

# **Distinct and common cortical activations for multimodal semantic categories**

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**Abstract**

**If semantic representations are based on particular types of perceptual features, then category knowledge that arises from multimodal sensory experiences should rely on distinct and common sensory brain regions depending on the features involved. Using a similarity-based generation and comparison task, we show that semantic categories activate cortical areas associated with taste and smell, biological motion, and visual processing. Fruit names specifically activated medial orbitofrontal regions associated with taste and smell. Labels for body parts and clothing activated lateral temporal occipitoparietal areas associated with perceiving the human body. More generally, visually-biased categories activated ventral temporal regions typically ascribed to visual object recognition whereas functional categories activated lateral frontotemporal areas previously associated with the representation of usage properties. These results indicate that semantic categories that are distinguished by particular perceptual properties rely on distinct cortical regions whereas categories that rely on similar types of features depend on common brain areas.**

Concepts are considered to be the building blocks of human higher-order cognition (Margolis & Laurence, 1999). Yet theories differ according to how these symbolic representations are instantiated within the brain. The amodal characteristics of word meaning (Landauer & Dumais, 1997) imply that knowledge is stored independent of perceptual experiences. However, mounting evidence suggests that concepts depend upon cortical regions typically ascribed to sensory input (Martin & Chao, 2001). This embodiment of semantic representations through perceptual mechanisms can explain how word meanings necessarily draw upon sensory experiences of the referenced objects (Barsalou, 1999). Yet theories of semantic knowledge differ according to the level at which object categories are said to rely on particular brain regions. These differences concern how semantic information is organized, either by the sensory features of items (Martin & Chao, 2001), innate domain-based mechanisms (Caramazza & Shelton, 1998), or based on a uniform distribution (Forde & Humphreys, 2002; Tyler & Moss, 2001). The resolution of this debate is critical to solving how conceptual understanding is acquired, maintained, and even hindered, by the supporting neural circuitry.

The neuropsychological literature is filled with case studies of individual who demonstrate a selective loss of semantic memory (for recent reviews, see Saffran & Schwartz, 1994; Caramazza, 1998; Capitani et al., 2003) even though such cases are relatively rare (Coltheart, 2001). A distinction between natural kinds and artifacts has been the most frequently reported among patients with semantic memory impairments (Mummery, Patterson, Hodges, & Price, 1998). Damage localized to inferomedial temporal cortex, usually resulting from encephalitis of the herpes simplex virus, has

been associated with impaired performance for natural kinds (e.g., animals, fruits, and vegetables) relative to a sparing of artifact (e.g., tools, household objects, vehicles) knowledge (Gainotti & Silveri, 1996; Hart & Gordon, 1992). The reverse pattern of category-specific deficits (i.e., artifacts impaired relative to a preservation of natural kind knowledge) usually from damage to frontoparietal areas, has also been found (Warrington & McCarthy, 1987; Hills & Caramazza, 1991; Sacchett & Humphreys, 1992) though significantly less often than selective impairments for natural kinds (Capitani et al., 2003). In sum, this double dissociation has led to the inference that semantic knowledge is organized on some level by category-specific information.

In the face of these category-specific deficits, and more diffuse semantic disturbances when stimulus factors are rigorously controlled, a number of proposals have been advanced to explain the natural kind / artifact dissociation found among patients. The most widely accepted view assumes that there are substantial differences in the saliency of semantic features for particular categories (Mummery et al., 1998) and that the neural instantiation of these features is thought to be biased to higher-order cortical areas mostly responsible for encoding them (e.g., visual features in extrastriate regions). The assumption is that natural kinds are distinguished from each other primarily through their visual or perceptual properties whereas artifacts are differentiated more by functional features. These category-specific deficits therefore suggest that semantic representations rely on dissociable sensory brain regions depending on the constituent features involved (Warrington & Shallice, 1984). Patients with such deficits show a disproportionate impairment for recognizing items within some object categories while other

categories are preserved (Capitani et al., 2003). These case studies suggest that natural kind categories, such as animals and fruits, tend to rely on visual areas in the temporal cortex (Gainotti & Silveri, 1996) to distinguish near associates in conceptual space. In contrast, categories of manipulable objects, for example tools and body parts, are thought to preferentially rely on function-biased areas in the lateral temporal and frontal cortex (Sacchett & Humphreys, 1992). These results suggest that category-specific deficits arise from how different types of features, and the categories that tend to rely on them, are localized to distinct brain regions, even as controversy surrounding this interpretation remains (Martin & Caramazza, 2003; Caramazza & Mahon, 2003).

