



In the present study, we wanted to investigate whether differences in the BOLD signal in response to animals and manipulable objects could be detected in the anterior temporal lobes (ATLs), paying particular attention to the quality of the signal (see Bellgowan, Bandettini, van Gelderen, Martin, & Bodurka, 2006). We presented grayscale images of animals and manipulable objects to 12 volunteers. On half of the trials, participants were asked to report whether the object in the image was an animal; on the remaining trials, they were asked to report whether it was a manipulable object (yes/no button press). To anticipate our results, we observed, in agreement with the lesion study by Brambati et al. (2006), greater BOLD signal in response to animals than to manipulable objects in the medial portion of the right anterior temporal pole and greater BOLD signal in response to manipulable objects in a lateral area of the left anterior temporal lobe. Previous PET studies, which do not have the susceptibility artifacts associated with fMRI, have reported greater activity in the temporal poles for natural kinds than for man made objects (Kellenbach, Hovius, & Patterson, 2005; Damasio et al., 2004; Devlin et al., 2002; Moore & Price, 1999; Mummery, Patterson, Hodges, & Wise, 1996). With the present study, we investigated in greater detail the response properties of the anterior temporal areas that showed preferential BOLD responses for animals and man-made objects, looking at whether information at different levels in the ventral stream is accessed flexibly as a function of the behavioral goals of the individuals. To address this issue, we compared the BOLD signal during object processing when the participants answered two questions: “Is the object in the image an animal?” and “Is the object in the image a tool?” The anterior temporal lobes showed greater task sensitivity than the posterior temporal lobes. This difference suggests that processing in the posterior temporal areas is more “automatic,” providing a perceptual analysis that is relatively independent of the specific behavioral goals of the individual, whereas the anterior temporal areas may process information more flexibly as a function of the goals of the individual. The present fMRI findings go a step farther in the investigation of the roles played by different areas within the temporal lobes, distinguishing anterior inferotemporal regions from posterior inferotemporal regions on the basis of their different patterns of BOLD signal with respect to baseline. The posterior regions in the ventral stream were more active than the baseline for objects of both the preferred and the nonpreferred category, whereas the BOLD signal in anterior temporal areas was, if anything, below baseline for objects belonging to the nonpreferred category. We speculated that this might be due to the retrieval of object representations during mind wandering. Whenever mind wandering takes place (e.g., during rest), the object representations in the anterior temporal lobes would be retrieved, leading to an increase in the BOLD signal. However, because of random variation, the object representations retrieved during mind wandering would belong sometimes to a cate-

gory and sometimes to others. Therefore, the BOLD signal in a region within the anterior temporal lobe during rest would result on average lower than during processing of objects of the preferred category but higher than during processing of objects of the nonpreferred category.

## METHODS

### Participants

Twelve participants between at age 18 and 32 years (all native Italian speakers) took part in the experiment. Data from one participant were excluded from the analysis because of excessive head motion. Thus, the data of 11 participants were analyzed. The participants’ consent was obtained according to the Declaration of Helsinki, and the project was approved by the human subjects committees at the University of Trento and at Harvard University.

### Stimuli

The set of stimuli consisted of 128 grayscale images, of which 64 depicted animals and 64 tools. There were 32 different basic-level animals and 32 basic-level tools, with two exemplars from each basic level. We presented two pictures for each object type, which depicted different exemplars of that object type. For instance, for the object type “hammer,” we had pictures of two different hammers.

Stimuli were presented with MATLAB PTB (MathWorks, Natick, MA; Brainard, 1997; Pelli, 1997) with the in-house add-on ASF (available from JS), using an Epson EMP 9000 projector. Images were projected on a frosted screen at the top of the bore, viewed through a mirror attached to the head coil.

## Experimental Design

### Structure of the Trial

Each trial was composed of five parts (see Supplementary Figure 1): blank with letter (400–800 msec); image (500 msec); delay, blank with letter (2–8 sec); response cue (400–800 msec); and blank with letter (4–8 sec). The timings were generated from distributions with hyperbolic density. On each trial, a single picture was presented. The participants were asked to decide whether a given picture was an animal or a tool (push button with right index finger for yes and left index finger for no). Specifically, the participants had to answer one of the two questions: “Is the object in the image an animal?” (“L’oggetto nell’immagine e’ un animale?”) or “Is the object in the image a tool?” (“L’oggetto nell’immagine e’ uno strumento?”). Participants were asked to wait until after the visual cue (a fixation cross) before responding.

