Object Activation from Features in the Semantic System

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Abstract

■ The human brain is thought to elicit an object representation via co-activation of neural regions that encode various object features. The cortical regions and mechanisms involved in this process have never been elucidated for the semantic system. We used functional magnetic resonance imaging (fMRI) to evaluate regions activated during a task designed to elicit object activation within the semantic system (e.g., presenting the words "desert" and "humps" with the task to determine if they combine to form an object, in this case a "camel"). There were signal changes in the thalamus for word pairs that activated an object, but not for pairs that (a) failed to activate an object, (b) were simply semantically associated, or (c) were members of the same category. These results suggest that the thalamus has a critical role in coordinating the cortical activity required for activating an object concept in the semantic system. ■

INTRODUCTION

Numerous models of semantic memory (Millikan, 1998; Schyns, Goldstone, & Thibaut, 1998; Lambert & Shanks, 1997; Estes, 1994; Hinton & Anderson, 1989; Fodor & Pylyshyn, 1988; Paivio, 1986; Collins & Loftus, 1975; Smith, Shoben, & Rips, 1974) have suggested the existence of specific subprocesses, including, but not limited to, making semantic choices from among multiple possibilities, feature-object correlation, noun-verb association, and adjective-noun association (Ricci et al., 1999; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Demb et al., 1995; Kapur et al., 1994; Saffran & Schwartz, 1994; Demonet et al., 1992; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Petersen, Fox, Snyder, & Raichle, 1990; Posner, Petersen, Fox, & Raichle, 1988; Shallice, 1988; Saffran, 1982). One other related process that has been investigated via a variety of tasks is semantic association. In a typical semantic association paradigm, two items are presented with the general instructions/question of, "Are these two stimuli related/ associated with each other?" The terms "related" or "associated" do not typically require a formal definition or instruction to the subject; their meaning or intent is conveyed by an example. ("For instance, salt and pepper are related.")

Within one theoretical framework, semantic associations have been shown to be behaviorally and anatomically dissociable into two major subtypes: (1) compositional associations (two items are associated but retain their individuality in the relationship—salt

and pepper), and (2) noncompositional associations (the two items become fused semantically—"computer" and "virus" forming "computer virus") (Kounios, Smith, Yang, Bachman, & D'Esposito, 2001; Fodor & Pylyshyn, 1988). Of interest, in the compositional associations, the two related items remain distinct both lexically and semantically, while in the noncompositional associations, the two stimuli fuse to form a third novel stimulus (as in the "computer virus" example) at the semantic, but not at the lexical, level. This concept of semantic fusion, where two entities combine to form a new representation, can be applied to other semantic relationships. One such application has been the proposal that features that are common to an object could "fuse" to activate a previously stored semantic object representation (Gray, 1999; Eichenbaum & Bunsey, 1995; Singer & Gray, 1995; Damasio, 1989, 1990; Warrington & Mc-Carthy, 1987; Allport, 1985). While this semantic fusion process has been proposed in theoretical form, a paradigm addressing it during object activation in semantic memory has not been formally developed.

To address the question of object activation within this framework, we have designed an analog of the semantic fusion task (a noncompositional association) where the stimuli are two features that are common to the target object. The particular features were chosen such that, in combination, they are both sufficient and specific to elicit the target object in semantic memory. The task instructions are to push a button if the two features (e.g., "desert" and "humps") combine to make you think of an object (e.g., "camel"). These task instructions are in contrast, yet analogous to, those of other semantic association tasks ("Are these items re-

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lated?"), since the feature stimuli may not be directly related/associated with each other on their own (e.g., "desert" and "dry" being typically associated as opposed to "desert" and "humps"). The other notable difference is that the two feature stimuli do fuse to activate/recall a third identity that differs from the input stimuli at both a semantic and lexical level.