Recent neuroimaging studies provide converging support for the view that the features of items, and not categories per se, are represented by disparate brain regions. Martin and colleagues (for a recent review see Martin & Chao, 2001) have shown across a number of studies that visual properties, and the semantic categories that preferentially rely on them (e.g., animals), tend to activate visual object recognition areas in the ventral temporal cortex. In contrast, action properties associated with manipulating an object tend to activate premotor and lateral temporal brain regions, providing converging support for the locations of category-specific properties of artifact categories (e.g., tools). These results argue for a distribution of object knowledge based on how cortical regions involved in encoding sensory features are used to discriminate among similar members of the same semantic category and to separate superordinate categories based on the collection of associated sensory experiences. For example, tigers are distinguished from leopards by the

presence or absence of the visual features of stripes or spots. In contrast, artifacts are distinguished more by their functional attributes. That is, the same object may be called a jar, a vase, or a glass based on how it is used. Different types of properties, and the cortical regions supporting them, may therefore distinguish one semantic category from another whereas semantic categories that rely on similar types of properties are likely to depend on common brain regions. For instance, Mummery and colleagues (Mummery, Patterson, Hodges, & Wise, 1996) found greater activation bilaterally in the anteromedial temporal lobe for the natural kind categories whereas the manipulable objects elicited posterior inferolateral temporal cortex, generally supporting the dissociation of these broad classes found in the lesion literature. Furthermore, activation differences between animals and artifacts have been replicated (Perani et al., 1995; Martin et al., 1996) with left occipitotemporal regions in the ventral visual stream more active for animals and left prefrontal and premotor regions more active for tools, supporting the specific locations predicted by the case studies.

These neuropsychological and neuroimaging findings may be interpreted more broadly in support of perceptual symbol theories, which presuppose that sensory experiences of objects support symbolic representations of them. Barsalou (1999) suggests that linguistic representations have their basis in perceptual mechanisms in which the recollection of object properties involves perceptual simulations of the objects themselves. For instance, subjects are faster to respond to properties that are perceptually, but not conceptually, similar to those verified previously (Solomon & Barsalou, 2001) and to pictures that match a described orientation of an item (Stanfield & Zwaan,

2001). The cortical organization of semantic knowledge may therefore be determined by the topography of perceptual representations (Simmons & Barsalou, 2003).

We examine the hypothesis that semantic representations for object categories are represented in multiple cortical areas based on the role of specialized sensory mechanisms in encoding perceptual experiences with the associated objects. If the constituent perceptual features of items can predict how semantic knowledge is instantiated with the cortex, semantic categories should dissociate when the perceptual properties differ, while common brain regions should support superordinate categories that tend to rely on common types of features to distinguish items within the category. Based on the central role of feature similarity in behavioral research (see for example Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976), we required participants to produce items and choose between alternatives based on the judged similarity among individual word referents. Participants were asked to covertly generate the most similar item they could think of in relation to a target item (e.g., What is the most similar item to ‘peach’?) and were then asked to choose, from among two alternatives (e.g., ‘nectarine’ or ‘pear’), the item most similar to the one they generated. We intentionally included items with very similar but often low lexical familiarity (e.g., ‘kiwi’) to induce careful evaluation of each item and its related properties. This manipulation therefore required between item comparisons rather than an explicit evaluation of the superordinate category or matching based on specific features, both of which are likely to evoke more analytic processing instead of the intended commonalities and differences between items and their associated classes. With this design, we

therefore expected multimodal category differences, and the brain regions underlying them, to emerge from participants' implicit knowledge of object similarity.

To investigate the cortical representation of object categories, we scanned participants using functional magnetic resonance imaging (fMRI) while participants generated and compared items from the judged similarity to a target. In a blocked design, items were drawn from superordinate categories that differed according to their predicted constituent features. Category contrasts were expected to show unique regions of activation if the constituent feature types differed, whereas contrasts were expected to demonstrate common areas of activation if categories relied on similar feature types. We hypothesized that these categorical similarities and differences would reflect the sensory processing associated with some object classes but not others. For instance categories assumed to preferentially depend on visual properties were expected to activate common regions of the extrastriate cortex, as indicated in by deficits for natural kinds with ventral temporal damage (Warrington & Shallice, 1984; Gainotti & Silveri, 1996) and the selective activation of ventral temporal regions when properties of object form knowledge are considered (Martin & Chao, 2001). Judgements of body parts, but not the other tested categories, were expected to specifically activate distinct cortical regions associated with perception of the human form similarly supported by evidence from lesion (Warrington & McCarthy, 1987; Sacchett & Humphreys, 1992) and neuroimaging studies (Downing et al., 2001; Beauchamp et al., 2002). By contrast, comparisons among fruit names were expected to elicit activation in

regions specifically involved in sensory processing for these items but not for any of the other categories.

## **Materials and Methods**

### ***Participants***

Sixteen right-handed, native English speakers were recruited from the University of Pittsburgh community (mean age = 23; standard deviation = 1.61). Three participants were removed from this sample due to excessive head motion ( $> 3$  mm) during the scanning session. Therefore, a total of 13 participants were included in data analyses. The protocol for this study was approved by the IRB at the University of Pittsburgh and informed consent was obtained from all participants.

### ***Stimuli and Design***

Word stimuli were drawn from one of four semantic categories: birds, fruit, body parts, and clothing based on the presumed role of multimodal features sets in each. All presented word items across the tested semantic categories were matched for letter length, number of syllables, and lexical familiarity. Lexical familiarity was derived from response times and accuracy data for each item when presented in a lexical decision experiment to a separate set of participants drawn from the same population as the neuroimaging sample. This effort aims to determine a direct empirical measure for how well word forms are known, in contrast to text-driven

frequency estimates (Francis & Kucera, 1982) which are susceptible to corpora selection bias and inconsistencies between how words are used in speech and in print. We have transformed the lexical decision data of about 90 subjects for over 600 words into a standardized z-space based on mean and variance measures for response time and accuracy for each item across the sample (Goldberg, in prep). This index therefore reflects the ease with which participants ascribe lexical status (e.g., ‘algae’ = -1.15 whereas ‘apple’ = +1.05) with the most positive scores representing items that are responded to on average very quickly and very accurately in the lexical decision task.