### Order of the Questions

Participants answered the same question for 32 consecutive trials. Thus, one question (e.g., Is it an animal?) was

presented at the beginning of the run and answered during the first half of the trials (32); then participants answered the other question (e.g., Is it a tool?) for the remaining half of the trials. Between trials, a blank screen with a letter in the middle (“A” for “animale” [animal], “S” for “strumento” [tool]) was presented to remind participants of the question that they should be answering. The order of the questions in the runs was counterbalanced within and between participants, using two different orders of question–presentation in the experiment. One half of the participants were presented with the questions in the order T(ool)A(nimal)-AT-AT-TA, whereas the other half were presented the questions in the order AT-TA-TA-AT. The dash denotes the separation between runs. Every image was presented with both questions for every participant, and this happened in different orders for the participants in the halves. That is, if for a given participant a given image was shown with the question “Is it an animal?” and later in the session with the question “Is it a tool?,” a different participant was shown that same image first with the question “Is it a tool?” and then with the question “Is it an animal?” This design ensured that all of the stimuli were evenly counterbalanced across participants.

### Structure of the Runs

The experiment was composed of four runs, each run lasting approximately 15 minutes. The stimuli were divided into two groups, A and B; each group (A and B) contained both exemplars of a given item. All items in Group A were presented in each of Runs 1 and 3, and all items in Group B were presented in each of Runs 2 and 4. Each run consisted of 64 trials. Stimuli were presented visually, subtending a visual angle of approximately 10 degrees.

Within each run, images of two different exemplars of every item type were presented. Because of the distribution of the questions, within a run, items repeated across question tended to have more trials between them than item types repeated within question. Therefore, we divided the images of item types repeated across question in two groups (repeated near and repeated far) so as to be able to match for number of intervening trials for the images repeated within question.

## Data Acquisition and Analysis

### MRI Scanning Parameters

The data were collected on a Bruker BioSpin MedSpec 4T at the Center for Mind/Brain Sciences (CIMEC) of the University of Trento using a USA Instruments eight-channel phased-array head coil. Before collecting functional data, a high-resolution ( $1 \times 1 \times 1 \text{ mm}^3$ ) T1-weighted three-dimensional MPRAGE anatomical sequence was performed (sagittal slice orientation, centric phase encoding, image matrix =  $256 \times 224$  [Read  $\times$  Phase], field of view =

