

Cortical Mechanisms Specific to Explicit Visual Object Recognition

Moshe Bar,^{*†‡} Roger B. H. Tootell,^{*}
Daniel L. Schacter,[†] Doug N. Greve,^{*}
Bruce Fischl,^{*} Janine D. Mendola,^{*}
Bruce R. Rosen,^{*} and Anders M. Dale^{*}

^{*}Massachusetts General Hospital
NMR Center

Charlestown, Massachusetts 02129

[†]Department of Psychology

Harvard University

Cambridge, Massachusetts 02138

Summary

The cortical mechanisms associated with conscious object recognition were studied using functional magnetic resonance imaging (fMRI). Participants were required to recognize pictures of masked objects that were presented very briefly, randomly and repeatedly. This design yielded a gradual accomplishment of successful recognition. Cortical activity in a ventrotemporal visual region was linearly correlated with perception of object identity. Therefore, although object recognition is rapid, awareness of an object's identity is not a discrete phenomenon but rather associated with gradually increasing cortical activity. Furthermore, the focus of the activity in the temporal cortex shifted anteriorly as subjects reported an increased knowledge regarding identity. The results presented here provide new insights into the processes underlying explicit object recognition, as well as the analysis that takes place immediately before and after recognition is possible.

Introduction

The ability to recognize visual objects is a crucial component of our everyday interaction with the environment. While many aspects of object recognition have been characterized behaviorally, little is known about their neural correlates. The purpose of this study was to define the cortical mechanisms specifically involved in conscious object recognition.

Previous human imaging studies of visual recognition have identified several brain regions that demonstrate "object-related" activity. In a typical neuroimaging study of "object-related" processes (Kosslyn et al., 1995; Malach et al., 1995; Martin et al., 1996; Kanwisher et al., 1997a; Ishai et al., 1999), activity elicited by the presentation of familiar objects has been compared with that elicited by presenting textures, abstract objects, and other nameless patterns. The objects in these experiments were usually presented for a relatively long duration and were not masked. Therefore, in addition to processes that are directly related to object recognition, the activity revealed in these studies may also reflect

other processes that occur when viewing meaningful, recognizable objects. For example, this activity may reflect both prerecognition processes such as segmentation, grouping, and parts analysis, as well as post-recognition processes such as activation of associated semantic knowledge, memory consolidation, and various effects of feedback (see Farah and Aguirre, 1999, for critical review). In a recent blocked-design study, pictures were masked and briefly presented (Grill-Spector et al., 2000), and the activity elicited by object presentations was compared with the activity elicited by nameless controls (e.g., scrambled masks). The resultant differential activity represents a combination of several recognition-related processes and not only those exclusively associated with explicit object recognition. (Indeed, the cortical activation in this study concentrated in several foci, though with different characteristics.) In summary, previous studies could not distinguish recognition itself from other related processes preceding and following it. Nevertheless, those studies have provided general clues regarding cortical regions that may be involved in object recognition.

We used a design that allowed a gradual accomplishment of object recognition such that the cortical activation elicited by different levels of recognition success could be compared for the same stimuli. Recent methodological advances make it possible to focus on conscious object recognition and to distinguish it from related processes. Specifically, the development of event-related fMRI methods (Dale and Buckner, 1997; Josephs et al., 1997) allows a selective post hoc comparison of correct and incorrect recognition attempts, and the use of cortical surface-based analysis (Dale et al., 1999; Fischl et al., 1999) facilitates a precise localization.

Our specific goal was to image cortical activity (as measured by the fMRI signal) elicited by trials in which participants were able to recognize pictures of familiar objects and to compare it with the activity elicited by trials in which the participants were very close but unable to recognize the same set of objects. The visual stimulation and the task requirements were identical in both cases; the only difference was subjects' recognition performance.

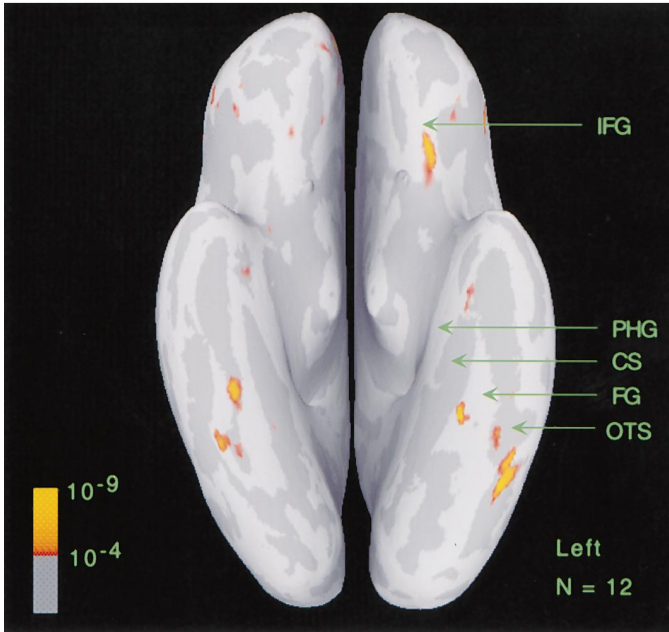
In addition, by comparing the cortical activation elicited in the different levels of recognition success, this design allowed addressing directly the question of whether visual awareness of identity is associated with a corresponding discrete or gradual change in cortical activation.