This study developed a similarity-based paradigm that required participants to generate and compare word items based on their shared relations. Each six-second trial (see Fig. 1) began with a the presentation of a fixation cross for 500 ms and consisted of the presentation of a target item for 2 seconds, followed by a two-second period for participants to generate the “most similar item they could think of” in relation to the target. A forced choice was then presented for 1.5 seconds in which participants were instructed to choose the item most similar to the one they had generated. Four trials within each category were presented consecutively in a blocked design with each category block randomly presented six times across the experiment. Thirty items were presented within each category across twenty-four trials. No item was presented as a target more than once and no forced choice pair was repeated.

Participants were not informed of the categorical grouping of items but rather were told only to consider the overall similarity between items. We expected that this manipulation would drive activation associated with the

relations between items instead of more passive decisions. This design allowed for the examination of regional activations specific to, and shared between, the tested categories without an explicit instruction to consider the superordinate class. The categories were chosen to maximize between category effects and to test differences between those that tend to rely on visual information (i.e., birds and fruits) versus those that are said to rely on functional differences (i.e., body parts and clothing), as indicated in prior case studies with patients (for a thorough review see Capitani et al., 2003). Therefore, this similarity-based generate and compare paradigm allowed us to analyse the distinct and common cortical regions associated with increased activation across the set of tested categories.

Prior to the scanning session, participants were trained on the paradigm using stimuli (e.g., insects) that were not presented in the neuroimaging session. This training aimed to familiarize participants with the task and to monitor and reinforce the goal of producing responses based on the overall similarity of items. Upon the presentation of the target stimulus, participants were asked to overtly generate, in contrast to covert generation during the experiment, the “most similar item they could think of” (e.g., tick → [gnat]) so that feedback could be given if generated items were not “similar to what the item represents”. Subjects were encouraged to generate more similar items when their overt responses were either too general (e.g., bug) or when items were associated with but not similar to the target (e.g., dog). Participants were encouraged to continue generating items until they found what they thought was the ‘best’ item or until the forced choice pair appeared. When the forced choice was presented (e.g., flea or ant), subjects were asked to choose the item

most similar to the one that they had generated. Participants were not instructed to consider the superordinate category to which the items belong or to use an imagery strategy. Rather their responses were expected to correspond only to judgements of inter-item similarity relations.

In visuo-motor control trials, participants were presented with a target stimulus consisting of a string of uniform symbolic characters (e.g., #####). During the generation phase they were asked to name the symbols, overtly during the training session and covertly during scanning. At the choice point, participants were asked to simply indicate the visual stimulus that they had named (e.g., ##### or +++++).

### ***Data Acquisition***

Anatomical and functional images were collected on a full body Signa 3 Tesla scanner (General Electric, Milwaukee, WI). The scanning session began with the acquisition of structural images including scout, high-resolution SPGR volume (256 x 256 matrix, 124 1.2mm sagittal slices), and T1 weighted (128 x 128 matrix, 30 3.0mm transverse slices with no gap) sequences. T2\* weighted functional images (TR = 3000, TE = 30, 64 x 64 matrix, 30 3.0 mm transverse slices with no gap), aligned to the inferior aspect of the temporal lobes, were collected while participants performed the task. Stimuli were presented and responses were collected using the E-Prime software package (Psychology Software Tools, Inc.)

### ***Data Analysis***

Behavioral response times to the forced choice decisions were analyzed using paired sampled t-tests among the semantic categories and between the semantic and control blocks. Neuroimaging data was preprocessed and analyzed using the BrainVoyager 2000 (BrainInnovation, Inc.) software. Preprocessing steps included: 6-parameter, 3D motion-correction, slice-scan time correction using linear interpolation, voxel-wise linear detrending, and spatial smoothing with an 8mm FWHM Gaussian kernel. Spatial normalization was performed using the standard 9-parameter Talairach landmark method (Talairach & Tournoux, 1988). For analyses, a general linear model was defined for each subject that included five regressors which modelled the BOLD response to the each semantic condition and the visuo-motor control. Each regressor was convolved with a standard gamma model (Boynton, Engel, Glover, & Heeger, 1996) of the hemodynamic impulse-response function. Following multiple regression from the general linear estimates of the conditions, first and second order random effect analyses were conducted in line with our a priori predictions. To isolate candidate regions-of-interest in the first order analysis, weighted ANOVA contrasts were conducted for each category relative to the other semantic categories ( $p < .01$ , uncorrected). For example, to localize regions preferentially active for body parts, this category was contrasted against the other three semantic object classes (i.e., Birds, Clothing, and Fruits). Increased activation for the specific category was assessed relative to the control condition in paired sample t-tests. Candidate semantic regions in which the category-of-interest did not significantly differ ( $p < .05$ ) from the control condition were excluded from

further analysis. Second-order orthogonal contrasts between these remaining categories were conducted to examine the category-specificity of average block activity in each of these candidate semantic regions. Any significant difference ( $p < .05$ , Bonferroni correction) in direct contrasts among the remaining semantic categories (e.g., among Birds, Clothing, Fruits) rejected the null hypothesis that only the category-of-interest (e.g., Body Parts) should show increased activation and were instead classified as category-selective areas (i.e. two or more categories showed significant increased activation). That is, regions in which this null hypothesis could be rejected are reported as category-specific areas (see Table 1). By contrast, areas in which this null hypothesis could not be rejected are reported as category-selective areas and correspond to the a priori predictions regarding cortical difference between visual and functional categories (see Table 2).