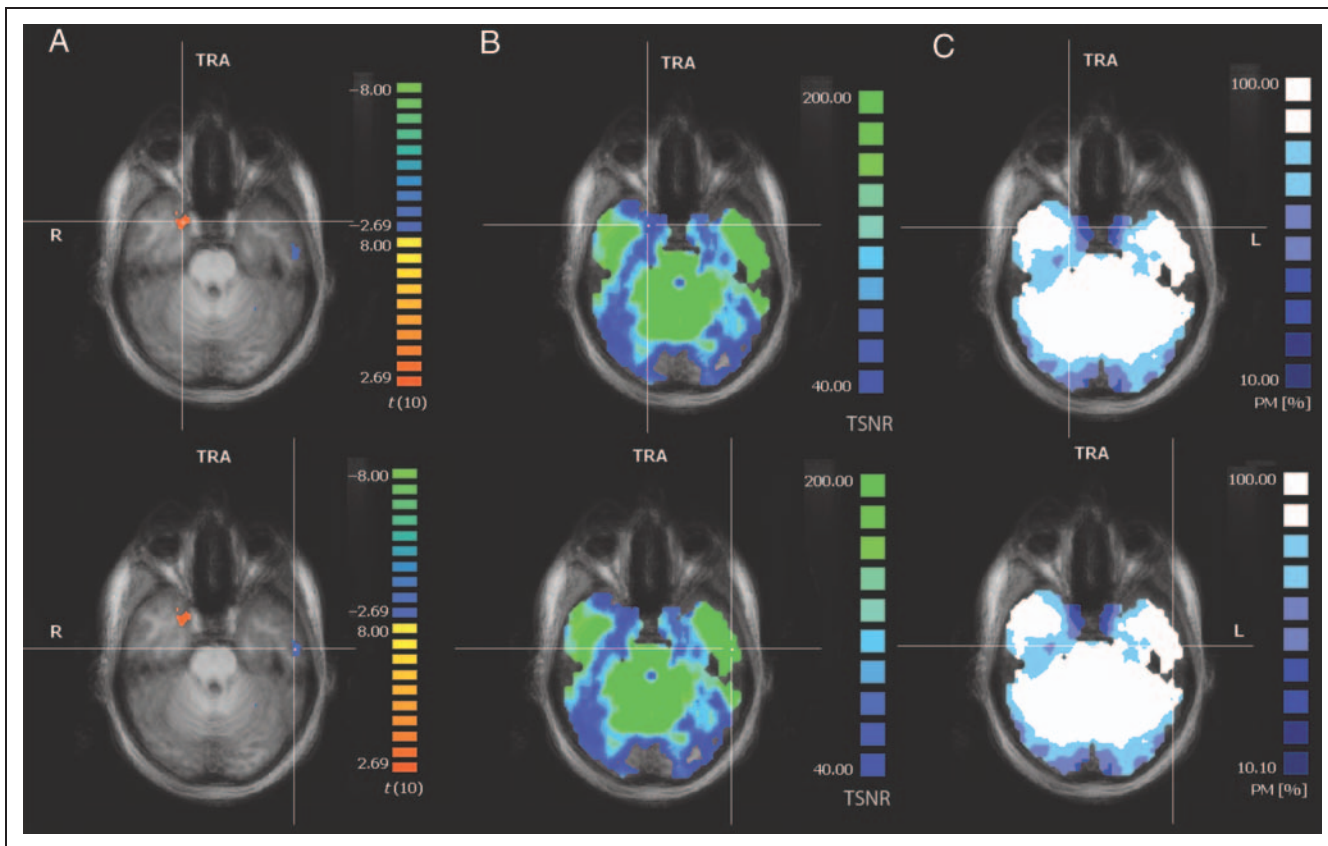
$256 \times 224 \text{ mm}$  [Read  $\times$  Phase], 176 partitions with 1-mm thickness, GRAPPA acquisition with acceleration factor = 2, duration = 5.36 minutes, repetition time = 2700, echo time = 4.18, TI = 1020 msec,  $7^\circ$  flip angle). Functional data were collected using an echo-planar two-dimensional imaging sequence with phase oversampling (image matrix =  $70 \times 64$ , repetition time = 2250 msec, echo time = 33 msec, flip angle =  $76^\circ$ , slice thickness = 3 mm, gap = 0.45 mm, with  $3 \times 3 \text{ mm}$  in plane resolution). Volumes were acquired in the axial plane, in 37 slices. The order of slice acquisition was ascending interleaved odd-even.

### Analysis of Temporal Signal-to-Noise Ratio

Given the known susceptibility issues associated with fMRI applied to frontotemporal regions (Devlin et al., 2000), we calculated temporal signal-to-noise ratio (TSNR) maps to ensure that the quality of the signal in the anterior temporal lobes was adequate to detect BOLD signal. We thresholded the TSNR map for every participant and run at 40, a value indicated by simulations as sufficient to detect effects reliably with fMRI (Murphy, Bodzurka, & Bandettini, 2007; see also Simmons, Reddish, Bellgowan, & Martin, 2010). The maps indicated high TSNR in individual participants, greatly exceeding the threshold of 40 in most of the anterior temporal lobes (see for instance Figure 1B). To check that signal quality in the anterior temporal lobes was consistent across participants, we generated probability maps indicating for each voxel the percentage of participants that showed TSNR above the threshold of 40 in that voxel (see Figure 1C). TSNR in the anterior temporal lobe was above threshold in the majority of the participants and runs, indicating that the quality of the signal was stable.