Twelve healthy human participants were scanned while they performed an object recognition task. In this task, pictures of familiar objects were presented very briefly (26 ms), interposed between two masks. Participants were required to recognize each of the objects and to respond by pressing one of four buttons, indicating their level of knowledge about the identity of the object (1 represented the lowest, and 4 represented successful recognition; see Experimental Procedures). The same object image was repeated, intermixed with the presentation of the other objects, up to five times.

[‡]To whom correspondence should be addressed (e-mail: bar@nmr.mgh.harvard.edu).

A

Recognized Objects vs. 'Almost' Recognized Objects



B

fMRI Signal in the Anterior Fusiform Gyrus is Linearly Related to Recognition Level

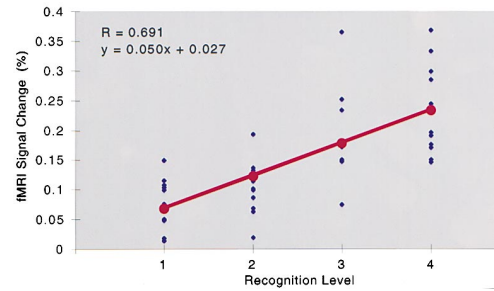


Figure 1. Statistical Activation Maps Illustrating the Comparison between Correct (4) and “Almost” Correct (3) Recognition Attempts of the Same Objects, under Identical Conditions

(A) The activity was averaged across all 12 participants and displayed on an “inflated” ventral view of each of the hemispheres. The brain was inflated to expose the sulci, and the result is a smooth surface. Gyri from the original brain are shown in light gray and sulci in dark gray. The view seen here is from the bottom looking up, such that the inferior part of the temporal lobes is visible. The activity was concentrated exclusively in the temporal lobes and in the inferior frontal gyri. The activity in the temporal lobe site that was modulated by recognition level was significant in eleven of the 12 subjects. PHG, parahippocampal gyrus; CS, collateral sulcus; OTS, occipital–temporal sulcus; FG, fusiform gyrus; IFG, inferior frontal gyrus.

(B) Percent fMRI signal change in the left fusiform gyrus as a function of level of recognition success. The fMRI signal was averaged across six different voxels in this region for each of the 12 subjects. Activation increased linearly with recognition level ($p < 0.000001$). The regression line is in red. The same analysis in the retinotopic areas (V1, V2, and V4v) yielded a flat line.

It has been shown that objects that are not recognized on a given brief presentation can nonetheless be recognized in a later presentation even under identical conditions, a phenomenon termed subliminal visual priming (Bar and Biederman, 1998, 1999). Therefore, by repeatedly presenting the same objects, subjects had multiple opportunities for successful recognition of those objects. In addition, some of the images appeared for a sixth time, without a mask and for longer duration (221 ms). These latter presentations were readily recognizable and provided another reference for successful recognition.

Results

As a result of the brief presentation duration and efficient masking, the task was extremely difficult. The average ratings for masked pictures, on the 1–4 scale, was 2.08 (± 0.06), compared with 3.92 (± 0.03) for the nonmasked pictures. Because subjects could not name objects overtly in the magnet, we ran a similar experiment out-

side the scanner, in which a different group of 12 subjects was required to name the objects aloud. Average percent correct naming was 21.37% ($\pm 1.52\%$) for the masked pictures, compared with 97.03% ($\pm 0.37\%$) for the nonmasked.

Figure 1A shows the differential activity elicited by trials in which subjects recognized the masked objects (pressing key 4) compared with trials in which they could “almost” recognize the masked objects (pressing key 3). We assumed that higher ratings reflected more successful processing. Therefore, when we subtract 3 from 4, the remaining activity is taken to reflect the processes directly associated with the transition from “almost” recognition to successful recognition. (Any other comparison [e.g., 4 versus 1 or 4 versus 2] would also include intermediate processes that precede recognition, as discussed later in the context of Figure 3.)