While the  $P$  values of the first order statistical parametric maps were not corrected for multiple voxel-wise comparisons, there are at least two reasons for why this threshold is warranted. First, the random effects analysis takes into account both the within- and between-subject variance allowing the results to be generalized to the population from which the sample was drawn and making the results robust statistically. In addition, the second order analyses were also based on variance within- and between-subjects from the summary condition data of each candidate semantic region. Areas not passing these second order random effects tests, with the statistical threshold Bonferroni corrected for multiple between category comparisons, are not reported, further lessening the chances of Type I errors.

## Results

The behavioral results indicated no significant differences in response times for the forced choice decisions between the visual (Mean = 883.10 ms, SE = 28.71 ms) and functional (Mean = 887.87 ms, SE = 20.46 ms) categories or between the individual categories (Birds: Mean = 874.31 ms, SE = 31.88 ms; Body parts: 910.94 ms, SE: 24.93 ms; Clothing: Mean = 864.80 ms, SE = 15.99 ms; Fruits: Mean = 891.88 ms, SE = 25.54 ms). Any observed differences therefore in the neuroimaging data between semantic categories is likely indicative of how this knowledge relies on specialized brain regions, rather than through domain-general mechanisms. Forced choice response took significantly longer ( $t(12) = 8.86, p < .001$ ), by about 300 milliseconds, for the semantic categories (Mean = 885.48 ms, SE = 24.58 ms) than for the visuo-motor control (Mean = 588.09 ms, SE = 29.09 ms).

The neuroimaging results indicate that cortical regions known to support the sensory encoding of object properties were specifically activated when participants considered similarities between word items. In particular, category-specific analyses identified cortical regions that were active for only one of the four tested categories, likely based on the role of these regions in supporting the sensory properties involved in perceptual experiences with the associated objects. Trials containing fruit items were specifically associated with increased activation in bilateral regions of the medial orbitofrontal cortex (Fig. 2A) in contrast to baseline activity for the other three categories and the control condition (Fig. 2B). Recent neuroimaging work suggests that these orbitofrontal areas are involved in representing distinct tastes (O' Doherty,

Rolls, Francis, McGlone, & Bowtell, 2001) and odors (Karenken et al., 2004), as well as the convergence of gustatory and olfactory information (de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003).

Trials that required similarity judgments between body part labels specifically activated the left lateral temporal occipitoparietal cortex (Fig. 2C, Table 1), in contrast to the other three categories (Fig. 2D). This region is also activated when images of the human body are viewed (Beauchamp, Lee, Haxby, & Martin, 2002). A specific aspect in this general region, the extrastriate body area (EBA), is consistently found in individual subjects, leading some investigators to suggest that this region is innately specified to perceptually process parts of the body (Downing, Jiang, Shuman, & Kanwisher, 2001). The prefrontal region, as especially close to premotor cortex, may be specifically involved in the retrieval of action knowledge (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995) associated with body parts. This set of regions specifically active for body parts showed robust activation and appear to be a part of a network of cortical regions involved in the perception of human actions and biological motion (Decety & Grezes, 1999; Grossman & Blake, 2002).

Direct contrasts between the visual and functional categories indicates how semantic knowledge that is likely to rely on similar properties, as initially suggested by Warrington and McCarthy (1983), activates common brain regions. The seminal distinction between these categories was replicated with the ventral temporal cortex associated with increased activity for the visual categories and lateral occipitotemporal and frontal cortical regions exhibiting

increased activity for the functional categories. That is, semantic categories that tend to preferentially rely on visual properties (i.e., fruits and birds) selectively activated a region in the parahippocampal gyrus of the left temporal lobe (Figure 3A, Table 2) whereas the functional categories were not associated with increased activity in this region (Figure 3B). This region of the ventral temporal cortex has been extensively associated with the visual properties of semantic knowledge through case studies (e.g., Warrington & Shallice, 1984) and neuroimaging work (e.g., Martin et al., 1995), as well as more generally in visual object recognition (Haxby et al., 2001). In particular, similarity judgements made on the basis of object color, specifically involving natural kinds (Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999), are associated with increased activity in ventral temporal cortex (Mummery, Patterson, Hodges, & Price, 1998). Martin and colleagues (1995) found that object colors activated the ventral temporal cortex but that the generation of object actions activated regions in the middle temporal cortex and the prefrontal cortex.

