

**From the holdings of the Department of Special Collections , Princeton University Library,
Princeton, NJ**

These documents are either in the public domain, or can only be used for educational and research purposes (Fair use) as per U.S. Copyright law (text below). By accessing this file, all users agree that their use falls in the public domain or within fair use as defined by the copyright law. We do not charge any permission or usage fees for the publication of images of material in our collections, including those provided by Princeton University Library, via our website, catalog, or directly from staff. For more information regarding copyright, credit, and citation please review the information on the Copyright, Credit and Citation Guidelines page of our website.

<https://library.princeton.edu/special-collections/policies/copyright-credit-and-citation-guidelines>. If you have any questions, including how to order higher-quality images from the collection, contact Special Collections Public Services via our Ask Us! Form. <https://library.princeton.edu/special-collections/ask-us>

Doctoral Dissertations, 2011-2026

Psychology

2012

The neural basis of compositionality: functional magnetic resonance imaging studies of conceptual combination

Baron, Sean George

Princeton, NJ : Princeton University

<http://arks.princeton.edu/ark:/88435/dsp01w08929975>

U.S. Copyright law: The copyright law of the United States (Title 17, §108, United States Code) governs the making of photocopies or other reproductions of copyrighted material. Under certain conditions specified in the law, libraries and archives are authorized to furnish a photocopy or other reproduction. One of these specified conditions is that the photocopy or reproduction is not to be used for any purpose other than private study, scholarship, or research. If a user makes a request for, or later uses, a photocopy or reproduction for purposes in excess of fair use that user may be liable for copyright infringement. This institution reserves the right to refuse to accept a copying order if, in its judgment, fulfillment of the order would involve a violation of copyright law. <https://www.copyright.gov/title17/title17.pdf>

**THE NEURAL BASIS OF COMPOSITIONALITY:
FUNCTIONAL MAGNETIC RESONANCE IMAGING STUDIES OF
CONCEPTUAL COMBINATION**

SEAN G. BARON

A DISSERTATION PRESENTED TO THE
FACULTY OF PRINCETON UNIVERSITY
IN CANDIDACY FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

RECOMMENDED FOR ACCEPTANCE
BY THE DEPARTMENT OF PSYCHOLOGY

ADVISOR: DANIEL OSHERSON

JUNE 2012

© Copyright by Sean G. Baron, 2012. All rights reserved.

Abstract

The use of concepts underlies the most basic cognitive processes. Consequently, psychologists have long been interested in understanding the behavioral and neural correlates of conceptual knowledge and its manipulation. This has led to a rich set of research results that have expanded our understanding of concepts. However, upon reviewing this literature it is clear that little of it expressly addresses the neural basis of conceptual combination. Conceptual combination is the mental construction of complex concepts (e.g., *GRADUATE STUDENT*) from simpler constituents (e.g., *GRADUATE* and *STUDENT*). The process of conceptual combination serves as the foundation for human conceptual creativity—our ability to create an infinite number of new ideas from a limited set. Across three functional magnetic resonance imaging (fMRI) studies, I explore the neural basis of basic conceptual combination. In the first I prove the feasibility of using fMRI to examine modifier-substantive combinations, and provide evidence for multiplicative combination (e.g., $YOUNG \times MAN \rightarrow YOUNG\ MAN$) in the left anterior temporal lobe. Studies two and three utilize non-phonologically dependent concepts (e.g., $MALE \times CHILD \rightarrow BOY$ and $WILD \times BIRD \rightarrow EAGLE$) and also point to the left anterior temporal lobe as a likely site of conceptual combination. Taken together, these results demonstrate the importance of the left anterior temporal lobe in conceptual combination, and also reveal a way for the cortex to store and process complex concepts in a non-redundant fashion.

Table of Contents

Abstract	iii
Table of Contents	iv
Acknowledgments.....	v
Introduction	
Dissertation Overview	1
Conceptual Combination	2
Conceptual Representation Across the Cortex	5
Cortical Regions Likely to be Involved in Conceptual Combination.....	8
Overview of Dissertation Studies	10
Study 1: Compositionality of Simple Social Concepts.....	12
Critical Concerns From Study 1 and Motivation for Studies 2 & 3	26
Methodologies and Analyses Common to Studies 2 & 3	28
Study 2: Compositionality of Phonologically-Independent Social Concepts.....	36
Study 3: Compositionality of Phonologically-Independent Non-Social Concepts.....	43
General Discussion	
The Left Anterior Temporal Lobe and Conceptual Combination	51
The Role of the Precentral Gyrus in Conceptual Combination	54
Other Cortical Regions Common to Studies 2& 3.....	56
Directions for Future Research	58
Final Comments	61
References.....	62

Acknowledgments

My exodus from Princeton was hurried, and as a result the feelings associated with my departure were proportionally intense. In the few days spent between finishing this dissertation and moving out of New Jersey I spent nearly all of my time experiencing one emotion most acutely: *gratitude*. The kindness shown to me by the community of professors, graduate students, support staff, and friends at Princeton can never be repaid or forgotten.