Two major sites were increasingly active as a direct function of recognition success. One was located in the ventral–temporal cortex, in the occipitotemporal sulcus (OTS). The mean Talairach coordinates of the center of

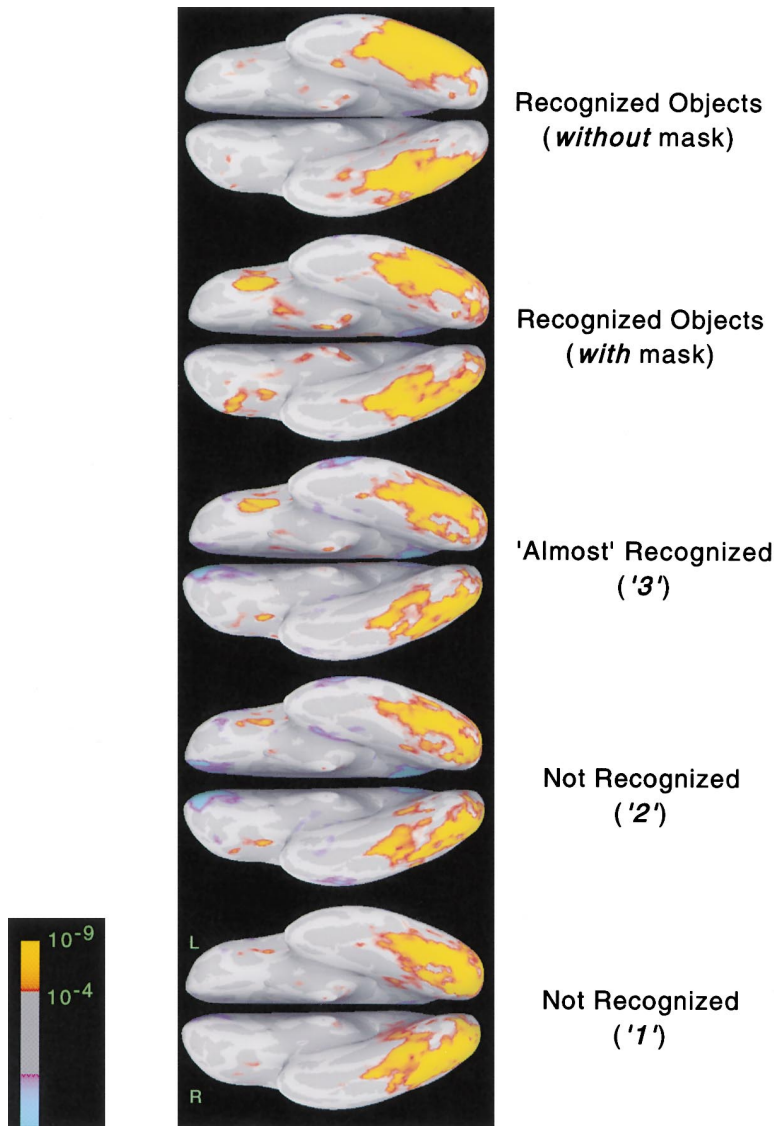


Figure 2. The Activity Associated with Recognition Ratings, Compared with Fixation

As knowledge about object identity increased (lowermost to uppermost panels in the figure), activity in temporal cortex strengthened and propagated anteriorly (see also Figure 3). Frontal activity increased with recognition ratings but dropped substantially for the recognized nonmasked trials. Signal decrease in the most anterior part of the temporal lobes and in the frontal lobe was unique to the conditions prior to successful, explicit recognition.

this activity were -50 , -61 , -12 in the left hemisphere and 41 , -56 , -18 in the right. This activation lies within a large region of the brain (LOC) previously linked to shape processing (Malach et al., 1995).

The second major focus was located in the fusiform gyrus, close to the collateral sulcus and anterior to the fusiform face area (Kanwisher et al., 1997b; McCarthy et al., 1997). The Talairach coordinates of the center of this activity were -34 , -45 , -16 in the left and 36 , -43 , -22 in the right.

The activation in this anterior fusiform focus, and to a smaller extent also in the OTS, increased linearly as a function of subjective rating of recognition success ($p < 0.00001$; Figure 1B; see Experimental Procedures for details of the statistical analyses). Consequently, this activation is suggested to reflect the processing of object identity.

An additional focus of consistent activation was revealed by this comparison, located in the inferior frontal gyri (IFG; 28 , 32 , -6 in the left hemisphere and 39 , 32 , -11 in the right). This activation was not directly modu-

lated by recognition performance. Instead, activity in this region was related to recognition by a U-shaped function such that it increased exponentially with recognition rating of the masked stimuli ($p < 0.0001$), was highest for the recognized masked objects, and lowest for the recognized nonmasked trials.

Other visual areas were not differentially activated in the 4 versus 3 comparison. We assume that processes that are mediated by regions that did not show differential activation in this comparison have been accomplished to the same extent in the "almost" recognition and in the successful recognition trials. Subsequently, because areas that are known to be involved in low- and midlevel visual processing (V1, V2, V4v, LO) did not show differential activation, it is reasonable to propose that the ventrottemporal foci in the fusiform and OTS were directly involved in the transition from "almost" to successful recognition, and not simply in low-level sensory processing.