The cognitive operations purportedly engaged by this object activation task are similar to those described in detail for standard semantic association (Kounios et al., 2001; Smith et al., 1974) until the semantic search stage. In a typical semantic association task, the search between related stimulus items likely ends when the subject determines that relevant conjunction criteria for association between the two items' semantic fields has been met (Smith et al., 1974). In contrast, the object activation task differs in that the semantic search likely can proceed via two routes: (1) the semantic fields of potential target objects are searched until both stimulus features are detected in a single object's field(s), thus ending the search and activating that object; and/or (2) the two features, by their saliency to a specific object, the frequency of their co-occurrence, or idiosyncratic nature of the feature combination, focus the search to a specific target object's semantic field(s), followed by feature detection and object activation as in (1). In either case, the end-result for the feature pairs that fuse is object activation.

The objective of this study is to assess the neural substrates of the object activation process within semantic memory, acknowledging that activation of an object in semantics can likely proceed along multiple pathways. Damasio (1989, 1990) proposed that the object activation from feature process exists in semantic memory and concluded that this is mediated by convergence zones or regions in the brain (e.g., prefrontal, anterior temporal pole), with no single convergence zone being sufficient to sustain object activation and recall. Our hypothesis is that there is an identifiable network of brain regions involved in object activation in semantic memory and that we can identify these with functional magnetic resonance imaging (fMRI) using the object activation and control experiments.

We studied 11 normal volunteers with fMRI during the performance of three tasks: (1) object activation from features (referred to as the "object activation" experiment), (2) semantic association (referred to as the "association" experiment), and (3) category activation from objects (referred to as the "category" experiment). Within each of the three experiments, the same words were used but paired differently to minimize stimulus-specific effects.

In the object activation experiment, word pairs for both the trials in which the features did elicit an object (O+ pairs) and in those pairs in which the features did not elicit an object (O- pairs) were admixed and visually presented, with the instruction being to push a button if these features combined to generate an object not presented in the stimulus words themselves (e.g., "desert" and "humps" produce "camel", while "bullets" and "milk" do not produce a third object). The cognitive operations associated with processing both the O+ and the O- pairs are quite similar until the object representation is activated. Thus, the primary comparison to best determine the brain region(s) associated with this object activation is the difference between the signal changes detected for the O+ pairs to those of the O- pairs.

The association and category experiments served as secondary controls in order to address the possibility that the activation observed in the O+ trials reflects simply an element of semantic relatedness between the stimulus pairs or a general process invoked whenever two elements in the semantic system combine to activate a third (or possibly higher level) entity. In the association task, participants were visually presented word pairs and were required to push a button if they were related (e.g., "hammer" and "nail" are related, A+, "nail" and "coffee" are not, A–). The category task required participants to view object word pairs and push a button if they are members of the same category (e.g., "skunk" and "monkey" are of the same category, C+, but "monkey" and " hammer " are not, C–).

RESULTS

For the object activation task, averaging over all the O+ trials, the signal changes were evident in the pre-supplementary motor areas [Brodmann's area (BA) 6], right more than left, and in the ventral occipito-temporal gyri bilaterally (BA 37). In addition, there was activation in the left thalamus when the object was activated (which was not present for the feature pairs that did not activate an object). These signal changes were centered in the dorsal thalamus (see Figure 1) and were evident in each participant's individual data as well (see Figure 2). The loci of signal changes in this and the other experimental conditions are summarized in Table 1.

In addition, the O+ pairs also demonstrated significant signal changes in the thalamus out to p < .0000005 using a random effects model, thus demonstrating the generalizability of the findings. These are displayed in Figure 3.

The single trial design facilitates examination of the signal changes that occurred as the participants were presented with feature word pairs that did not meet the target criteria for each experiment, in this case the O–pairs in the object activation task. The loci of signal changes in this condition are seen only in the ventral occipito-temporal regions bilaterally (Figure 4).

