FEATURE ARTICLE

Person- and Place-Selective Neural Substrates for Entity-Specific Semantic Access

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Object-category has a pronounced effect on the representation of objects in higher level visual cortex. However, the influence of category on semantic/conceptual processes is less well characterized. In the present study, we conduct 2 fMRI experiments to investigate the semantic processing of information specific to individual people and places (entities). First, during picture presentation, we determined which brain regions show category-selective increases during access to entity-specific semantic information (i.e., nationality) in comparison to general-category discrimination (person vs. place). In the second experiment, we presented either words or pictures to assess the independence of entity-specific category-selective semantic representations from the processes used to access those representations. Convergent results from these 2 experiments show that brain regions exhibiting a category-selective increase during entity-specific semantic access are the same as those that show a supramodal (word/picture) category-selective response during the same task. These responses were different from classical “perceptual” category-selective responses and were evident in the medial precuneus for people and in the retrosplenial complex as well as anterior/superior sections of the transverse occipital sulcus and parahippocampal gyrus for places. These results reveal the pervasive influence of object-category in cortical organization, which extends to aspects of semantic knowledge arbitrarily related to physical/perceptual properties.

Keywords: concepts, domain, face, semantic, unique entities

Introduction

Semantic knowledge refers to a broad range of factual knowledge that informs our beliefs and guides our day-to-day behavior. This diverse range of knowledge relates not only to facts general to kinds of objects (people wear clothing, dogs are quadrupeds) but also to facts specific to particular individuals (Sally is a lawyer, Bill likes Jazz). This latter form of semantic knowledge relates to individual people (president Obama, my mother) as well as “unique entities” from other object-categories (the Eiffel Tower, Lassie). It remains an open question whether object-category influences the representation of semantic knowledge about unique identities (Damasio et al. 2004). To put this another way, would accessing a similar semantic detail, such as the entity’s nationality (e.g., French), involve the same or distinct neural substrates for individual persons (e.g., Descartes) and places (e.g., Eiffel Tower)?

One reason to think that dissociable substrates may exist for semantic knowledge of individual persons and places is provided by neuropsychological investigations that have documented the existence of category-specific semantic impairments of one or another object-category that could not be attributed to damage to perceptual or linguistic processes (for a recent review, see Mahon and Caramazza 2009). Moreover, similar category-specific semantic deficits have been reported for individual people in the context of relatively spared semantic knowledge about specific places (e.g., Miceli et al. 2000).

Another reason for thinking that semantic knowledge of individual persons and places might have partially distinct neural substrates is provided by the neuroimaging literature, which has consistently reported category-selective effects in perceptual and cognitive processing for these 2 categories of objects. The perception of places and scenes leads to the selective activation of ventral (the parahippocampal place area, PPA; lingual gyrus, LG), dorsal (transverse occipital sulcus, Tos), and medial (retrosplenial complex, RSC) brain regions (Epstein and Kanwisher 1998; Maguire et al. 2001; Grill-Spector 2005). By contrast, viewing faces preferentially recruits the occipital and fusiform face areas (OFA/FFA) and the posterior superior temporal sulcus (pSTS; Kanwisher et al. 1997; Gauthier et al. 2000). More importantly for current purposes, category-selective regions for person knowledge have been identified outside classical visual perceptual areas, presumably representing extraperceptual, semantic knowledge about people. During face perception, personally familiar people more strongly activate an extended network of regions including the anterior temporal lobes (ATL), medial prefrontal cortex (mPFC), and a region at the junction of the hippocampus and amygdala (Gobbini et al. 2004; Leibenuft et al. 2004). However, there is considerable variability in the regions activated. A recent study compared active access to semantic detail about specific individuals (occupation of famous people) to a perceptual matching task (identity matching between 2 unknown faces; Gesierich et al. 2011). The results implicated the left temporoparietal junction and middle temporal gyrus, but not the ATL, in the ability to later retrieve the name of the famous person. The study also revealed an extensive network of regions (including the ATL) that are more active during access to semantic knowledge about people. The activations revealed in these various studies appear to reflect nonperceptual characteristics associated with individual, familiar people (semantic, emotional, social: Haxby et al. 2000; Gobbini and Haxby 2007). However, such results do not distinguish between 2 possible interpretations: these regions could represent person-selective knowledge related to individual people or these regions selectively represent knowledge about individuals of all sorts (e.g., both people and places). To distinguish between these alternatives, we need to include control conditions that allow comparison between types of unique entities (e.g., Obama vs. Washington Monument).