Figure 2 shows the gradual changes that occurred as subjects' recognition rating increased. Activity in the

'4' vs. '3'



'3' vs. '2'



Figure 3. Average Activity in Left Hemisphere, for the Comparisons 4 versus 3 (upper panel) and 3 versus 2

Before participants were able to recognize the objects (and press 4), activation concentrated in the posterior OTS. Successful recognition was associated with activation more anterior in the OTS and in the fusiform gyrus.

temporal lobe strengthened and propagated anteriorly and laterally as recognition rating increased from 1 to 4 [anterior direction: $F(4,6) = 15.9$, $p < 0.0001$ in the left hemisphere and $F(4,6) = 16.6$, $p < 0.0001$ in the right; lateral direction: $F(4,4) = 13.0$, $p < 0.0001$ in left hemisphere and $F(4,4) = 12.4$, $p < 0.0001$ in the right; see Experimental Procedures for analysis details]. This anterior shift was further illustrated when we compared the statistical map of 4 versus 3 with that of 3 versus 2 (Figure 3).

In addition to activating the fusiform gyrus, the recognized trials differentially activated a more anterior region in the temporal lobe, within the parahippocampal gyri (PHG) (-27 , -37 , -20 in the left and 41 , -38 , -21 in the right). This activation was substantially stronger in the nonmasked recognized trials than in the masked recognized trials. In other words, although recognition was possible in both conditions, the activity that was elicited in the PHG for masked and nonmasked recognized trials was different. Consequently, it appears that the PHG is not directly involved in explicit recognition. This parahippocampal activation may instead reflect postrecognition processes such as semantic analysis and visual memory consolidation, which occur more often when recognition is easy and uninterrupted. This supports the proposal that—of all the activated sites—the cortical region that mediates explicit recognition lies in the anterior fusiform gyrus and possibly also in the OTS.

There was also a substantial MR signal decrease, compared with the fixation baseline, in the most anterior regions of the temporal lobe and in the frontal cortex. This decrease occurred during the conditions before successful recognition was possible (i.e., 2 and 3), and it may therefore reflect prerecognition processes (e.g., local competition).

When designing the experiment, we initially predicted that recognition would improve consistently with each repetition. The data, however, reveal that subjects' ratings did not increase monotonically during the five repetitions. On average, ratings peaked on the third presentation (average 2.16). (Average rating was 2.07 on the first presentation, 2.06 on the second, 2.16 on the third, 2.03 on the fourth, and 2.06 on the fifth.) Afterward, recognition performance declined somewhat (perhaps due to fatigue or boredom). In other words, significant

average priming was present only on the third presentation [$t(11) = 1.80$; $p < 0.02$], although priming of individual objects occurred on all repetitions. Nevertheless, to compare “almost” successful recognition with successful recognition, the important factor was that priming occurred, regardless of when in the experiment it happened for each object.

Reaction time for each recognition rating was as follows: 1212 ms (± 65) for 1, 1364 ms (± 76) for 2, 1348 ms (± 76) for 3, 1156 ms (± 58) for 4 in masked trials, and 914 ms (± 34) for 4 in nonmasked trials. Neither reaction time nor stimulus repetition significantly covaried with the fMRI signal change. (Our analysis has revealed, however, a significant linear covariation [$p < 0.0001$] between RT and signal change in a new prefrontal site [the circular sulcus of the insula]). Therefore, the only explanatory variable for cortical signal change in the fusiform gyrus and the OTS was subjective rating of recognition success. In other words, fMRI signal changed as an exclusive function of recognition level.

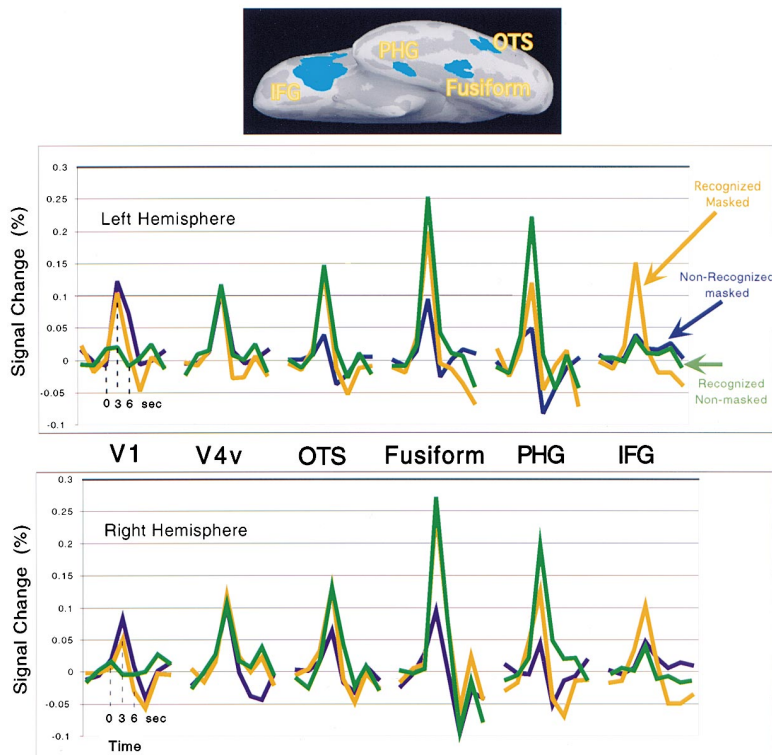
Figure 4 illustrates the average activity over time in specific regions of interest (ROIs). These ROIs include retinotopic areas (V1, V2, V4v), as well as regions in which activation was both consistent among subjects and related to explicit recognition (see Experimental Procedures). Several patterns are worth emphasizing.