To Daniel Osherson, I'm not sure that "thank you" is enough for all that you've done for me. Your incredible intelligence is matched by the expansiveness of your selflessness and warmth. The debt I owe you for teaching me how to think, write, and prioritize my life and work is staggering. Moving forward, I know that an overwhelming proportion of my successes will be the direct result of the things I've learned from you.

To Alexander Todorov, I would not be here without you. You took a chance on me six years ago and in that time I've seen you do the same for so many others. I've always admired your openness and I hope that someday I can pay forward the opportunity you afforded me. Thank you for being such a wonderful advisor.

To Danny Oppenheimer, the pedagogical maestro, you showed me how to communicate ideas passionately and effectively. You always stressed the importance of finding your own voice when teaching, and I like to think that I was able to find mine because of your guidance. Even if I'm never at the head of a classroom again, the skills you helped hone will remain invaluable.

To Sam Wang, thank you for showing me that those "Mol Bio" folks aren't so

bad. It was an honor to have taught with you. I hope to use “Welcome to Your Child’s Brain” soon.

To Tamara Thatcher, I’m fairly certain that no one would ever graduate without your help. Thank you.

To the staff in the Princeton Psychology Department—RoseMarie Stevenson, Keisha Craig, Ray Lee, and the list continues—without you, the Department would grind to a messy halt.

To my cohort—Avani & Atul Sood, Julia & Anthony Caponiti, Sara Verosky, and Timothy Schoenfeld—our time at Princeton is near the end. Without each of you, I wouldn’t have enjoyed my time here half as much as I did. You are all such wonderful, brilliant, and funny people. Thank you for being so awesome.

To my friends—Anuj Shah, Chris Said, Daniel Torres, Greg Whelan, Mike North, Matt Roche, Peter Mende-Siedlecki, Tyson Aflalo, and assorted soft-ballers & Green-hallers—each of you made the unbearable parts of graduate school bearable and the great parts even better.

To the Morrison family—Doug, Sue, & Danny—during my time here you’ve gone from being like family to actually being family. Without your love and encouragement graduate school would have been much, much harder.

To the Baron family—Dad, Mom, Dawn, & Grandma— this is where acknowledgements simply aren’t enough. Each of you has provided endless support and love. Your sacrifices humble me, and I only hope I can make you proud by living my life with the sort of dignity and goodness I see in each of you.

To Julie—without you, any accomplishment, any goal, anything, would be pointless. Here we go.

Dissertation Overview

In this dissertation, I will present a suite of research that explores the neural basis of conceptual combination. First, I will introduce conceptual combination and an influential cognitive model used to describe it. The current state of knowledge regarding the cortical representation of conceptual knowledge will then be addressed. Subsequently, I will present and motivate two brain regions as candidate loci of conceptual combination. After this general introduction, I will describe three studies meant to evaluate the neural correlates of conceptual combination. Across all three studies I will show that, regardless of concept-type, compositional processes critical to the creation of complex concepts occur in the left anterior temporal lobe. These results fit well with the current literature and provide the first direct elucidation of the neural correlates of conceptual combination.

Conceptual Combination

Concepts are mental representations of categories, e.g., *CARS*, *COMPUTERS*, *CATS* (Murphy, 2004). Their manipulation underlies cognitive processes as fundamental as reasoning and language acquisition (Fodor, 2008; Murphy, 2004). Because of the importance of concepts to our cognitive lives, researchers have sought to understand their nature (Armstrong, Gleitman, & Gleitman 1983; Fodor & Lepore, 1996; Hull, 1920; Hampton, 1979; Keil, 1989; Medin & Schaffer, 1978). Much of this research examines only the mental representations of unitary concepts or the acquisition of completely novel concepts. A separate area of research has focused on conceptual combination—our ability to create complex conceptual representations from existing concepts.

In the process of conceptual combination, constituent concepts (e.g., *PARTY* and *ANIMAL*) are combined to create complex concepts (e.g., *PARTY ANIMAL*). The generation of such combinations is essential to the creative nature of human cognition, and allows for the production of an unlimited set of ideas from a finite base (Fodor, 2008). These combinatorial processes facilitate the comprehension of language by allowing the projection of our finite lexicon to a virtual infinity of thoughts. These thoughts are embodied by linguist structures such as noun phrases (e.g., *PARTY ANIMAL*), adjectival phrases (e.g., *BROWN DOG*), gerundive phrases (e.g., *WALKING IN THE SNOW CAN BE TREACHEROUS*), prepositional phrases (e.g., *UNDER THE ROILING SEA*), and so forth.