Some studies directly compared the cortical responses produced in the course of processing unique people and places.
A complicated picture has emerged from these studies with some results suggesting the possibility of a specialized neural substrate for all types of unique entities and other results suggesting the existence of regions specialized in representing unique entities of a specific category. Comparisons of famous to unknown people and places during perception (Gorno-Tempini and Price 2001) and naming tasks (Grabowski et al. 2001) have implicated the left ATL for both categories. This is consistent with the idea that unique entities share a common neural substrate (Damasio et al. 2004; but see also Simmons and Martin 2009; Simmons et al. 2010). However, these studies also produced contrasting results regarding category-specificity in representing unique entities. While Gorno-Tempini and Price (2001) found indication of person-selectivity in the right ATL at uncorrected statistical thresholds, Grabowski et al. (2001) did not replicate this finding. Although these studies compared unique persons and places, they did not explicitly compare semantic retrieval for such items to semantic retrieval for the general kinds “person” and “place.” The absence of this control limits the conclusions we can reach regarding the representation of unique entities versus general types.

Thus, it remains unclear whether the retrieval of semantic information about unique entities engages category-selective or category-neutral neural substrates. In the study reported here, we assessed the degree to which the explicit instruction to retrieve entity-specific information about people and places produces an increase in cortical activity selectively for those semantic categories. In Experiment 1, we tested whether the retrieval of entity-specific semantic information (nationality) produces enhanced person- and place-selective neural responses when compared with general-category discrimination (person vs. place). In Experiment 2, we used picture and word stimuli in a task that required participants to retrieve entity-specific semantic information in order to test the independence of semantic representations from the processes used to access those representations (i.e., via word and picture stimuli). We hypothesized that those brain regions showing maximal category-selective responses during semantic retrieval will be the same category-selective regions that are found across the picture and written word tasks.

Materials and Methods

Participants

Sixteen subjects participated in Experiment 1 (9 females, mean age 26.2 years). Seventeen subjects participated in Experiment 2 (8 females, mean age 26.9 years, 3 subjects participated in both experiments). All participants were right handed native Italian speakers. All procedures were approved by both the University of Trento Human Research Ethics Committee and the Harvard University Committee on the Use of Human Subjects in Research.

Experiment 1: Stimuli and Procedures

The experiment consisted of 3 runs (7 min, 40 s each) of 12 blocks each. Each block was composed of 7 person and 7 place trials (randomly intermixed) comprising a 400 ms image presentation followed by the 1600 ms presentation of a fixation cross. In 3 different block types (Fig. 1), subjects performed a categorization task based upon either: (a) “General Category,” indicating whether an image was of a

<table>
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<tr>
<th>Person or Place?</th>
<th>Unfamiliar</th>
<th>Famous</th>
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<td>Italian or Foreign?</td>
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<td>Celebrity or politician?</td>
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Figure 1. Schematic of Experiments 1 and 2. In Experiment 1, participants performed a categorization task based either upon “General Category” (person or place) or “Entity-Specific” semantic information (Italian or foreign) for people and places. The contrast of interest was the interaction between category (person/place) and task for famous stimuli. In Experiment 2, stimuli were presented as both words and pictures. Participants performed an Entity-Specific categorization task for people and places as well as 2 control categories composed of nonunique basic objects. In this experiment, the critical analysis was the conjunction of person-/place-selective effects evident in both word and picture modalities.
person or a place, with separate blocks for Unknown (1/3 of blocks) and Famous stimuli (1/3 of blocks); or (b) “Entity-Specific semantic information,” where participants indicated whether the famous person or place was Italian or foreign (1/3 of blocks). Entities readily identified by Italian participants were selected from various internet sources (for a complete list of stimuli, see Supplementary Materials). The semantic question was selected to be arbitrary in nature, not encouraging perceptual, spatial, or social cognition, so as to encourage the retrieval of “comparable” conceptual knowledge across categories. Blocks were separated by the 6-s presentation of a fixation circle, the color of which also served to cue the trial type of the upcoming block. Stimuli consisted of 84 images of faces and 84 images of places. One-third of stimuli in each category were unknown: one-third Italian, and one-third foreign. Each stimulus was presented once per run. Images were grayscale and subtended ∼7° of visual angle horizontally and vertically.