The posterior activity in retinotopic areas V1 and V2 was similar for masked presentations, regardless of recognition performance. Thus, V1 and V2 have only an indirect role in the conscious perception of object identity. In these areas, the activity elicited by the nonmasked presentations was smaller than that elicited by the masked conditions, likely due to the lack of visual stimulation and transients caused by the mask.

In area V4v (Tootell et al., 1997), the response to masked and nonmasked trials was similar, perhaps reflecting the sensitivity of cells in V4v to features more complex than those contained in the masks (Gallant et al., 1996; Pasupathy and Connor, 1999).

Response patterns were quite different in the fusiform gyrus and the OTS. In these regions, the recognized objects in the masked and nonmasked conditions produced similar activity, which was stronger than the activity elicited in this region by the nonrecognized trials. The fusiform activation was considerably higher than that of the OTS (Figure 4). These are the first cortical

fMRI Signal Change in Regions of Interest



–2.05, $p < 0.05$ in the right]. The frontal activation caused by recognized nonmasked trials was also significantly lower than that of masked recognized trials [$t(11) = 5.38$, $p < 0.0005$ in left hemisphere and $t(11) = 2.14$, $p < 0.05$ in the right]. The pattern of activity as a function of time was computed for each of these ROIs and each subject, and then averaged across the 12 participants (except V1–V4v, which represents the average of 6–7 subjects for which these areas were mapped previously; courtesy of N. Hadjikhani).

foci in which the activity level was not modulated by stimulus properties (as in V1 and V2) but was instead dependent on recognition success.

Discussion

Several processes are subsumed under the broad category of “object recognition.” In what follows, we propose an association between the activity we observed and subprocesses involved in object recognition.

Confining our discussion to bottom-up models of object recognition, visual features are first extracted in lower-level areas (e.g., V1, V2, V3, V3A, V4v) and are later projected to higher-level regions (e.g., inferior temporal cortex), where a visual representation of the input image is formed. Presumably, this representation is then compared with object representations stored in memory. When a match is found, a representation of object identity is activated, and the association of the input image with an object is accomplished. Studies of brain-damaged human patients support this division of object recognition into several subprocesses (Behrmann et al., 1992; Sheridan and Humphreys, 1993). For example, some patients lose the ability to recognize objects by name, class, or function, although their perception of the image remains intact, as suggested by their ability to copy pictures. Other patients are unable to recognize

Figure 4. Activity as a Function of Time in the Various Regions of Interest in Left (upper panel) and Right Hemispheres

In early retinotopic visual areas V1 and V2 (only V1 is shown), the nonmasked presentation elicited significantly less activity [V1: $t(5) = 2.49$, $p < 0.05$ in left hemisphere and $t(5) = 3.18$, $p < 0.05$ in the right; V2: $t(5) = 2.95$, $p < 0.05$ in left hemisphere and $t(6) = 2.35$, $p < 0.05$ in the right]. In V4v, which presumably processes more complicated features than V1 and V2, the response to masked and nonmasked presentation was similar [$t(6) < 1$ in both hemispheres]. In the anterior fusiform region, both masked and nonmasked recognized trials resulted in an equally strong activity [$t(11) = -1.73$ in the left hemisphere and $t(11) = -1.41$ in the right], which was significantly higher than the activity elicited in this region by the unrecognized trials [masked recognized versus masked unrecognized: $t(11) = -2.23$, $p < 0.05$ in left hemisphere and $t(11) = -2.46$, $p < 0.005$ in the right]. In the parahippocampal gyri, however, the nonmasked trials elicited more activity than the masked recognized [$t(11) = -2.2$, $p < 0.05$ in left hemisphere and $t(11) = -2.3$, $p < 0.05$ in the right], which also elicited significant activity in that region [$t(11) = -2.7$, $p < 0.05$ in left hemisphere and $t(11) = -3.6$, $p < 0.005$ in the right]. In the frontal sites, masked objects that could not be recognized elicited significantly less activity compared with masked recognized trials [$t(11) = -3.37$, $p < 0.005$ in left hemisphere and $t(11) =$

objects due to impairment in grouping and segmentation. Nonetheless, these patients may be able to imagine objects and draw them from memory, indicating intact representations.