With both the associated (A+) and nonassociated (A-) stimulus pairs, the signal changes are strikingly similar to those in the O- condition, with activation seen in the ventral occipito-temporal gyri bilaterally (BA



Figure 1. Signal changes with object activation (O+ trials). The sections are angled perpendicular to the intercommisural line. The group data images show the loci of fMRI signal changes (p < .001) superimposed upon a normalized T1-weighted image gathered at the same location. Nine axial-oblique sections are displayed, showing foci of signal changes at representative levels through the dorsal cerebral hemispheres, the thalamus, and the ventral temporal lobes. The color bar at the right side of each figure reflects the range of *t* scores evident in the depicted data.

37), and minimally in the pre-supplementary motor area (BA 6). See Figures 5 and 6.

The signal changes in the categorization task, averaging over the object word pairs that were from the same category (C+), irrespective of the specific categories, reach a less robust level of statistical significance than do the changes in the other conditions (Table 1); they are focused in medial BA 6, slightly to the left of midline (Figure 7). There was no significant difference in the participants' reaction times across these three tasks [F(2,7) = .86; p = .44].

DISCUSSION

These experiments delineate neural regions associated with object activation resulting from a semantic search task involving feature stimuli, and point to one region that appears to be specifically involved when objects are activated—the thalamus.

Signal Changes with Object Activation

The signal changes detected during the O- trials in the object activation experiment, the associated A+ and nonassociated A- trials of the semantic association experiment, and the C+ trials of the category experiment provide a series of useful comparisons to those changes detected when object activation from features did occur (the O+ pairs).

We found robust activation in the thalamus only during the O+ trials, indicating that the thalamus is strongly associated with object activation. These thalamic signal changes were evident in both the group data, and in each participant's data examined individually. The fact that the thalamic activation was not detected as the participants evaluated feature word pairs that did not activate an object (O- trials), nor with searching for or finding semantic associations or categories, argues strongly for the specificity of the thalamic activity in this experimental context. For both the O+ and O- trials in the object activation task, the instructions and task were the same,



Figure 2. Images through the thalami from each of the participants' O+ trials (p < .001 for each individual participant), showing that each of the participants exhibits signal changes in the thalamic hemispheres.

Condition	Aznatomic Location of Maximal Signal Change	Talairach Coordinates			t Scora
		x	У	z	Naximum Value
Object activation pairs (O+)	Right pre-SMA (BA 6)	-3.0	19.4	47.4	3.34
	Left dorsal thalamus	11.4	-19.6	2.1	3.45
	Left fusiform gyrus (BA 37)	40.7	-52.5	-12.3	4.00
	Right fusiform gyrus (BA 37)	-37.8	-61.3	-10.7	3.32
Object nonactivation pairs (O-)	Left fusiform gyrus (BA 37)	40.3	-53.5	-12.3	4.07
	Right fusiform gyrus (BA 37)	-38.5	-61.3	-11.3	3.94
Association pairs (A+)	Left pre-SMA (BA 6)	3.6	13.5	51.3	3.45
	Left fusiform gyrus (BA 37)	41.2	-53.1	-12.3	3.88
	Right fusiform gyrus (BA 37)	-38.0	-59.1	-11.0	3.87
Nonassociated pairs (A-)	Left pre-SMA (BA 6)	1.9	16.5	49.8	3.26
	Left fusiform gyrus (BA 37)	40.8	-52.8	-12.3	4.12
	Right fusiform gyrus (BA 37)	-36.9	-60.8	-10.6	3.97
Category pairs (C+)	Left pre-SMA (BA 6)	3.9	19.8	46.0	1.92

Table 1. Locations of Maximal Signal Change for Each Major Locus of Activation in Each of the Four Conditions Depicted in Figures 1, 4, 5, 6, and 7

Both approximate anatomic localizations, as well as coordinates in standard stereotaxic (Talairach & Tournoux, 1988) space, are provided. The centroids of activation were determined after plotting the group data at a statistical threshold of p < .001.

the stimulus words were identical, and the semantic search was the same. The only difference was that in one condition, O+, the words were paired such that the semantic search resulted in object activation, whereas in the O- condition, the same feature word stimuli were combined differently so that they did not activate an object. Under both circumstances, the search strategies are presumably the same. Therefore, the cognitive processes should be similar when participants evaluated the stimulus pairs that activated an object versus those that did not, until the actual object activation is initiated.