### Data Analysis

The data were analyzed using Brain Voyager (Version 1.10) and MATLAB (release 2008b). The first two volumes of functional data from each run were discarded before the analysis. Functional data were preprocessed with the following steps (reported in the order in which they were performed): slice time correction (sinc interpolation), motion correction (trilinear interpolation) with respect to the first (remaining) volume in the run, and linear trend removal in the temporal domain (cutoff: three cycles within the run). They were then coregistered (after contrast inversion of the first remaining volume) to the high-resolution deskulled anatomy on a participant-by-participant basis in native space. For each individual participant, echo-planar and anatomical volumes were transformed into the standardized Talairach and Tournoux (1988) space. Data were smoothed with a Gaussian spatial filter (4.5 mm FWHM). The presentations of the images were modeled as events. A standard dual gamma hemodynamic response function was used to convolve the events in the experiment.



**Figure 1.** Foci of activation in the anterior temporal lobes (A), temporal signal-to-noise maps in a specific run (B), and probability maps reporting the percentage of participants showing TSNR more than 40 for each voxel (C). The threshold of 40 has been shown by simulations to be sufficient for detecting differences between conditions reliably with fMRI (Murphy et al., 2007). The maps show that the TSNR was more than 40 in the anterior temporal lobes for most of the participants.

The data were modeled with a random effects general linear model (GLM). As described in the section about the design, in each run, every item type was presented twice, and in the two presentations, two different images (i.e., different exemplars) of that item type were shown. We modeled these properties of the design, which led to 26 regressors overall: 12 for the animal stimuli (Exemplar 1, Exemplar 2 by Presentation 1, Presentation 2 presented within question, presented across question (near or far), 12 for the tool stimuli (analogous to the animal case), 1 for the response cue, and 1 for the presentation of the questions.

The GLM was masked with the deskulled average brain extending anteriorly to  $y = -75$  in the Talairach coordinate system (see Pietrini et al., 2004) so as not to bias the analysis by effects in early visual regions, such as those described in Damasio et al. (2004), Martin and Chao (2001), and Martin, Wiggs, Ungerleider, and Haxby (1996) (Figure 2; see the Supplementary materials for a figure of the unmasked data). The threshold was corrected for cluster size using alpha-sim in the Brain Voyager cluster-level plug-in (1000 iterations). Custom MATLAB software using the BVQX toolbox for MATLAB was used to perform further analyses on the data extracted from Brain Voyager (Figures 1 and 3).

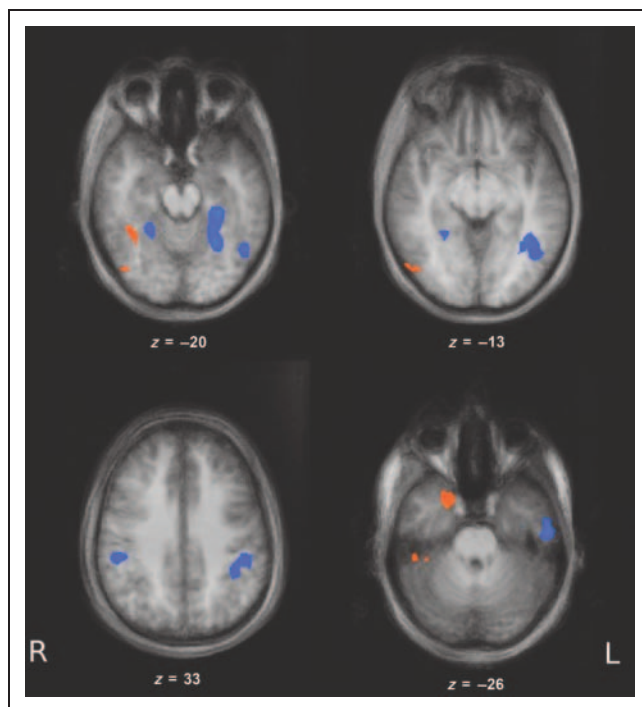
## RESULTS

### Analysis of Category Effects

Using the random effects GLM, we performed an analysis of category effects on the basis of the contrast of all animal stimuli versus all tool stimuli, collapsing across the other nested factors. In Table 1, we report the regions that showed significantly different activity ( $p < .05$  corrected) for the two categories of objects, the coordinates of the centers of mass and the numbers of voxels. We found greater activity for animals than for tools in the right fusiform and STS ( $p < .01$  corrected) and greater activity for tools in the medial fusiform gyrus bilaterally ( $p < .001$  corrected). In agreement with lesion studies (Brambati et al., 2006), we also found greater BOLD signal for tools than for animals in the left MTG ( $p < .001$  corrected), a region frequently associated with impairments for the recognition of nonliving objects (Brambati et al., 2006; Gainotti, 2000).