Our data suggest that, of all these subprocesses, the anterior fusiform gyrus mediates explicit identification. Post-recognition mechanisms (e.g., activation of semantic knowledge and memory consolidation) are mediated by the PHG and the prefrontal cortex, while prerecognition analysis (e.g., feature extraction and intermediate shape processing) is presumably handled by more posterior areas. Because of the gradual manner by which activation increased with recognition level in the fusiform, however, it is clear that this region was already active before explicit recognition was possible. This early activation in the fusiform may also be considered as prerecognition analysis. Unlike the posterior foci, however, this activation is more likely to reflect “high-level” prerecognition processes such as matching with stored object representations, rather than midlevel shape analysis. Future studies are required to discriminate the exact cortical distribution of prerecognition processes.

What mechanisms are manifested by the OTS activity? Generally, the OTS (anterior “LOC”) is a region that is believed to subserve shape analysis. Processes that fall under this category include segmentation, grouping, surface extraction, and texture analysis. Consequently,

this region was previously more associated with sensory processing than with explicit recognition. It is therefore interesting that activity there was modulated by recognition success, as in the fusiform region (although in a significantly lower magnitude) and not by stimulus parameters. Further analysis (Figure 3) reveals that before subjects could recognize the objects explicitly (comparison 3 versus 2), activation concentrated more posteriorly in the OTS. Therefore, our data suggest that while the posterior activation reflects intermediate shape analysis, the anterior OTS activation is associated with late stages of shape analysis, and maybe also actual recognition.

Finally, activation in the fusiform gyrus increased gradually with subjective rating of recognition success (Figure 1B). Therefore, awareness of object identity is more likely to be characterized by a threshold activity in this region rather than by an abrupt onset.

Conclusions

A major visual cortical focus in the fusiform gyrus was identified in which activity increased directly as a linear function of the ability to recognize objects. Unlike the activity in retinotopic areas, activity in this site was modulated by recognition success and not by stimulus properties. Visual awareness of an object's identity seems associated with a continuous rather than abrupt change of cortical activity. As subjects gained more information about an object's identity, activity in the temporal lobe intensified and propagated anteriorly. These findings support reports of single-unit studies in monkeys that revealed a cortical hierarchy of object representation in the temporal lobe (Tanaka, 1993).

Furthermore, our results suggest that the inferior frontal gyrus may have a special role in coping with difficult tasks such as recognition of briefly presented objects. Because the activity in the frontal lobe was more substantial in the masked presentations, it may reflect a general increased effort during the recognition attempt, or the manifestation of feedback processes that may have had a more central role in the brief masked trials. This activation may be related to the semantic analysis involved in recognition (Gabrieli et al., 1998). It cannot be determined whether this frontal activity started before or after recognition was accomplished. It is conceivable, however, that when recognition is difficult (e.g., brief and masked presentations), top-down processes could facilitate successful recognition (e.g., Ullman, 1995) and therefore might be active even before recognition has been accomplished.

Experimental Procedures

Subjects

Twelve subjects (8 females; aged 24–38) participated in the experiment. All had normal or corrected-to-normal vision. None were aware of the purpose of the experiment. Informed written consent was obtained from each subject prior to the scanning session. All procedures were approved by Massachusetts General Hospital Human studies Protocol number 96-7464.

Stimuli

The pictures were line drawings, 6.8° in their largest dimension, drawn with black lines, two pixels in width, on a white background. The stimuli depicted familiar objects such as tools, furniture, animals, clothes, and means of transportation. The thickness and contrast of the mask lines was similar to those of the stimuli.

Design and Procedure

Stimuli were back projected (NEC LCD projector, MultiSync MT800) onto a translucent screen that subjects viewed through a mirror mounted on the head coil. A custom-designed magnet-compatible panel of four keys was used for subjects responses. The image presentations and response collection were controlled by a Macintosh PowerBook G3, with a resolution of 1024 × 768 pixels and a refresh rate of 75 Hz, and by the PsyScope experimental software. Each subject had 21 practice trials (prior to image acquisition) with images that were not presented again, 504 masked presentations of 154 different objects, and 84 nonmasked presentations of 84 of these objects. In addition, there were 351 presentations of a fixation dot that were used both as a baseline for subsequent comparisons and as "null-events" that are typically necessary for varying the intervals between object presentations in rapid event-related designs. The experimental trials and fixations were equally and randomly distributed across nine consecutive scans.

Before the beginning of the scanning session (and after the practice trials), there were 210 presentations of a subset of the experimental images (70 objects). This was used as an "alignment" block so that it would be possible to present a certain object for the second, third, fourth, or fifth time, already on the first scan session. Subjects were required to recognize each of the objects and to respond by pressing one of four buttons, indicating their level of recognition success.