Experiment 2: Stimuli and Procedures
In a blocked design (8 trials per block), participants performed Entity-Specific semantic categorization of famous people and places (Fig. 1). Additionally, 2 nonunique basic-object-categories, animals and inanimate objects, were included as a control condition, (e.g., “dog,” “fork”). In the conditions of interest, participants indicated by button press if a famous person was a politician or celebrity, or if a famous place was constructed before or after AD 500. For the control conditions, participants indicated whether an animal was normally used for food or whether an object was associated with food (either something edible or something used for cooking).

Forty-eight exemplars were drawn from each of the 4 categories (192 in total; 46% of the unique entities were also used in Experiment 1). Participants were presented with word stimuli in the first 2 runs and picture stimuli in the third and fourth runs (9 min, 42 s per run). This order was chosen so that word presentation was not confounded by prior exposure to particular images. Each run consisted of 30 blocks of 8 stimulus presentations, 6 blocks for each of the categories and 6 blocks of a control (fixation) condition. The block presentation sequence was pseudorandom. Consecutive sequences of 5 blocks contained the randomized presentation of each condition. Each exemplar was presented once per run. The trial type of the upcoming block was indicated by the presentation of a written cue (2 s) at the start of each block. Stimuli were presented for 400 ms followed by the 1600 ms presentation of a fixation cross against a phase-scrambled background (subtending 7.4° of visual angle horizontally and vertically). To create the picture stimuli, color images were isolated from their original background and matched for root mean square contrast, luminance, and size. Foreground images and word stimuli were presented against a phase-scrambled background to minimize overall differences in visual input between categories and between word and picture presentation. The images used to form the phase-scrambled backgrounds were selected equally from among the 5 categories. The passive baseline condition consisted of 8 repetitions of a 400- and 1600-ms presentation of a fixation cross against alternating phase-scrambled backgrounds.

MRI Scanning Parameters
Participants lay in the scanner (BrukerBioSpin MedSpec 4T) and viewed the visual stimuli through a mirror system. Data collection was conducted at the Center for Mind/Brain Sciences (CIMEC), University of Trento using a USA Instruments 8-channel phased-array head coil. In Experiment 1, a sequence was selected to maximize the signal-to-noise ratio in the ATLs (for details, see Gesierich et al. 2011). Functional data were collected using an echo-planar 2D imaging sequence with phase oversampling (image matrix = 70 × 64, repetition time = 2000 ms, echo time = 33 ms, flip angle = 76°, slice thickness = 3 mm, gap = 0.45 mm, with 3 × 3 mm in plane resolution). Over 3 runs, 712 volumes of 43 slices were acquired in the axial plane, aligned along the long axis of the temporal lobe. In Experiment 2, a standard functional sequence was used to maximize signal quality over the whole brain. One thousand one hundred and sixty-eight volumes of 34 AC–PC aligned slices were acquired over 4 runs (image matrix = 70 × 64, repetition time = 2000 ms, echo time = 33 ms, flip angle = 76°, slice thickness = 3 mm, gap = 0.45 mm, with 3 × 3 mm in plane resolution).

An additional high-resolution (1 × 1 × 1 mm³) T₁-weighted MPRAGE sequence was performed (sagittal slice orientation, centric phase encoding, image matrix = 256 × 224 [Read × Phase], field of view = 256 × 224 mm [Read × Phase], 176 slices with 1-mm thickness, GRAPPA acquisition with acceleration factor = 2, duration = 5.36 min, repetition time = 2700 ms, echo time = 4.18, TI = 1020 ms, 7° flip angle).