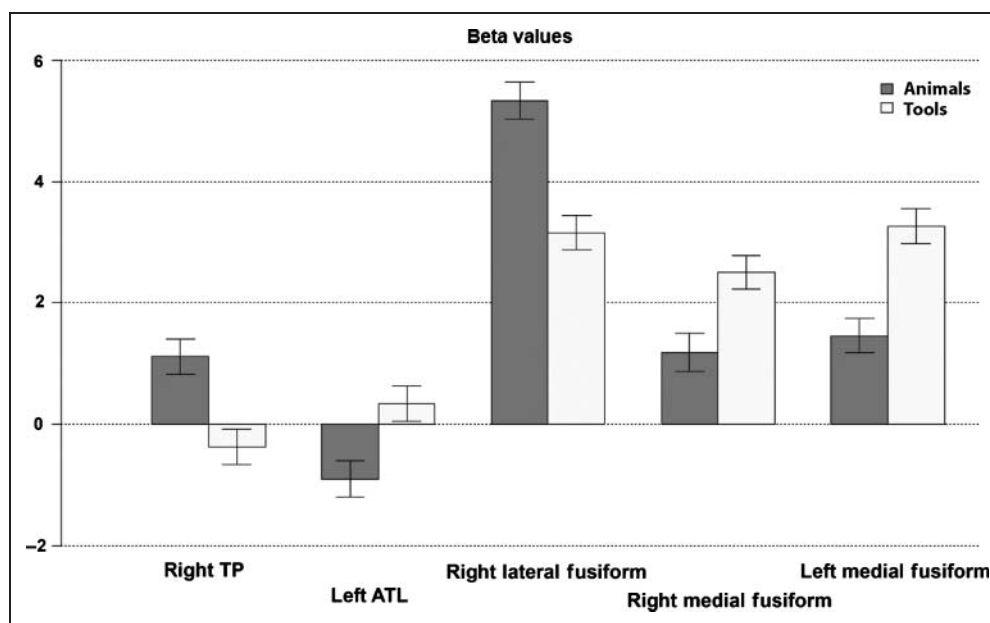
In addition, we found greater BOLD signal for animal pictures in the right temporal pole, significant at  $p < .001$  (corrected). The identified area is compatible with a broader region reported by Brambati et al. (2006), where a volume of gray matter correlates with patient performance at animal recognition (Figure 4). We also found greater BOLD signal





**Figure 2.** Replication of category effects (animals vs. tools). The data are shown at  $p < .05$  uncorrected for visualization purposes. The data thresholded at  $p < .05$  corrected are shown in Figure 1, and a table of all areas showing a significant ( $p < .05$  corrected) difference in the bold signal for animals and manipulable objects is reported in the Supplementary materials (Supplementary Table 1). The functional data were masked to include activation anterior to  $y = -75$ . Areas showing stronger BOLD signal for animals are shown in red, and areas showing greater BOLD signal for manipulable objects are shown in blue. The top left panel shows BOLD signal in the fusiform gyri, the top right BOLD signal in the left MTG, the bottom left BOLD signal in parietal areas, and the bottom right BOLD signal in the anterior temporal lobes.

**Figure 3.** Beta values for ROIs in the ventral temporal lobes. The error bars depict the *SEM*. The mean beta values in the anterior temporal lobe are significantly lower than that in the posterior temporal lobe (lateral and medial fusiform gyri), with the BOLD signal showing a trend toward deactivation for the nonpreferred category. The fusiform gyri show BOLD signal above baseline for images of both the preferred and the nonpreferred category.



for tools in the left anterior temporal lobe ( $p < .005$  corrected).