Categories that tend to rely on functional properties (i.e., body parts and clothing) activated a set of regions in the left lateral temporal and prefrontal cortex. These effects appear to be driven by the network of regions specifically sensitive to body parts. However, an area just anterior to the extrastriate body area in the lateral temporal cortex (Figure 3C) also showed preferential activation for clothing stimuli in contrast to the visual categories (Figure 3D). This result suggests that semantic knowledge for articles of clothing depends on areas associated with the perception and manipulation of body parts. These results are consistent with a recent meta-analysis of 24

studies by Grezes and Decety (2001) that identified a network of cortical regions, including the observed prefrontal and lateral temporal areas, active not only for action knowledge retrieval but also action execution, observation, simulation and verb generation. Indeed, the relationship between clothing and body parts appears much more pragmatic than simply getting dressed in the morning. Articles of clothing take their shape from the parts of the body on which they are worn, and so knowledge of this semantic category appears to depend on regions specialized to process the human form.

### **Discussion.**

The present results suggest that semantic decisions rely on multiple cortical areas based on the roles of those regions in encoding perceptual and functional properties of objects. Multimodal semantic categories appear to activate multiple specialized regions based on the role of sensory brain regions in representing the perceptual properties of the referenced objects. Semantic categories that are likely to depend on unique types of object properties, such as flavor and biological motion, activate distinct cortical regions. In contrast, categories that rely on similar types of features, including visual or functional attributes, are associated with increased activation in common brain regions. These results suggest that similarity-based comparisons of word meanings evoke categorical distinctions in the patterns of cortical activation.

Category-specific sensory regions were found for fruits and body parts, likely based on based on the roles of perceptual properties in distinguishing

these semantic categories. In contrast, categories more likely to rely on either on visual or functional properties were associated with selectively increased activity in regions implicated in representing these different types of object features from patient and previous neuroimaging studies. In this regard, sensory mechanisms used to encode experiences with the given items also seem to represent the meaning of words and the superordinate categories to which they belong. In this regard, semantic representations appear to depend on cortical activation patterns based on the constituent features involved. Categories that rely on separable types of features are likely to dissociate based on the cortical regions involved. In contrast, categories that are similar in their reliance on one feature dimension are likely to depend on common cortical areas.

Orbitofrontal areas associated with the reward values for taste and smell (Rolls, 2000) and their integration (Small et al., 2004) were specifically activated by fruit stimuli. This region appears to support semantic decisions that require the flavor and reward properties of objects, even when photographs are presented (Simmons, Martin, & Barsalou, 2005). None of the other tested categories activated this region but importantly none could generally be considered to be edible. Since the activation of this region was likely driven by properties of taste and smell, other food items should similarly rely on this region. Indeed, we have recently found that this orbitofrontal region is specifically activated by the verification of a taste property in contrast to other modalities (Goldberg, Perfetti, Schneider, under review). A design more sensitive to individual trials could perhaps isolate activity in this region by categories generally lacking in such attributes (e.g.,

birds) but that contain specific instances with taste and smell properties (e.g., chicken and turkey).

Labels for body parts activated a set of regions in the left lateral temporal occipitoparietal and prefrontal cortex that have previously been implicated in recognizing parts of the human body (Downing et al., 2001), in perceiving biological motion (Grezes et al., 2001), and in accessing knowledge of actions (Tranel et al., 2001; 2003). These areas may be selectively involved in the representation of functional properties more necessary for some semantic categories but not others. In particular, a lateral temporal region most active for comparisons between body parts also showed increased activation to articles of clothing but not to more visually-biased categories. In contrast, similarity-based comparisons within visual categories produced increased activity in the ventral temporal cortex irrespective of the particular visual category. This dissociation between visually and functionally biased categories replicates effects apparent in patients with focal brain damage and in neuroimaging studies with unimpaired individuals (Martin & Chao, 2001). In this regard, common brain regions appear to support object knowledge across semantic categories when decisions rely on similar types of properties.

Table 3 shows the pattern of activation associated with each of the tested categories. Some categories (i.e., birds and clothing) were associated with a single area of significant activation while the other categories (i.e., fruits, body parts) were associated with multiple areas of increased activation. The cortical activation patterns provide a unique discrimination of each of the

four categories. This result suggests that in accessing semantic knowledge it might be possible to make a rapid response based on the overall set of areas activated. For example, non-overlapping regions may be selectively used to discriminate items that share many features in one perceptual modality but differ significantly in others, such as when determining whether a ‘ball’ is a fruit. Such semantic judgements that involve multimodal categories with distinct and common regions (e.g., fruits) the comparison could be tuned to operate in an area that is not typically shared with other items. In contrast, comparisons made between categories that rely on the very similar types of features (e.g., fruit and vegetables), and likely common cortical areas, may lead to increased activation in each region in order to discriminate near neighbors (e.g., apple and tomato) in the semantic space.

These results suggest that other sensory brain regions should be activated when object knowledge is considered. Indeed, evidence is emerging which indicates that sound judgments elicit selective activity in auditory association areas of the superior temporal cortex (James & Gauthier, 2003; Kellenbach, Brett, & Patterson, 2001). In addition, action words based on specific motor movements (e.g., *lick* and *kick*) activate areas directly adjacent to or overlapping with regions in the primary motor cortex associated with the actual body part movements (Hauk, Johnsrude, & Pulvermueller, 2004). These findings indicate that semantic representations, and the specific categories that rely upon them, activate multiple sensory brain regions that encode visual, gustatory and olfactory, auditory, and motor experiences. Similarly, we (Goldberg, Perfetti, Schneider, under review) have found that the somatosensory cortex in the postcentral gyrus supports tactile judgments in

addition primary and pre-motor regions. Specific categories may preferentially rely on each on these modality-based representations based on the diverse experiences one has with the indicated objects. For instance, object categories not tested (e.g., musical instruments) are likely to specifically rely on a specific, and predictable, subset of perceptual properties and therefore to selectively drive the associated regions of sensory cortex.