The association task serves as a secondary control to assess the possibility that the signal changes observed during the object activation task reflect searching for and detecting semantic associations, as distinct from object activation itself. Within this framework, the signal changes detected in the ventral occipito-temporal areas for the O+ pairs do not appear to be specific to object activation itself as they are also detected in all pairs in the association task (A+ and A-), and in the O- pairs. Further support for this claim comes from Thompson-Schill et al. (1997) who had participants make a judgment of a semantic relationship between a feature and an object (e.g., "expensive" and "car" are related but "heavy" and "apple" are not). They detected activation in the fusiform gyrus, inferior frontal gyrus, and SMA. These investigators and others have attributed activation in the ventral occipito-temporal gyri and SMA to visual object recognition/imagery (Kraut, Hart, Soher, & Gordon, 1997) and preparedness to make a motor response, respectively. These processes, and, therefore, neural regions, would likely also be engaged during performance of our tasks-both when target responses

were detected and when they were not (Lotze et al., 1999; D'Esposito et al., 1997; Kraut et al., 1997; Kosslyn, Thompson, Kim, & Alpert, 1995). In addition, the pre-SMA (BA 6) activation in nearly all of our tasks suggests that this region is involved in directing the search for semantic relationships in general, perhaps interacting with the ventral temporal cortex as part of a network searching through multiple candidate object representations that fulfill the task-specific criteria. That the signal changes in BA 6 are most obvious with O+ (as opposed to O-) stimuli may reflect prolonged, or perhaps biphasic, neuronal activity under the conditions during which the subjects' searches culminated in activation of an object representation. Such prolonged neuronal firing, with its presumably greater metabolic requirements, might translate into a higher amplitude, or larger area of apparent signal change in the O+, versus the O-, conditions. Overall, however, deciding whether two items are semantically associated (A+ or A-) elicits signal changes in cortical regions quite similar to those detected during the object activation task (O+ or O–), but without signal changes in the thalamus.

The category task serves as a further secondary control for the object activation task, as it parallels the analogous process in semantics, yet, it does not represent object activation phenomenon as we have defined it. It similarly engages a "two items combine to elicit a third item" process, but in this case presents two semantic items (in this instance objects) and also requires the participant to decide if the two together activate a third semantic representation not directly presented in the two stimuli, namely, a category. Thus, while our object activation experiment assayed the



Figure 3. Signal changes with O+ pairs analyzed with a random effects model (p < .000005).

features-to-object level of semantic relationships, the category task explores the comparable, objects-to-category relationship and provides a secondary control to this type of process in semantic memory. In this regard, the lack of thalamic activation in the category experiment is further support that the observed thalamic activation is indicative of object activation in semantic memory, at least in this experimental context.

Possible Role of the Thalamus During Object Activation from Features in Semantic Memory

The thalamus is uniquely situated for object activation in semantic memory because of its central location, extensive thalamo-cortical connectivity, role as a relay station, and as mediator of cortico–cortical interactions (e.g., via corticothalamic and thalamocortical connections, etc.). There is evidence from previous studies suggesting that the thalamus performs a critical role in language and cognitive functions, some of which could be relevant to object activation in the semantic system. PET investigations of patients with thalamic lesions resulting in aphasia have shown hypometabolism of perisylvian cortical regions typically associated with language functions (Metter et al., 1988), consistent with the notion that subcortical aphasia in this case may result from a disruption of the thalamic coordination of cortically based language operations. Patients with lesions in the dominant thalamic hemisphere (usually the left) appear to primarily affect language functions, especially word finding (Nadeau & Crosson, 1997; Raymer, Moberg, Crosson, Nadeau, & Rothi, 1997). These pathophysiologic findings are concordant with our detection of left thalamic signal changes in the O+ condition, wherein the subjects' searches culminated in activation of object representations. A recent review of a series of patients with anterior thalamic nuclei lesions showed that all of the patients had word finding difficulties and over half had impaired naming, as well as deficits in memory retrieval and the sequencing of mental tasks (Ghika-Schmid & Bogousslavsky, 2000). The pulvinar nucleus has direct connections to SMA (BA 6) and the ventral temporal regions that are routinely co-activated with the thalamus in our O+ pairs (Nieuwenhuys, Voogd, & van Huijzen, 1988). In addition, lesions in the pulvinar have been associated with language disruption, including word finding, semantic paraphasias, and comprehension, suggesting