### Dissociation between Anterior and Posterior Temporal Regions

Within the ventral temporal lobes, we found a qualitatively distinct pattern of BOLD responses in posterior and anterior regions. Responses to animals and tools in the anterior temporal lobes are centered on the baseline, whereas responses to both animals and tools activate the more posterior areas well above baseline (see Figure 3). This pattern is represented by the significant differences between the means of the betas in the anterior and posterior regions, collapsing together the animal and the tool conditions. Comparing the mean activity of the right temporal pole and of the left anterior temporal lobe separately with each of the three areas in the fusiform, the differences are highly significant ( $p < .001$  corrected in all comparisons). On the other hand, the difference between the means of the right temporal pole and the left anterior temporal lobe was not significant ( $p > .05$  corrected). In particular, the fusiform gyri showed BOLD signal above baseline for pictures for both animals and tools, with greater BOLD signal for the preferred category and smaller BOLD signal for the non-preferred category. Instead, activity in the anterior temporal lobes showed activity around baseline, with a trend toward a decrease below baseline of the BOLD signal in response to the nonpreferred category (Figure 3).

### Question Effects

We were interested in studying whether the BOLD signal in the ventral stream is modulated as a function of the question asked (Is it an animal? Is it a tool?) and in which

**Table 1.** Regions Showing Greater BOLD Signal for Tools and for Animals

<i>Region</i>	<i>Center of Mass Coordinates (x, y, z)</i>	<i>No. Voxels</i>
<i>Tools</i>		
Left medial fusiform	(-26, -38, -19)	1065
Right medial fusiform	(24, -46, -13)	293
Left MTG	(-44, -59, -11)	748
Left anterior temporal lobe	(-52, -12, -27)	249
Left posterior temporal pole	(-35, -8.6, -32)	291
Left anterior temporal pole	(-44, 5.2, -33)	236
Left intraparietal sulcus	(-25, -78, 31)	311
Left posterior IPL	(-37, -42, 34)	240
Left anterior IPL	(-44, -34, 34)	319
Right anterior IPL	(48, -32, 36)	228
Left superior parietal lobe	(-30, -53, 44)	253
<i>Animals</i>		
Right LOC	(45, -73, -10)	468
Right lateral fusiform	(36, -47, -21)	611
Right STS/STG	(34, -50, 11)	223
Right anterior temporal pole	(20, 8.6, -26)	273

regions this might be the case. Inside the ROIs defined above, we ran an ANOVA to test for question effects. The BOLD response in the fusiform gyrus bilaterally did not differ significantly for the two questions asked ( $p > .1$ ). On the other hand, activity in the right temporal pole was significantly modulated by question type,  $t(1, 10) = -2.25$ ,  $p < .05$  (see Table 2). Importantly, in the right temporal pole, there were no interaction effects of question by any of the other dimensions manipulated in the experiment (all  $p$  values  $> .1$ ). In particular, the interaction between question type and category of the stimulus was nonsignificant,  $F(1, 10) = 0.01$ ,  $p = .94$ . Furthermore, the question dimension was orthogonal to the category dimension (and to the item dimension, as both questions were asked for all items in every participant). For these reasons, the test of question effects is independent of the way in which we selected the voxels.

## DISCUSSION

Our observations replicate several studies of object recognition showing differential BOLD signal in response to animal pictures and pictures of manipulable objects (for a review, see Martin, 2007). In particular, we replicated previous reports of greater activity for tools in the medial fusiform gyri, the left MTG, and the parietal cortex as well as reports of greater activity for animals in the right lateral fusiform and

the right STS (Mahon et al., 2007; Martin & Chao, 2001; Chao, Haxby, et al., 1999; Chao, Martin, et al., 1999).

The observation of differential activation for animal pictures in the right medial-temporal pole reconciles the results of functional imaging with neuropsychological findings of category specific deficits after damage to the temporal poles (e.g., Papagno, Capasso, & Miceli, 2009; Noppeney et al., 2007; Brambati et al., 2006). This result motivates the use of fMRI longitudinally in patients to study the deterioration of object knowledge with the progression of neurodegenerative diseases.

We observed a left hemisphere bias for manipulable objects and a right hemisphere bias for living things in the anterior temporal lobes, in line with the differential involvement of the left and right posterior temporal lobes in the processing of objects from different categories. Thus, it seems that the pattern of greater activity in the right hemisphere for animals and greater activity in the left hemisphere for tools (see Mahon et al., 2007; Martin & Chao, 2001) generalizes from the posterior temporal lobe to the anterior temporal lobe.