fMRI Analysis
Analysis was performed in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). After discarding the first 4 volumes of each run, all images were corrected for head movement. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the standard SPM8 EPI template (Montreal Neurological Institute [MNI] stereotactic space), resampled to a 3-mm isotropic voxel size, and spatially smoothed using an isotropic Gaussian kernel of 8-mm full-width half-maximum (FWHM). The time series at each voxel for each participant were high pass filtered at 128 s and prewhitened by means of an autoregressive model AR(1). Subject-specific beta weights were derived through a general linear model (GLM). For each subject, the data were best fitted at every voxel using a combination of effects of interest. These were delta functions representing the onset of each of the experiment conditions, convolved with the SPM8 hemodynamic response function (HRF). The 6 head-motion parameters were included as additional regressors of no interest. Subject-specific beta values were entered directly into a group-level random-effects GLM to allow statistical inference, and reaction time (RT) data were included as an additional regressor of no interest. Unless otherwise stated, statistics maps were generated using an initial voxelwise threshold of P < 0.001. Correction for multiple comparisons was subsequently performed at the cluster level using the familywise error (FWE) correction as implemented in SPM8.

Results

Experiment 1: Enhanced Category-Selective Effects During Entity-Specific Semantic Retrieval
In this experiment, we sought to identify person- and place-selective changes in the neural response during Entity-Specific semantic retrieval in comparison to the General-Categorization of these same stimuli. As anticipated, RTs were significantly faster for the General-Category (mean = 682 ms, SD = 77 ms) than the Entity-Specific task (mean = 896 ms, SD = 108 ms; t(15) = 6.28, P < 0.001). Additionally, RTs were faster for persons than places in both the General-Category (persons: mean = 664 ms, SD = 78 ms; places: mean = 700 ms, SD = 81 ms; t(15) = 3.47, P < 0.005) and Entity-Specific tasks (persons: mean = 848 ms, SD = 105 ms; places: mean = 945 ms, SD = 115 ms; t(15) = 9.52, P < 0.001). Critically, there was no interaction between Task and Category (the effect-of-interest in the fMRI analysis). However, to minimize the contribution of RT effects, all fMRI analyses were performed with RT as a covariate.

The contrast of all faces versus all places revealed the expected network of domain selective brain regions (see Fig. 2A and Table 1). Faces preferentially activated the right OFA, bilateral FFA, pSTS, the anterior hippocampus/amygdala, and the mPrec. For places, activation was seen to extend dorsally from the middle and superior occipital gyri to TOS and the superior parietal lobe. Ventrally, place-selective activation spread anteriorly from the lingual to parahippocampal gyrus. Mesially, places selectively activated the RSC bilaterally.
The general category discrimination of unknown people and places produced largely the same pattern of person- and place-selective responses (Fig. 2B). This confirms that many of the “extended” category-selective areas also respond to images of people and places that possess only general semantic associations. A notable exception to this pattern was the mPrec. Even at lenient thresholds (P < 0.01, uncorrected), no voxel in this region was more active for faces than places when Entities-Specific semantic information was absent.

To assess the influence of category on Entity-Specific semantic retrieval, we considered the interaction between Task (General-Category/Entity-Specific) and Category (person, place) (Fig. 2C). This contrast revealed that Entity-Specific semantic retrieval produced a significant person-selective increase in the mPrec (see Fig. 2C) but not in right OFA or bilateral FFA (even at very lenient thresholds; P < 0.05). Entity-specific semantic retrieval for places led to an increase in place selectivity in the RSC, PPA, and TOS. For both the dorsal (TOS) and ventral (PPA) regions, Entity-Specific semantic retrieval produced place-selective increases in regions anterior (and superior) to those showing the maximal overall place-selectivity (see Table 1).

Next, we performed a conjunction analysis to determine if there were any effects of semantic processing common to both
domains (such category-neutral effects would be missed in the Category by Task interaction). A whole-brain conjunction analysis of the effect of Task for famous persons and famous places was performed ([PlaceEntSpec > PlaceGenCat] ∧ [PersonEntSpec > PersonGenCat]; P < 0.001). No region survived correction for multiple comparisons although bilateral clusters in ventrolateral PFC were evident at uncorrected (P < 0.001) thresholds (left: x y z = −36, 20, −8; 43 voxels; right x y z = 30, 23, −11; 31 voxels).