One potential difficulty with the present results is in the limited number of categories that were examined. However, the generation and comparison paradigm is likely to yield robust patterns of activation for other categories that rely on similar conjunctions of properties. Distinguishing between similar categories may specifically involve not only magnitude differences in distinct regions but also voxel-wise patterns of correlated activity in the common areas, as suggested from visual object recognition (Haxby et al., 2001). Therefore the differences between similar categories (e.g., fruit and vegetables), and perhaps even specific items (e.g., peach from nectarine), may arise from variation in activity within the indicated sensory cortical regions.

While semantic categories seem to rely on sensory cortical regions, it is not clear how these disparate modality-specific representations link together to give rise to the intuition of a holistic concept in memory. One possibility for such an integration of disparate elements of categorical knowledge may arise from multimodal convergence zones (Damasio, 1989; Damasio et al., 2004) or from how similar representations depend on a common cortical topography (Simmons & Barasalou, 2003). Alternatively, sensory brain regions may be

automatically activated whenever an object or its symbolic representation is presented (Martin et al., 1995). The representation of some objects may depend on the activation of related features (e.g., apple + green = sour; apple + red = sweet) and perhaps mediated by higher-order areas (e.g., convergence zones) or by direct connections between sensory pathways. More passive tasks, such as simply identifying an item as a member of a given category, may not necessarily activate all of the modality-specific properties involved in representing the category. For instance, identifying a peach as a fruit or naming a picture of the object could involve simply accessing prototypical visual properties that distinguish common fruits from other natural kinds. In a more demanding task, such as the similarity generation and comparison that we required, participants were expected to necessarily go beyond visual similarities to generate and select the ‘best’ item while implicitly considering the other sensory properties associated with the items. In this way, by comparing cortical activation patterns across task contexts, it may be possible to determine whether certain properties are accessed initially with supplementary sensory features used as necessary to resolve a given semantic decision and at which stage higher-order representations, such as those theorized in convergence regions (Damasio, 1989; Damasio et al., 2004), become necessary to mediate conceptual comparisons.

In conclusion, the present results reveal a reliance on sensory brain regions when participants consider the similarities between object names. Semantic categories that rely on different types of perceptual properties activated distinct brain regions while classes that depend on common sets of features activated common brain regions. These results support and extend

feature-based views on the organization and wide distribution of semantic knowledge. By activating cortical regions associated with taste and smell, visual processing, and biological motion, these findings indicate that object knowledge generally relies on multiple cortical regions associated with object perception, specifically when word items are used. The cortical distribution of multimodal semantic categories appears to reflect the feature differences and similarities apparent in the perceptual experiences with the associated objects.

**References**

- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4), 577-660.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, 34(1), 149-159.
- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, 16(13), 4207-4221.
- Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, 20, 213-261.
- Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences*, 7(8), 354-361.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience*, 10(1), 1-34.
- Damasio, A.R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, 33, 25-62.

- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179-229.
- de Araujo, I. E. T., Rolls, E., Kringelbach, M. L., McGlone, F., & Phillips, N. (2003). Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain. *European Journal of Neuroscience*, *18*, 2059-2068.
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences*, *3*, 172-178.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470-2473.
- Forde, E. M. E., & Humphreys, G. W. (2002). *Category specificity in brain and mind*. New York, NY: Psychology Press.
- Friston, K. J., Penny, W. D., & Glaser, D. E. (2005). Conjunction revisited. *NeuroImage*, *25*, 661-667.
- Gainotti, G., & Silveri, M. C. (1996). Cognitive and anatomical locus of lesion in a patient with a category-specific semantic impairment for living beings. *Cognitive Neuropsychology*, *13*(3), 357-389.
- Goldberg, R.F., Perfetti, C.A., Schneider, W. (under review). Representation of word meaning in sensory brain regions.

- Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping, 12*, 1-19.
- Grezes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *Neuroimage, 13*, 775-785.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron, 35*, 1167-1175.
- Hauk, O., Johnsrude, I., & Pulvermueller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*, 301-307.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science, 293*(5539), 2425-2430.
- James, T. W., & Gauthier, I. (2003). Auditory and action semantic features activate sensory-specific perceptual brain regions. *Current Biology, 13*, 1792-1796.
- Karenken, D. A., Sabri, M., Radnovich, A. J., Claus, E., Foresman, B., Hector, D., et al. (2004). Olfactory system activation from sniffing: Effects in piriform and orbitofrontal cortex. *NeuroImage, 22*, 456-465.
- Kellenbach, M. L., Brett, M., & Patterson, K. (2001). Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of

perceptual attribute knowledge. *Cognitive, Affective, & Behavioral Neuroscience*, 1(3), 207-221.

Landauer, T. K., & Dumais, S. T. (1997). A solution to plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review*, 104(2), 211-240.

Margolis, E., & Laurence, S. (1999). *Concepts: Core readings*. Cambridge, MA: MIT Press.