We detected greater BOLD signal for manipulable objects than for animals in a more posterior region of the left anterior temporal lobe, not reported to our knowledge in the PET studies that described a right anterotemporal locus of greater activity for animals. The location of this region is consistent with a recent neuropsychological report of deficit for tool naming after left anterior temporal

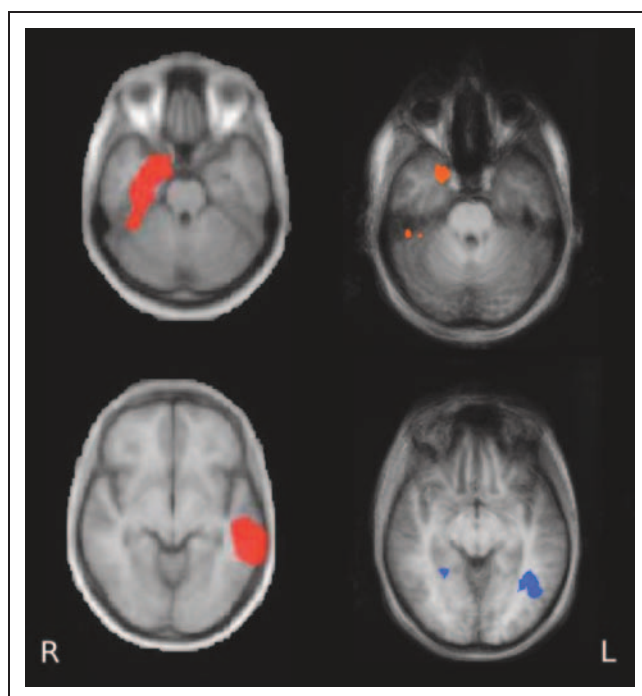


Figure 4. Comparison between the present findings and those by Brambati et al. (2006). The top row shows areas involved in processing animals, with the areas found to correlate with patient performance at animal naming on the left and the temporal pole area showing stronger BOLD responses to animal pictures in this study on the right. The bottom row shows areas involved in processing tools, again comparing the findings of Brambati et al. (on the left) and our findings (on the right) thresholded at  $p < .05$  corrected. Left panel reproduced from Brambati et al.

lobe resection (Bi et al., 2011). The finding of a region more responsive for manipulable objects than for animals in the left anterior temporal lobe converges with the finding of a region more active for knowledge of context of use of manipulable objects versus knowledge of action (Canessa et al., 2007).

A recent fMRI study has shown that the anterior temporal lobes are more active when participants learn facts about unfamiliar people than when they learn facts about hammers or buildings (Simmons et al., 2010). The authors propose that the anterior temporal lobes are part of a domain-specific social cognition system. This hypothesis, however, does not account for the deficits for animals and especially for plants observed as a consequence of anterior temporal lobe damage (e.g., De Renzi & Lucchelli, 1994). Without excluding an important role of the anterior temporal lobes for knowledge about persons and social cognition, our results support the view that the anterior temporal lobes are also involved in processing objects belonging to other semantic categories (see also Hodges, Patterson, Oxbury, & Funnell, 1992).

Converging with the findings by Simmons et al. (2010), Rajimehr, Young, and Tootell (2009) described a region in the right anterior temporal lobe that shows greater BOLD signal in response to faces than to place stimuli. It remains

an open question whether and to which extent the regions described by Simmons et al. and by Rajimehr et al. and the animal area that we described overlap. This question would be best addressed by studies that show images of both animals and faces because they would permit a comparison of the different regions within single subjects thus avoiding the difficulties deriving from the intersubject variability of the foci of activity.

We found a qualitatively different pattern of BOLD signal in the anterior and posterior regions of the ventral temporal cortex. The pattern of activity in posterior regions is well above baseline for both animals and tools. On the other hand, the pattern of activity in anterior regions is centered around baseline, with a trend toward a decrease in the BOLD signal for the nonpreferred category. Importantly, under the standard assumption that noise is symmetrically distributed around the actual value, the difference in the mean BOLD signal relative to baseline in the PTL with respect to the anterior temporal lobe is unlikely to be explained by a greater amount of noise in the anterior areas. This is because greater levels of noise in the anterior temporal lobe would lead to a larger variance in the BOLD signal reducing the significance level, but they would not alter the observed mean value.