**Experiment 2: Supramodal Person and Place Selectivity During Entity-Specific Semantic Retrieval**

In this experiment, we tested whether the Entity-Specific category-selective responses evident in Experiment 1 were dependent on input modality. The assumption being tested is that a central semantic representation should be activated irrespective of modality of input. Participants were presented with words and pictures in separate blocks while they performed a task that required Entity-Specific semantic retrieval (occupation for people and vintage for buildings). RTs for persons and places did not differ significantly either for words (person: mean = 960 ms, SD = 130 ms; place: mean = 983 ms, SD = 109 ms) or for pictures (person: mean = 776 ms, SD = 61 ms; place: mean = 795, SD = 88 ms). There were large overall differences in RTs between the person and place conditions and the baseline conditions (all P < 0.001: For inanimate objects, words: mean = 832 ms, SD = 168 ms; pictures: mean = 707 ms, SD = 80 ms; for animals, words: mean = 823 ms, SD = 75 ms; pictures: mean = 766 ms, SD = 66 ms). While RTs for person and place categories did not differ significantly, there was a trend (P < 0.08). Therefore, RT was included as a covariate to minimize its contribution to the reported results.

To verify that category-selective semantic representations were truly selective for person and place domains, we required that any person or place effects were also greater than the control conditions (animals and inanimate objects; P < 0.05 uncorrected, implemented using inclusive masking). Looking first at the cortical response during pictorial conditions, all person/place-selective regions identified in Experiment 1 were replicated (Fig. 3A). Additionally, the mPFC showed a selective response for people. Similar mPFC activations were present in Experiment 1 but did not survive correction for multiple comparisons. In the word presentation conditions, several category-selective regions evident in the picture conditions were also apparent (Fig. 3B). For people, the mPrec and mPFC were more active during person-related semantic retrieval (see Table 2). However, an expected supramodal person-selective effect in the right pSTS was not significantly greater than the control conditions. Place-related semantic retrieval during word presentation produced place-selective increases in the RSC, PPA, and TOS (Table 2). The loci of place-related processing for words in the PPA and TOS were seen to undergo an anterior shift with respect to the maxima observed during picture presentation. To quantify the consistency of category-selective effects across modalities, a conjunction analysis was performed ([PersonWord vs. PlaceWord] ∩ [PersonPic vs. PlacePic]). This analysis confirmed the significance of supramodal clusters in the mPrec, RSC, PPA, and TOS (Pcorr < 0.05; Fig. 3C).

We did not find clear category-selective effects for persons and places in bilateral ATL. A whole-brain analysis revealed that both words and pictures depicting people produced more activation than the control categories (significant at the peak but not cluster level - Left: MNI = −60, −7, −20; Pcorr < 0.005, 70 voxels: Right MNI: 60, −4, −26; Pcorr = 0.001, 70 voxels) but not more than places. Similarly, for the places condition, words (but not pictures) also produced uncorrected activation of the left ATL (MNI = −57, −4, −23; Funcorr < 0.00005), but again no difference when compared with

**Figure 3.** Surface maps of category-selective activation during Entity-Specific semantic retrieval. (A) Picture cuing. (B) Word cuing. (C) The conjunction between words and pictures. This conjunction reveals input-independent (supramodal) category-selective semantic processing. All contrasts are inclusively masked by the contrast of persons > [animals and objects] and places > [animals and objects]. Surface maps have been thresholded at P < 0.001 (uncorrected). See Table 2 for further details.
people. These results are not inconsistent with a category-general role of the ATL in entity-specific semantic processing (Damasio et al. 2004). This is in contrast to the effects seen in Experiment 1 where there was no evidence that the instruction to recall detailed entity-specific information modulated the ATL response compared with that seen during the General-Categorization (and automatic recognition) of unique entities.

Finally, comparable analyses carried out for the control conditions (animals and objects) revealed no significant supramodal category-selective effects. This was true both in comparison to each other and to the person and place categories.

Convergence Between Experiments 1 and 2

All semantic regions identified in Experiment 1, the mPrec, RSC, PPA, and TOS showed a supramodal response in Experiment 2. To formally determine whether the brain regions overlapped in the 2 experiments, we performed a conjunction analysis across experiments. The analysis was performed by determining the overlap between 1) the effects of Entity-Specific semantic retrieval in comparison to General-Categorization discrimination in Experiment 1 (interaction; Fig. 2C) and 2) the supramodal category-selective effects in Experiment 2 (conjunction of words and pictures, Fig. 3C). Figure 4A shows the supramodal response in those voxels showing a Category by Task interaction in Experiment 1 (P < 0.001). All clusters were significant (P < 0.05, FWE corrected) after correction for multiple comparisons over the mask volume. When the reverse comparison was performed, determining the Category by Task interaction in Experiment 1 within voxels showing the supramodal conjunction effect in Experiment 2, all reported clusters were again significant (P < 0.05, FWE corrected). A region of interest (ROI) analysis confirmed the congruency of effects across the studies. Beta values for each study were extracted from ROIs independently defined from the contrast of interest in the other study (thus avoiding any circularity in ROI definition/interrogation). All effects of interest were present in this ROI analysis (P < 0.001, see Fig. 4B,C for the signal plots).