Figure 4. Signal changes with O- pairs. Signal changes remain evident in the right supplementary and pre-supplementary motor area and ventral temporal lobes bilaterally, but are not detected in the thalamus (p < .001).

strongly that this nucleus is involved in semantic processing (Johnson & Ojemann, 2000; Crosson, 1999; Crosson et al., 1986). It is therefore possible that a component of the thalamic signal changes we observe during object activation reflect neural activity within the pulvinar. This is consistent with electrophysiologic evidence (Johnson & Ojemann, 2000) showing disruption of verbal memory processing with left pulvinar electrical stimulation. In conjunction, these studies show that disruption of thalamically mediated cortical operations results in cognitive deficits (e.g., word finding, naming) that appear to be associated with the object activation process. While the signal changes appear to be maximal at the dorsomedial aspects of the thalamic hemispheres, the spatial resolution of our techniques does not allow for accurate localization of the sources of the signal changes within the thalamus. Although thalamic activation has been demonstrated with changes in levels of attention and vigilance (Kinomura, Larsson, Gulyas, & Roland, 1996), the comparable reaction times for all three tasks in our experiment argue against that explanation of our findings of thalamic signal changes only in the O+ condition.



Figure 5. Signal changes with semantic association (A+), gathered at the same locations as the data in Figure 1 (p < .001).

While it is clear from our investigation that the thalamus plays an active role during our object activation task, it is unclear how this is mediated. The presumed underlying neural activity that evokes the observed signal changes during the semantic object activation could be associated with the functions of stimulus recognition and stimulus–stimulus association, both of which may be necessary in object activation and have been attributed to the dorsal medial nucleus of the thalamus (Mottaghy et al., 1999; Nadeau & Crosson, 1997; Steriade, Jones, & McCormick, 1997). Other plausible operations include coordinating a search or detection circuit for correlated features and possible target objects, pointing to object representations in the imagery or lexical system, or mediating shifts in selective attention.

Nevertheless, based upon previous investigations in other cognitive systems, we suggest that the process that elicits object activation involves coordinating and synchronizing feature representations via an oscillating rhythm (Roelfseman, Engel, Koning, & Singer, 1996; Singer, 1993). In humans, the thalamus has been associated with oscillatory rhythms in multiple frequency ranges (Klimesch, 1996; Joliot, Ribary, & Llinas, 1994). Thus, both the animal and human data are consistent with the notion that the thalamus mediates object activation through the synchronization of oscillatory



Figure 6. Signal changes with the word pairs that were not semantically associated (A–) (p < .001).

neural activity in cortical regions encoding features (from multiple sensorimotor and lexical-semantic systems) of that object (Steriade, 2000; Engelborghs, Mariën, Martin, & De Deyn, 1998).

Object activation, as we have defined it in our experimental context, is essential to activating a conceptual representation in the semantic system, which, in turn, is basic to word finding, naming, comprehension, and translating thought into language. Among patients with neurodegenerative disorders and focal brain lesions, word finding is one of the most prevalent cognitive impairments, but little is known about the mechanisms by which objects are identified and named. The pathophysiological disruption of these mechanisms similarly remains unknown. The intermittent nature of word finding difficulties (e.g., being able to recall a name at one time, but not at another) may suggest transient disruptions of synchronizing electrical rhythms; however, further investigations will be necessary to delineate what appears to be the thalamus' critical role in semantic object activation.