The neural significance of BOLD signal below baseline is a complex issue (Kannurpatti & Biswal, 2004; Smith, Williams, & Singh, 2004; Harel, Lee, Nagaoka, Kim, & Kim, 2002; Gusnard & Raichle, 2001; Raichle et al., 2001). However, a recent article (Shmuel, Augath, Oeltermann, & Logothetis, 2006) showed that negative BOLD can reflect neural activation below baseline. Shmuel et al. (2006)

**Table 2.** Effects of Question Type

ROI	<i>t</i>	<i>p</i>
Left medial fusiform	0.64	.5342
Right medial fusiform	0.26	.7937
Right lateral fusiform	0.46	.6553
Left anterior temporal lobe	1.85	.0932
Left posterior temporal pole	0.14	.8978
Left anterior temporal pole	0.54	.6033
Right anterior temporal pole	-2.25*	.0483*
Left IPS	0.89	.3959
Left posterior IPL	0.76	.4636
Left anterior IPL	1.02	.3307
Right anterior IPL	0.57	.5764
Left superior parietal lobule	0.89	.3960
Left MTG	0.22	.8353
Right STS	1.24	.2431
Early visual cortex	1.43	.1824

\* $p < .05$ .



suggest that negative BOLD responses that are located in the gray matter and far from other positive BOLD responses may be interpreted as reflecting a decrease in neural activity. The areas in the anterior temporal lobes showing a trend toward a decrease in the BOLD signal are most likely located in the gray matter and are far from other positive BOLD responses; therefore, the same interpretation may be tentatively applied to our findings.

In this study, the different pattern of BOLD signal in the posterior and anterior areas of the ventral temporal cortex could be due to relatively high activity in the anterior temporal areas during baseline. In fact, portions of the anterior temporal lobes are part of the default network (Ingvar, 1974, 1979; for a review, see Buckner, Andrews-Hanna, & Schacter, 2008), and it is thus possible that the areas we found are within a set of regions that show greater activity during rest than during performance of most active tasks. It is possible that the anterior temporal lobes are particularly active even when we retrieved representations of objects “top-down,” in the absence of a corresponding bottom-up sensory stimulation. Mind wandering also involves the retrieval of object representations, and according to this account, it would thereby raise the BOLD signal in the anterior temporal lobe during rest.

Another possibility is that the BOLD signal in the anterior temporal lobes reflects active suppression of the non-preferred category in the anterior temporal lobes but not in the fusiform gyri (see Egner & Hirsch, 2005). These two possibilities are not mutually exclusive.

The BOLD signal in posterior areas of the temporal lobe (e.g., the fusiform gyri) did not show any significant modulation by task. The BOLD signal in the right temporal pole, on the other hand, was mildly but significantly modulated by question type, suggesting a greater influence of top-down connections. A study by Rogers, Hocking, Mechelli, Patterson, and Price (2005) has shown task-dependent modulations of the activity in posterior temporal areas. The results obtained by Rogers et al. are compatible with our findings. The different tasks used in the present experiment were matched very closely: They required categorization at a similar level of specificity and the relative instructions differed by a single word. Therefore, our study does not imply that posterior areas are totally unaffected by any possible task differences, but rather it shows that by choosing carefully matched tasks, it is possible to reveal differences between posterior and anterior areas in terms of their task sensitivity. Further studies will be needed to deepen our understanding of how different types of tasks modulate anterior temporal lobe activity and what role this modulation plays in the performance of the tasks.

In conclusion, dimensions other than semantic category might differentiate anterior from posterior regions in the ventral temporal lobe (e.g., the integration of information from different modalities; see Patterson, Nestor, & Rogers, 2007). On the other hand, semantic category could be a factor shaping neural organization within different levels along the anterior to posterior axis.

## Acknowledgments

The authors thank Scott Fairhall and Thomas McKeeff for their comments; Alex Martin and Yanchao Bi for discussing some neuropsychological findings; Jorge Jovicich for assistance with organizational issues; and Gianpaolo Basso, Manuela Orsini, Claudio Boninsegna, and Hanna Liisa Inkala for technical assistance with fMRI. The research was supported by a grant from the Fondazione Cassa di Risparmio di Trento e Rovereto.

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