part of the right inferior temporal gyrus seem to be involved in access to stored visual knowledge, being associated only with the processing of recognizable stimuli. This finding is difficult to account for in models that do not distinguish between perceptual and memorial stages of object processing (see e.g. [8,9]). It is, however, in keeping with a long-standing distinction between apperceptive (perceptual) and associative (memorial) deficits in agnosia [21].

Another notable aspect of the present data is that the parietal lobes did not seem to be involved in wholistic integration. This negative finding is at odds with accounts of integration processes proposed by the well-known feature integration theory [43,44]. According to this theory, features can only be integrated by use of focused visual attention mediated by the parietal lobes [43]. Evidence consistent with this proposal comes from studies where activation of the parietal lobes has been found during conjunction search in multiple element displays [5]. It may be that our failure to find activation of the parietal lobes was related to the display of only single objects. This would limit competition in integration processes across objects, which may be influenced by parietal activation (e.g. biasing attention to one region of the field). Alternatively, the parietal lobes may be important for maintaining links between features and locations [6]. In contrast, more ventral visual areas, as found in the present study, may mediate integration within objects [22]. Indeed problems in organizing the relations between perceptual features within objects are found after ventral rather than dorsal brain lesions [21].

4.2. Automatic object recognition and effects of object category

In all the present tasks, subjects were required only to attend to the global shape of the stimuli. Nevertheless, we found evidence suggesting that the activation of structural knowledge of objects did take place. This supports the finding by Boucart and Humphreys [1] that subjects may not attend to global shape without automatically recognizing the objects, and also that shape integration takes place within an attended region of space at the boundaries of an object [25].

The clearest evidence in favor of the proposal that object recognition took place automatically was the fact that activation of the anterior part of the left fusiform gyrus (BA 20) and the more anterior part of the right inferior temporal gyrus (BA 37) was affected by category (natural versus artifact). Such an effect of category would be difficult to account for had the subjects not recognized the stimuli. Moreover, these category effects are interesting in their own right. It has been proposed by Humphreys and coworkers [24,28] that category-specific recognition impairments for natural objects may be caused by natural objects being globally more visually similar than artifacts, and therefore, harder to discriminate perceptually. We recently found support for this hypothesis in an imaging study where subjects had to perform easy and difficult object decisions to natural objects and artifacts [17]. In this study, rCBF increased in the right inferior temporal gyrus and the anterior part of the right fusiform gyrus during difficult compared with easy object decisions. In addition, the size of the activated areas increased more for natural objects and were more bilateral compared with the activation associated with artifacts, suggesting that activation differences in these regions reflected the greater perceptual differentiation required to recognize natural objects (see [31] for a similar finding). The fact that very similar activations were observed in the present study, using a paradigm stressing wholistic integration processes, lends further support to this hypothesis. Thus, in the present experiment, the greater activation found for natural objects may reflect that stimuli within this category resemble each other more perceptually than stimuli within the category of artifacts, and therefore, activate a greater range of structurally related representations in visual long-term memory.

Before leaving the issue of category-specificity, it is worth noting that no category-specific effects were observed for

artifacts although this category has previously been associated with activation of the left prefrontal cortex (premotor area) and the left middle temporal gyrus (see [31] for a recent review). One reason for this may lie in the stimuli used. Thus, studies that have reported specific activation for artifacts have typically contrasted tools with animals. Accordingly, the category-specific activations reported for artifacts may only apply to a subset of objects from this category—namely tools. Evidence suggesting that this is probably not the sole explanation comes from the studies by Gerlach et al. [17,18], in which the category of artifacts comprised other objects besides tools. In these studies, no category-specific effects were observed for artifacts on neither easy nor difficult object decision tasks [17]. However, category-specific effects were found on tasks requiring access to semantics. Thus, activation of the left premotor cortex was significantly greater during categorization of artifacts compared with both categorization of natural objects and object decisions to artifacts [18]. Considered together, these findings suggest: (i) that category-specific effects may occur for other artifacts besides tools and (ii) that category-specific effects for artifacts may not emerge on early stages of visual object recognition, where objects are matched to visual memory, but only on later stages when there is contact with semantics. Given that the tasks employed in the present study are more likely to cause access to structural than to semantic knowledge, as the subjects were not required to identify the stimuli, the present failure to find any category-specific activation for artifacts is compatible with the latter suggestion.

5. Conclusion

We report evidence that the ventral parts of the occipital lobes (the inferior occipital gyri) and the posterior parts of the fusiform and inferior temporal gyri are involved in wholistic integration of contours in object processing. Of these areas, the fusiform and inferior temporal gyri were found to be more activated by recognizable than by unrecognizable stimuli. We propose that whilst integration in the ventral parts of the occipital lobes (the inferior occipital gyri) is primarily a bottom-up process, integration in the posterior parts of the fusiform and inferior temporal gyri is modulated also by stored structural knowledge about objects. Evidence in favor of this interpretation comes from the additional finding that activation of the anterior part of the left fusiform gyrus and a more anterior part of the right inferior temporal gyrus, areas previously associated with access to stored structural knowledge [17,18], were found during the processing of recognizable stimuli, but not during the processing of unrecognizable stimuli. This latter finding also indicates: (i) that subjects may not refrain from (automatically) identifying objects even if they only have to attend to the objects' global shape, and (ii) that perceptual and memorial stages of object processing can be dissociated on both functional and anatomical grounds.

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