Anterior Shift in PPA and TOS

In both ventral and dorsal place-Selective regions, compared with the maximal response to picture stimuli, a more anterior/superior locus was apparent in regions preferentially involved in Entity-Specific semantic retrieval in Experiment 1 (compare B and C in Fig. 2) and in regions showing a supramodal response in Experiment 2 (compare A and C in Fig. 3). To verify this statistically, the peak activations in ventral and dorsal regions were identified in each subject. This was accomplished objectively by selecting the maxima for each contrast within a stereotaxically defined volume (P < 0.05, extent >10). Post hoc paired t-tests were performed comparing the stereotaxic location of each subject’s peak during the General Category task for unknown stimuli to the interaction of Category by Task (see Fig. 5). These tests revealed a significant anterior shift in the PPA (left: t(12) = 3.42, P < 0.005; right: t(13) = 2.64, P < 0.05) and an anterior (left: t(11) = 3.43, P < 0.05; right: t(10) = 4.59, P = 0.005) dorsal shift (left: t(11) = 2.88, P < 0.05; right: t(10) = 3.54, P = 0.05) in TOS. Similar effects were seen in Experiment 2. Compared with the place-selective response in the picture presentation condition, a more anterior region of the PPA (left: t(16) = 4.66, P < 0.005; right: t(15) = 3.38, P < 0.005) and a more anterior (left: t(15) = 4.73, P < 0.005; right: t(12) = 3.34, P < 0.01) and superior (t(15) = 4.57, P < 0.005; right: t(12) = 3.73, P < 0.005) region of the TOS showed a place-selective response in the word condition.

Discussion

In 2 experiments, we investigated whether the retrieval of Entity-Specific semantic information engages person or place-selective neural substrates. We identified category-selective semantic processes using 2 criteria: enhanced category-selectivity in the Entity-Specific semantic retrieval task and category-selective responses during both picture and word presentation (supramodal responses). In Experiment 1, we observed that Entity-Specific semantic retrieval modulated category-selectivity medially, in the precuneus (persons) and RSC (places), as well as in anterior/superior regions of the

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**Table 2**

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<th>Picture stimuli</th>
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<td>Cluster, Peak, T</td>
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<td></td>
<td>Person, Vol,</td>
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<tr>
<td>RSTS</td>
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<td>mPrec</td>
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<td>MFG</td>
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<td>0.005 7.16</td>
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<tr>
<td>RATL</td>
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<td>RHIPP</td>
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<td>rTOS</td>
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<td>lTOS</td>
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<td>Left</td>
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<td>Right</td>
<td>0.001 143</td>
<td>0.001 32</td>
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Note: To increase statistical power, P values, and cluster extent for the interaction are reported masked by the main effect. (No regions were evident outside of this mask. See Fig. 3 for unconstrained whole-brain results).

†Region does not survive correction for multiple comparisons, but see later sections for significant effects using anatomically informed analyses.
PPA and TOS for places. Experiment 2 showed the supramodal category-selective response produced by Entity-Specific semantic retrieval in these same regions. Across these 2 studies, there was a striking concordance between brain regions meeting each criterion. The findings indicate that category-selective systems exist for Entity-Specific semantic retrieval and that the neural substrates of this category-selective response are dissociable from the classical “visual” category-selective architecture.