Martin, A., & Caramazza, A. (2003). Neuropsychological and neuroimaging perspectives on conceptual knowledge: An introduction. *Cognitive Neuropsychology*, 20, 195-212.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, 11(2), 194-201.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270(5233), 102-105.

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

Mummery, C. J., Patterson, K., Hodges, J. R., & Price, C. J. (1998). Functional neuroanatomy of the semantic system: Divisible by what? *Journal of Cognitive Neuroscience*, 10(6), 766-777.

Mummery, C. J., Patterson, K., Hodges, J. R., & Wise, R. J. (1996). Generating 'tiger' as an animal name or a word beginning with T:

differences in brain activation. *Proceedings of the Royal Society of London Series B: Biological sciences*, 263, 989-995.

O' Doherty, J., Rolls, E., Francis, S., McGlone, F., & Bowtell, R. (2001). The representation of pleasant and aversive taste in the human brain.

*Journal of Neurophysiology*, 85(3), 1315 -1321.

Perani, D., Cappa, S. F., Bettinardi, V., Bressi, S., Gorno Tempini, M., Matarrese, M., & Fazio, F. (1995). Different neural systems for the recognition of animals and man-made tools. *Neuroreport*, 6, 1637-1641.

Rolls, E. T. (2000). The orbitofrontal cortex and reward. *Cerebral Cortex*, 10, 284-294.

Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology*, 382-439.

Sacchett, C., & Humphreys, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwam: A category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, 9(1), 73-86.

Saffran, E. M. (2000). The organization of semantic memory: In support of a distributed model. *Brain & Language*, 71(1), 204-212.

Saffran, E. M., & Schwartz, M. F. (1994). Of cabbages and things: Semantic memory from a neuropsychological perspective--a tutorial review. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance xv*:

*Conscious and nonconscious information processing* (pp. 507-536).

Cambridge, MA: The MIT Press.

- Simmons, W. K., & Barsalou, L. W. (2003). The similarity-in-topography principle: Reconciling theories of conceptual deficits. *Cognitive Neuropsychology*, 20(3-6), 451-486.
- Simmons, W. K., Martin, A., & Barsalou, L. W. (2005). Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cerebral Cortex*.
- Small, D. M., Voss, J., Mak, Y. E., Simmons, K. B., Parrish, T., & Gitelman, D. (2004). Experience-dependent neural integration of taste and smell in the human brain. *Journal of Neurophysiology*, 92(3), 1892-1903.
- Solomon, K. O., & Barsalou, L. W. (2001). Representing properties locally. *Cognitive Psychology*, 43(2), 129-169.
- Stanfield, R. A., & Zwaan, R. A. (2001). The effect of implied orientation derived from verbal context on picture recognition. *Psychological Science*, 12(2), 153-156.
- Talairach, J., & Tournoux, P. (1988). *A co-planar stereotaxic atlas of the human brain*. New York, NY: Thieme Medical Publishers.
- Thompson-Schill, S. L., Aguirre, G. K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, 37(6), 671-676.
- Tranel, D., Adolphs, R., Damasio, H., & Damasio, A.R. (2001). A neural basis for the retrieval of words for actions. *Cognitive Neuropsychology*, 18, 655-670.

- Tranel, D., Kemmerer, D., Damasio, H., Adolphs, R., & Damasio, A.R. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, 20, 409-432.
- Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, 5(6), 244-252.
- Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, 106(Pt 4), 859-878.
- Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge. Further fractionations and an attempted integration. *Brain*, 110(Pt 5), 1273-1296.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107(Pt 3), 829-854.

**Author's Note**

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**Table 1. Areas showing category-specific activation.**

Category	Region	BA	Talairach Coordinates			Spatial Extent (3 mm <sup>3</sup> voxels)	t value
			x	y	z		
<b>Birds</b>	Left Ventral Temporal Cortex	19/36/37	-24	-40	-14	62	3.560
<b>Body Parts</b>	Right Inferior Frontal Gyrus	47	40	16	-4	214	3.589
	Left Temporal Occipitoparietal	22/37/39	-45	-60	15	1050	4.225
	Left Inferior Frontal Cortex	44/45	-41	15	11	379	3.707
	Left Middle Frontal Cortex	6/9	-36	7	33	8	3.306
<b>Fruits</b>	Right Orbitofrontal Cortex	11/12	22	36	-3	74	3.939
	Left Orbitofrontal Cortex	11/12	-19	41	-3	109	3.997
	Left Superior Frontal Gyrus	10	-19	52	17	72	3.515
	Left Fusiform Gyrus	37	-30	-50	-12	29	3.672
	Left Middle Frontal Gyrus	10/46	-40	39	17	39	3.381

**Table 2. Areas showing category-selective activation for visual or functional categories.**

Categories	Region	BA	Talairach Coordinates			Spatial Extent (3 mm <sup>3</sup> voxels)	t value
			x	y	z		
<b>Visual</b>	Right Lingual Gyrus	17	16	-86	-2	8	3.28
	Left Parahippocampal Gyrus	19/37	-25	-51	-13	29	3.36
<b>Functional</b>	Left Inferior Frontal Gyrus	44/45	-50	11	13	104	3.41
	Left Middle Temporal Gyrus	21/37	-51	-43	-3	18	3.62

**Table 3. Distinct and common activations for the tested categories**

Semantic Category	Distinct ROI's		Common ROI's	
	Orbitofrontal	Lateral Frontotemporal	Ventral Temporal	Lateral Temporal
Fruits	⊙		⊙	
Birds			⊙	
Body Parts		⊙		⊙
Clothing				⊙

## List of Figure Captions.

**Figure 1.** The paradigm was designed to elicit between item similarity comparisons. In each trial, participants were asked to covertly generate the most similar item they could think of in response to a target word. They were then asked to choose the item most similar to the one they generated from among two alternatives.