The instructions required explicitly that subjects would press 4 when they could recognize the object, 3 when they had some idea about the shape (e.g., elongation and orientation) but could not recognize the object, press 2 when they noticed a presentation of an image but nothing about the shape and identity, and 1 when they could not even distinguish the presentation of the image from the presentation of the masks. In addition, because of the extraordinary difficulty of this task, we emphasized to the subjects at the beginning of the experiment that they should not reserve the 4 key for trials in which they were absolutely sure what the object identity was but rather use 4 even when they only had a "good guess." These instructions were designed to minimize cases in which subjects presses 3 although they were able to recognize the objects, just because they were not completely sure. Subjects had ~3 s to respond before the next presentation of another object. The presentation order for each object was intermixed and randomized among the presentations of the other objects such that, for example, the second presentation of a given object could appear after the fifth presentation of another object. The first mask, preceding the object presentation, was presented for 65 ms and the second for 130 ms. The sixth, nonmasked presentations were displayed for 221 ms (the total duration of a picture and two masks in the other conditions). The presentation order was balanced such that half of the subjects had a different presentation sequence than the other half. The subjects were never informed about possible repetitions. No feedback was provided. On average, eighty-five images and nine minutes intervened between two presentations of the same object.

Imaging Details

Subjects were scanned in a 3T General Electric magnetic resonance (MR) scanner, retrofitted with ANMR echoplanar imaging. Head motion was minimized using pillows and cushions around the head and a forehead strap. In addition, the SPM package (Friston et al., 1995) was used for motion correction before functional analysis. MR images were acquired using a custom-built head coil. MR slices were oriented ~10° axially, 4 mm thick with 1 mm skip and with an in-plane resolution of 3.125 mm. Each scan lasted 4 min 16 s, during which 2040 images were acquired (85 images per slice; 24 slices). The functional images were acquired using a gradient-echo sequence (TR = 3 s, TE = 20 ms, flip angle = 90°).

For each subject, a series of conventional structural images was first collected to provide detailed anatomic information. Then, a series of echoplanar functional images was collected to provide both anatomic and functional images sensitive to BOLD contrast. The entire session, including both structural and functional sequences, lasted between 2 and 2.5 hr.

Statistical Analyses

Event-Related Analysis

The procedures for selective averaging have been described previously (Dale and Buckner, 1997). Data from individual fMRI runs

were first normalized to correct for signal intensity changes and temporal drift. The normalized data were then averaged selectively in relation to the beginning of each trial type, both within and between subjects. Finally, statistical activation maps were constructed, based on the averaged event-related responses for each trial type.

Cortical Surface-Based Analysis

Once all trials were selectively averaged, the mean and variance volumes for each subject were resampled onto the cortical surfaces for that subject. Each hemisphere was then morphed into a sphere in the following manner: First, each cortical hemisphere was morphed into a metrically optimal spherical surface (Dale et al., 1999; Fischl et al., 1999a). The pattern of cortical folds was then represented as a function on the unit sphere. Next, each individual subject's spherical representation was aligned with an average folding pattern constructed from a large number of individuals aligned previously. This alignment was accomplished by maximizing the correlation between the individual and the group, while prohibiting changes in the surface topology and simultaneously penalizing excessive metric distortion (Fischl et al., 1999b).

Analysis of Activity Propagation

To assess the propagation of activity with increasing ratings, the following analysis was performed: The inferior temporal cortex of each of the subjects was divided into seven regions that were progressively more anterior (i.e., the first was the most posterior part of the temporal lobe and the seventh was the most anterior) and five regions that were progressively more lateral. Interaction between fMRI signal strength and rating was then tested along the posterior–anterior axis and along the medial–lateral axis in both hemispheres. For analysis purposes we considered five possible ratings: 1 to 4 in masked presentations, and 4 in the nonmasked condition.

Testing Covariance

We examined the statistical power of recognition rating, stimulus repetition, and reaction time to explain the data. For each of these possible covariates, we used a random-effect model to create significance maps indicating voxels in which the fMRI signal changed as a direct function of a change in the specific variable. This was done both for linear and exponential models, comparing them for the best fit with the data.

ROI Selection

The ROIs for the retinotopic areas (V1, V2, V4v) were taken from additional area-labeling scans in the same subjects, as described elsewhere (Tootell et al., 1997). The other ROIs (OTS, fusiform gyrus, PHG, and IFG) were selected from the differential activity elicited by the recognized, nonmasked trials (i.e., nonmasked versus fixation), averaged across the 12 subjects. Those ROIs were then analyzed for each individual subjects, on their individual brains, in the comparison 4 versus 3 of the masked trials, therefore minimizing any possible bias in the analysis.