It has been proposed that the specific demands associated with accessing unique semantic features for both person and places is met in a category-neutral manner by the ATL (Gorno-Tempini and Price 2001; Damasio et al. 2004; see also, Ross and Olson 2012). That is to say, the unique associations connected to specific entities put them in an exclusive semantic class, one that requires the highest level of discrimination with respect to perceptual and contextual knowledge as well as the lexical retrieval of proper names (Grabowski et al. 2001; Damasio et al. 2004). This, in turn, may lead to dedicated cortical structures that serve these demands in a category-neutral fashion. The predominance of category-neutral semantic representation is also supported by the observation that, of the extensive network of regions associated with the semantic processing of words, only a small fraction of these regions show modulation by object-category (Binder et al. 2009). Based on these considerations, one might expect the demands of accessing entity-specific rather than general-category information to result in category-neutral alterations in brain activity. In contrast, we observed extensive supramodal category-selective systems that were more active when entity-specific semantic information must be accessed.

In both experiments, “Extended” face-selective regions show a strong preference for people over places during visual presentation. This was evident even during the General-Category task of unknown stimuli. However, the majority of these regions did not meet our conservative criterion for Entity-Specific semantic processing. Only the mPrec and mPFC showed supramodal selectivity for people and only the mPrec also showed an increased person-selective response during Entity-Specific semantic retrieval. The prefrontal’s strong connections to frontal and association (but not sensory) cortices and its central involvement in internalized “default-mode” cognition, has led to the proposal that it is involved in elaborating highly integrated information (Cavanna and Trimble 2006). Functionally, this region has been associated with an extensive range of high-level cognitive processes, including imagery and episodic memory (see Cavanna and Trimble 2006 for review). Previously, activation of the mPrec during the viewing of personally familiar people has been attributed to the incidental retrieval of episodic memories, (Gobbini and Haxby 2007; see also Sugiura et al. 2009). In the present study, we observed no significant modulation of this region during the person/place categorization of famous faces (and presumably automatic recognition). In contrast, the mPrec was strongly modulated during Entity-Specific semantic retrieval of information of a biographical and not episodic nature. While it is almost impossible to completely disentangle semantic and episodic memories, the minimal autonoetic knowledge associated with famous stimuli and the high sensitivity of the mPrec to Entity-Specific semantic retrieval strongly suggest that this region plays a role in person-specialized semantic processing extending beyond the retrieval of episodic knowledge.
Another medial region, the RSC, showed a category-selective semantic response. This place-selective region covered BA 30 (RSC proper) and extended along the fundus of the parietal-occipital sulcus, consistent with previous reports (Nasr et al. 2011). During rest, the RSC forms a coupled unit with the mPrec but is also tightly connected to medial temporal structures, including the hippocampus, perirhinal, and parahippocampal cortices (Greicius et al. 2009; Vann et al. 2009). Functionally, the RSC is associated with higher level processing related to places. These functions include the location of a place within its immediate spatial environment (e.g., north or south of a reference location; Epstein et al. 2007), the retrieval from memory of spatial relationships between elements within a scene (Burgess et al. 2001) and familiarity judgments about places (Sugiura et al. 2005). Here, we observe a semantic response in this region, showing that the scene-selective response extends beyond spatial representations.

The semantic processing of places also activated anterior sections of classic place-selective PPA in a region adjacent to BA 36 (perirhinal cortex). Recruitment of anterior regions of the parahippocampal gyrus may be less bound to visual processing. This region has been reported for spatial navigation (Rosenbaum et al. 2004) and episodic recall (Summerfield et al. 2009) and more anterior regions of the parahippocampal/perirhinal cortex functionally couple with ATL rather than place-selective visual cortex (Kahn et al. 2008). Furthermore, in the left hemisphere this more anterior section of the parahippocampal gyrus has been implicated in the semantic processing of words (Binder et al. 2009).

A notable dissociation was seen between the PPA and its ventral stream counterpart, face-selective FFA. While the anterior PPA showed both a place-selective increase during Entity-Specific access and a supramodal representation, neither effect was seen in the FFA (even at uncorrected statistical thresholds). The dissociation between the PPA and FFA is consistent with their characteristic profiles during perception. The PPA responds almost exclusively to scenes while the FFA shows a bias towards faces but is activated during the perception of multiple categories of objects (Downing et al. 2006; Schwarzlose et al. 2008). Thus suggesting that the PPA encodes information specific to the processing of scenes that is relatively independent of the perception of images in general. The supramodal semantic representation in the PPA in this study provides support for the possibility that the activation of PPA during perception also reflects processes less intimately bound to the perception of the physical characteristics of places, while the FFA is more tightly linked to the perceptual process.