**Figure 2.** Category-specific regions implicated in mediating sensory processing. **(a)** Map of the  $t$  statistic ( $p < .01$ , uncorrected) for fruit items in bilateral orbitofrontal cortex. **(b)** Fruit specifically activate these regions in contrast to the other categories. **(c)** Map of the  $t$  statistic ( $p < .01$ , uncorrected) for regions specifically active for labels of body parts, including the left temporal occipitoparietal cortex (outlined). **(d)** Body parts specifically activate this region in contrast to the other categories.

**Figure 3.** The reliance of visual and functional categories on sensory brain regions. **(a)** Map of the  $t$  statistic ( $p < .01$ , uncorrected) for a visual semantic area in the left lingual gyrus. **(b)** This region is significantly activated for the visually-biased categories in contrast to the functionally-biased categories. **(c)** Map of the  $t$  statistic ( $p < .01$ , uncorrected) for a left lateral temporal regions showing greater activation for functional categories. **(d)** This region is responsive to Body Part names and Clothing items in contrast to the visually-biased categories.

**Figure 1.**

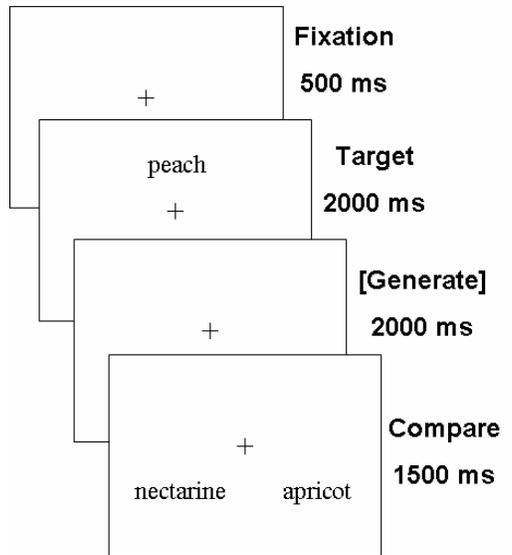


Figure 2.

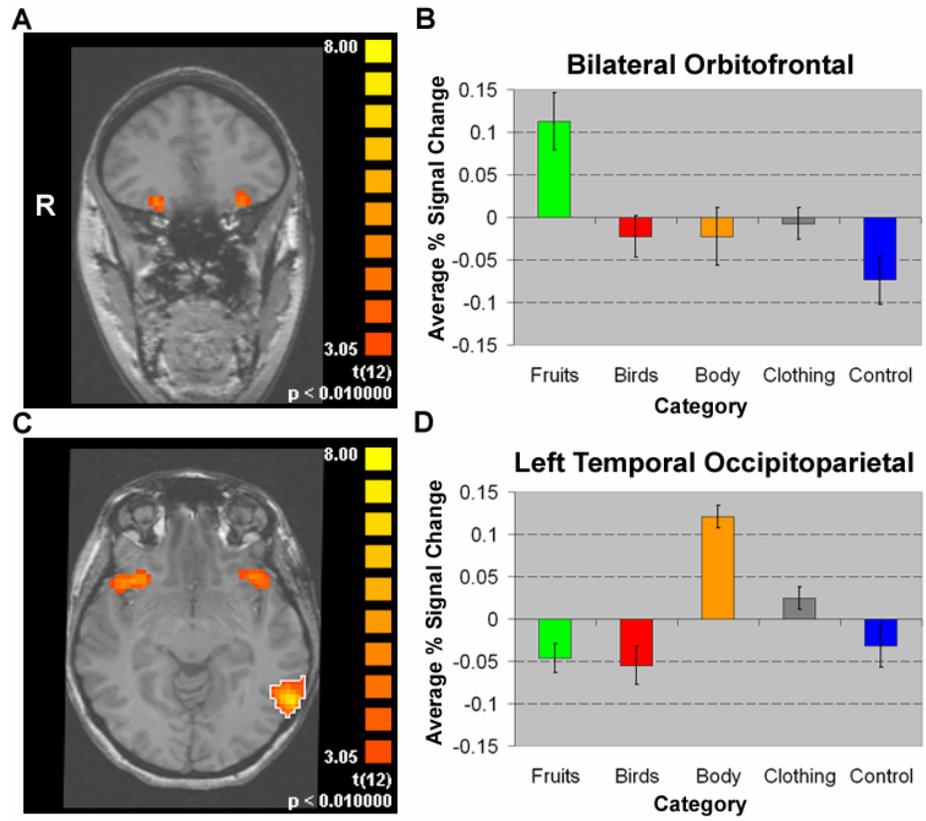


Figure 3.