METHODS

Research Participants

Eleven normal right-handed individuals, seven women and four men, between the ages of 23 and 48 (mean age 31.45 years, SD = 8.57) participated in the object activation and association experiments. Ten of these individuals from the group above (seven women and three men, mean age of 31.2 years [SD = 8.99]) participated in the category experiment.

Stimuli

The stimuli for the three tasks consisted of visually presented word pairs printed in lower case, with one word above the other.



Figure 7. Signal changes (p < .05) with the object pairs from the category task where both objects were from the same category, irrespective of the specific categories.

Object Activation

For the object activation experiment, the stimulus words were all features of objects, length range 3–7 letters (mean 5.3 letters, SD = 1.2) and syllable range 1–3 (mean 1.3 syllables, SD = 0.5). The features chosen were not specific to one particular perceptual or verbal domain. The target objects came from seven different categories. There were two types of word pairs: (a) 16 O+ pairs, where the two words describing features of an object combine to elicit an object that was not presented (e.g., the words "desert" and "humps," which produce the object "camel"), and

(b) 16 word pairs that do not combine to activate an object not presented, O- pairs, and are semantically unrelated (e.g., "humps" and "alarm").

To minimize stimulus-specific effects based on the words themselves (vs. the relationship between the words), the same feature words used in the O+ pairs were the stimuli in the O- pairs, being paired in these cases with a semantically unrelated word (e.g., "humps" and "alarm"). Serial position in the word pairs (upper vs. lower positions on the screen) was counterbalanced between the O+ and O- word pairs.

Choice of the O+ word pairs was determined by constructing a list of feature pairs (initiated from a list of feature norms for individual objects, see Tanaka & Szechter, unpublished manuscript) that potentially, in pairs, activated object representations, which were presented as word pairs to 11 normal individuals who did not participate in the imaging portion of this study. They were asked to determine whether the pair of words combined to form an object not presented in the stimulus words, with an example given for demonstration. Only those pairs that elicited the same object for all 11 were used in the experiment.

The participants in the imaging study were preinstructed as to the meaning of "object activation," as this term pertained to our experiment, immediately prior to the scanning session. The O+ and O- feature word pairs were all admixed, pseudorandomized, and presented to the participants with the instructions to "Push the button if the words combine together to form an object not presented in the stimulus words themselves."

Semantic Association

For the semantic association experiment, the stimulus words were all nouns depicting features/objects, length range 3–9 letters (mean 4.8 letters, SD = 1.6) and syllable range 1–3 (mean 1.4 syllables, SD = 0.6). The stimulus pairs consisted of two types: (a) 16 semantically related features/objects ("pot" and "stove"), and (b) 16 unrelated features/objects ("stove" and "car"). The words used in the semantically associated pairs were also used to make the unrelated pairs, being re-paired so that the words were semantically unrelated. The stimulus pairs were again screened by 11 normal individuals and only those pairs that all 11 agreed were related (or unrelated) were used. The related and unrelated word pairs were admixed, pseudorandomized, and presented to the fMRI study participants with the instructions to "Push the button if the two items are related to each other."

Category Activation

The stimuli for the category task consisted of 54 stimulus pairs, comprising: (a) 24 nouns representing animals with a length range from 3 to 12 letters (mean of 5.4 letters, SD = 2.3) and a syllable range of 1–5 (mean of 1.8 syllables, SD = 1.1), (b) 24 nouns representing tools with a length range of 3–11 letters (mean 5.5 letters, SD = 1.8) and syllable range 1–3 (mean 1.6 syllables, SD = 0.7), and (c) 24 nouns representing fruit and vegetables with a length range from 3 to 9 letters (mean 5.9 letters, SD = 1.6) and syllable range 1–3 (mean 2.0 syllables, SD = 0.8).