The region of the TOS that was maximally active during the viewing of images was located in the lateral occipital gyrus (LO), rather than in its namesake sulcus (see Nasr et al. 2011). Classic perceptual TOS is highly sensitive to mirror reversal (Dilks et al. 2011) and spatial location (Schwarzlose et al. 2008), and appears closely bound to the visual properties of the stimulus. In contrast, the TOS region identified as being involved in semantic processing was located about a centimeter dorsally, covering the extreme dorsal edge of LO and extending into the angular gyrus. The anterior/dorsal locations of this TOS region may reflect an abstraction of information away from original sensory features that is consistent with semantic representation (Thompson-Schill 2003). Of note, all person and place-selective regions were either located within the putative “semantic system” proposed by Binder et al. (2009, i.e., the precuneus and RSC) or in regions abutting this system (the anterior/superior PPA TOS).

The left ATL showed some evidence of entity-specific representations when famous people and places were compared with nonunique basic-level animals and inanimate objects in Experiment 2. However, in Experiment 1 there was no increase in the activation of this region when participants retrieved entity-specific information compared with the General-Categorization of famous people or places. This could be because ATL is involved in the differentiation between individual entities (Rogers et al. 2006), and this function is performed automatically in both tasks.

Collectively, these brain regions—the mPrec for people, the RSC as well as sections of the TOS and PPA for places—showed both a category-selective increase and supramodal response during Entity-Specific semantic retrieval. While this response profile is highly consistent with semantic processes, the exact nature of the contribution of these areas to semantic retrieval/representation remains unknown. It is unlikely that the reliable activation of these brain regions during Entity-Specific semantic retrieval is epiphenomenal. Parsimony and neural economy would suggest that the consistent activation of a brain region during a cognitive operation must contribute at some level to that operation. Brain regions contributing to semantic processing may reflect the symbolic or abstract representations themselves or they may reflect conceptual
processes that enrich and provide relational context to abstract semantic concepts such as nationality (Mahon and Caramazza 2008). It is appealing to speculate that the latter possibility may be the case for the PPA and TOS. Medially, paired Entity-Specific semantic structures exist for both people and places (the mPrec and RSC) while the anterior PPA and TOS have no person-selective equivalents. Arguably, this may reflect a stronger association between places and visual features that are more likely to be recruited during the retrieval of Entity-Specific semantic details about places. However, 2 facts argue against this possibility. First, Entity-Specific retrieval led to place-selective increases in the anterior PPA and TOS when full visual information was available during Experiment 1. Second, the anterior shift does not match the pattern reported for the top-down activation of place-related visual associations during imagery (where classical “perceptual” PPA is activated; O’Craven and Kanwisher 2000).

Our results indicate that the neural responses occurring during retrieval of entity-specific semantic information are organized by object-category. However, this does not necessarily imply that semantic information about individual entities and semantic information about nonunique entities (e.g., basic-level categories) is represented in different brain regions. In fact, the study contrasted the process of retrieving specific semantic information about individual entities and the process of performing superordinate categorization of individual entities. It did not directly compare the execution of the same kind of process for individual entities and basic-level entities within the same superordinate category. Therefore, the present results are compatible with accounts of semantic knowledge in which categories emerge from generalization across exemplars (e.g., Rogers et al. 2006).

The findings of this study show that a set of brain regions are selectively involved in the process of retrieving specific semantic information about individual entities, as opposed to the process of categorizing individual entities as members of a superordinate category. This entity-specific activation might reflect increased demands when participants have to access semantic information as a function of the identity of the specific entities that are being processed, when compared with a more automatic process of categorization that does not need to interrogate semantic knowledge in different ways as a function of the identity of the different entities.

In short, in this study, we asked whether person and place object-categories influence the cortical organization of entity-specific semantic knowledge that is arbitrarily related to physical/perceptual properties. We used 2 criteria to identify semantic processing: category-selective increases during Entity-Specific semantic retrieval and independence from perceptual input. Convergent results from 2 groups of subjects showed that object-category does influence the neural representation of entity-specific semantic knowledge. The regions showing the maximal category-selective semantic responses were not the same as those showing maximal category-selectivity during perception, although their anatomical locus appears to be influenced by the classical perceptual response.

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