Acknowledgments

We thank I. Biederman for insightful comments; two anonymous reviewers for constructive advice; E. Halgren, F. Newell, A. Wagner, and C. West for helpful discussions; E. E. Cooper for providing some of the stimuli; and U. Viswanathan for assistance with the experiment. Supported by the McDonnell-Pew Program in Cognitive Neuroscience 99-6 #CNS-QUA.05 (to M. B.), NEI #EY07980 (to R. B. H. T.), NIMH #RO1 MH60941 (to D. L. S.), and NIH #R01 RR13609 and Whitaker Foundation (to A. M. D.).

Received August 2, 2000; revised December 31, 2000.

References

Bar, M., and Biederman, I. (1998). Subliminal visual priming. *Psychol. Sci.* 9, 464–469.

Bar, M., and Biederman, I. (1999). Localizing the cortical region mediating visual awareness of object identity. *Proc. Natl. Acad. Sci. USA* 96, 1790–1793.

Behrmann, M., Winocur, G., and Moscovitch, M. (1992). Dissociation

between mental imagery and object recognition in a brain-damaged patient. *Nature* 359, 636–637.

Dale, A.M., and Buckner, R.L. (1997). Selective averaging of rapidly presented individual trials using fMRI. *Hum. Brain Mapp.* 5, 329–340.

Dale, A.M., Fischl, B., and Sereno, M.I. (1999). Cortical surface-based analysis: I. Segmentation and surface reconstruction. *Neuroimage* 9, 179–194.

Farah, M.J., and Aguirre, G.K. (1999). Imaging visual recognition: PET and fMRI studies of the functional anatomy of human visual recognition. *Trends Cogn. Sci.* 3, 79–186.

Fischl, B., Sereno, M.I., and Dale, A.M. (1999a). Cortical surface-based analysis: II. Inflation, flattening and a surface-based coordinate system. *Neuroimage* 9, 195–207.

Fischl, B., Sereno, M.I., Tootell, R.B.H., and Dale, A.M. (1999b). High-resolution intersubject averaging and a coordinate system for the cortical surface. *Hum. Brain Mapp.* 8, 272–284.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.P., Frith, C.D., and Frackowiak, R.S.J. (1995). Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.

Gabrieli, J.D.E., Poldrack, R.A., and Desmond, J.E. (1998). The role of left prefrontal cortex in language and memory. *Proc. Natl. Acad. Sci. USA* 95, 906–913.

Gallant, J., Connor, C., Rakshit, S., Lewis, J., and Van Essen, D.V. (1996). Neural responses to polar, hyperbolic, and cartesian gratings in area V4 of the macaque monkey. *J. Neurophysiol.* 76, 7060–7078.

Grill-Spector, K., Kushnir, T., Hendler, T., and Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nat. Neurosci.* 3, 837–843.

Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., and Haxby, J.V. (1999). Distributed representation of object in the human ventral visual pathway. *Proc. Natl. Acad. Sci. USA* 96, 9379–9384.

Josephs, O., Turner, R., and Friston, K. (1997). Event-related fMRI. *Hum. Brain Mapp.* 5, 243–248.

Kanwisher, N., Woods, R.P., Iacoboni, M., and Mazziotta, J.C. (1997a). Locus in human extrastriate cortex for visual shape analysis. *J. Cogn. Neurosci.* 9, 133–142.

Kanwisher, N., McDermott, J., and Chun, M.M. (1997b). The fusiform area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.

Kosslyn, S.M., Alpert, N.M., and Thompson, W.L. (1995). Identifying objects at different levels of hierarchy: a positron emission tomography study. *Hum. Brain Mapp.* 3, 107–132.

Malach, R., Reppas, J., Benson, R., Kwong, K., Jiang, H., Kennedy, W., Ledden, P., Brady, T., Rosen, B., and Tootell, R.B.H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl. Acad. Sci.* 92, 8135–8139.

Martin, A., Wiggs, C.L., Ungerleider, L.G., and Haxby, J.V. (1996). Neural correlates of category-specific knowledge. *Nature* 379, 649–652.

McCarthy, G., Puce, A., Gore, J.C., and Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 9, 605–610.

Pasupathy, A., and Connor, C.E. (1999). Responses to contour features in macaque area V4. *J. Neurophysiol.* 82, 2490–2502.

Sheridan, J., and Humphreys, G.W. (1993). A verbal-semantic category-specific recognition impairment. *Cogn. Neuropsychol.* 10, 143–184.

Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science* 262, 685–688.

Tootell, R.B.H., Mendola, J.D., Hadjikhani, N.K., Ledden, P.J., Liu, A.K., Reppas, J.B., Sereno, M.I., and Dale, A.M. (1997). Functional analysis of V3A and related areas in human visual cortex. *J. Neurosci.* 17, 7060–7078.

Ullman, S. (1995). Sequence seeking and counter streams: a computational model for bidirectional information flow in the visual cortex. *Cereb. Cortex* 7, 1–11.