The stimuli were object word pairs where the objects were either: (a) from the same category ("bear" and "mouse"), or (b) unrelated objects. The object words were paired to form 12 animal category pairs ("lion" and "rat"), 12 tool category pairs ("screwdriver" and "drill"),

12 fruit and vegetable category pairs ("raisin" and "peach"), and 18 unrelated object pairs that consisted of select objects from the above category pairs that were re-paired to be unrelated ("drill" and "bear"). The 12 matching word pairs in each category consisted of the following: (a) four pairs where both objects were highly typical for the category, (b) four pairs of low typicality objects, and (c) four pairs with one high typicality and one low typicality object (Battig & Montague, 1969).

These word pairs were all admixed, pseudorandomized, and presented to the participants with the instructions to "Push the button if both items are members of the same category." The participants were specifically not told what the target categories could be, how many categories the stimuli were from, or the names of any possible categories. They were instructed prior to the experiment that the items could be from any category and the participants' decision about whether the two objects were from the same category should be based on their experience and judgment of what is a category and what items are members of a category.

Procedures

For each of the three experiments, the stimulus word pairs were presented one at a time on a rear projection screen, projected from a video system located outside of the MRI scanner room. These stimuli subtended approximately the central 3° of visual field. Word pairs were presented for 2.7 sec, with 15 sec between stimuli for the object activation and association experiments and 8.2 sec for the category experiment. The total run time for object activation and association experiments was 8 min, 15 sec each. Run time for the category experiment was 7 min, 33 sec. The participant was instructed to push a button held in their right hand if the stimuli met target criteria (e.g., if they were semantically related) and to not push if they did not meet those conditions. Stimulus presentation, responses, and reaction time recording were performed with the SuperLab software package (Cedrus, San Pedro, CA).

Scanning Procedures

The fMRI data were acquired in a 1.5-T MRI scanner, using a standard head coil. fMRI data covering the entire supratentorial brain were acquired using echo planar imaging with fifteen 7-mm-thick sections using a TR/TE = 1,000/50 msec and a flip angle of 70°. The field of view was 24 cm, with a 64×64 acquisition matrix, yielding pixels that were 3.75×3.75 mm in-plane.

Image Analysis

As a first step analysis, we segregated the recorded responses to each of the stimulus subtypes, in order to average and evaluate the responses separately. Thus, we analyzed the responses of the participants to the O+ stimulus pairs separately from the responses to the O– pairs in the object activation experiment, pairs that are associated versus those that are not associated in the association experiment, and same-category pairs versus different-category pairs in the category experiment.

We performed an event-related analysis for each individual using SPM99 (K. Friston, London, UK). Because the acquisition was 2-D, nominally contemporaneous slices were acquired as much as \sim TR apart. Therefore, the slices were time-adjusted using sinc interpolation (Calhoun, Adali, Kraut, & Pearlson, 2000). The data were motion-corrected, spatially smoothed (6 × 6 × 8 mm Gaussian kernel), and normalized into a standardized Talairach template.

Signal changes were modeled as delta functions located at stimulus presentation onset convolved with a canonical hemodynamic response function, and then entered into a linear model. The data were effectively bandpass-filtered by temporally smoothing using a 4s Gaussian kernel and removing harmonic frequencies up to one-half the fundamental frequency of the word pair occurrences (15 sec).

The model was fit to each participant's data, a t statistic image was generated, and the individual t statistic images were averaged across participants to create a group statistic image (p < .001 for the object activation and association experiments, and p < .05 for the category experiment), which were then overlaid on T1 images for display. To verify that the signal changes of primary interest, in the thalamus for the object activation experiment, were present in all participants, we plotted the data at the level of the thalamus on a participant-by-participant basis, in addition to evaluating the group data.

We then performed a second level analysis in which the SPM contrast images were entered into a one sample t test (random effects analysis) using SPM99 for the object activation experiment for both the I+ and I- pairs (Woods, 1996).

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The data reported in this experiment have been deposited in the fMRI Data Center (http://www.fmridc.org). The accession number is 2-2001-111YX.

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