While combinatorial processes are used to create complex concepts from triadic (or quartic, quintic, etc) combinations of concepts (Hagoort, Baggio, & Wilems, 2009),

the simplest and most readily examined types of combinations are modifier-substantive dyads (e.g., *PARTY ANIMAL*). In this case, a modifier concept (e.g., *PARTY*) is applied to a substantive concept (e.g., *ANIMAL*). During this process, aspects of each constituent are used to construct the mental representation of the complex concept. The exact nature of this process has been the subject of intense investigation and many theorists have sought to fully describe it (e.g., Murphy 1990; Smith, Osherson, Rips, & Keane, 1988; Wisniewski, 1997; for a general review, see Murphy, 2004). Currently, the most complete theory is the selective modification model (SMM) of Smith, Osherson, Rips, and Keane (1998). This model was originally meant to apply only to adjective-noun phrases of the sort *RED WAGON*; however, it can also apply more generally to modifier-substantive combinations.

In the SMM, the mental representation of a substantive concept (e.g., *WAGON*) consists of a set of dimensions (e.g., ‘color’, ‘size’, ‘brand’). Each dimension contains a collection of possible features (e.g., for ‘color’: red, green, black) that are weighted according to their typicality. During the process of conceptual combination, the modifier adjusts both the named feature and its weight. In the example of *RED WAGON*, the color feature of *WAGON* is switched to *red* and the weight of the color attribute is increased (Smith et al., 1988). The SMM is particularly effective in describing conceptual combinations that directly affect particular attributes (*RED* nearly always applies to a color-related attribute). This model can encounter difficulties when the effect of the modifier—typically in the form of a relative adjective—depends on the substantive. For example, *HARD* in *HARD TEST* affects different substantive attributes than in *HARD BALL*. The SMM model also fails to

explain emergent features (Hampton, 1995). The complex concept *BEACH TOWEL* evokes a brightly colored towel of larger than average surface area meant to keep its user off of the sand. However, these important features (i.e., bright color, very large, to protect from sand) are not prominently available in the natural representation of *BEACH* or *TOWEL* separately.

Other models of conceptual combination have attempted to address compositions that result in emergent features or utilize relative adjectives (e.g, Gagne & Shoben, 1997; Hampton, 1988; Murphy, 1988; Wisniewski, 1996), but none are as clearly delineated as the SMM. Notice also that the issues arising when considering relative adjectives do not deny the functionality of the SMM in describing *how* combinations occur; rather, they only show issues involving the accurate selection of specific features to be modified. Additionally, properties that appear to be emergent might reflect phonological conflation of distinct concepts (e.g., *FAST in FAST CAR* vs. *FAST FRIEND*). Because the problem is of conceptual uniqueness in such cases, criticism of the SMM with respect to relative or emergent concepts might be unwarranted.

At any rate, all models—regardless of how they address the weakness of the SMM—suggest that conceptual combination relies on the integration of constituent concept representations to create complex concepts (Gagne & Shoben, 1997; Hampton, 1988; Murphy, 1988; Smith et al., 1988; Wisniewski, 1996). Because of this, my work will assume that *neural representations*—operationally defined herein as voxel-wise representations—of complex concepts must be similar to some combination of their constituents (i.e., the neural representation of *PARTY ANIMAL* must contain aspects of

the representations of both *PARTY* and *ANIMAL* activated separately). Additionally, to avoid any concerns related to relative adjectives or emergent features, I will only use modifier concepts that clearly modify one feature of the substantive (i.e., how *RED* modifies the color feature of the substantive in *RED WAGON*).

Conceptual Representation Across the Cortex

Neuroscientists have long been interested in characterizing the cortical underpinnings of conceptual competence (Cohen & Walter, 1966; Grabowski et al., 2001; Grossman et al., 2002; Martin & Chao, 2001; Warrington, 1975). When reviewing this literature it becomes clear that there is no single neural location for conceptual processing. In fact, there is strong evidence that large portions of each cortical lobe are involved in handling conceptual information (Ashby & Ell, 2001; Binder et al., 2009; Kellenbach, Brett, & Patterson, 2001; Martin, 2007; Patterson, Nestor, & Rogers, 2007; Pobric, Jeffries, & Lambon Ralph, 2007; Wiggs, Weisberg, & Martin, 1999). Perhaps because so many brain regions have been implicated in conceptual processing, multiple theories regarding the neural basis of concepts have emerged.

One early theory suggested that concepts are organized in *category-specific* regions of cortex (e.g., Caramazza & Shelton, 1998; Mahon & Caramazza, 2003; Tranel, Damasio, & Damasio, 1997). Evidence for this comes from lesion studies showing category-specific deficits related to damage in isolated regions of cortex (Gainotti, Silveri, Daniele, & Giustolisi, 1995; Warrington & Shallice, 1984). For example, it seems as though damage to the anterior medial temporal lobes directly affects knowledge of living things (Gainotti & Silveri, 1996), while damage to regions

of the left frontal and parietal lobes (Tranel, Damasio, & Damasio, 1997) affects knowledge of man-made artifacts (e.g., *WRENCH*, *HAMMER*, *SCISSORS*). Such evidence is compelling but it is unclear what kinds of processes these deficit-related regions are actually responsible for. For example, these regions may only process *perceptual* correlates of specific categories and have little to do with conceptual representation (e.g., Forde et al., 1997).

Another theory posits that the representation of a concept (e.g., *WRENCH*) is based in the *distributed* activations of the perceptual (e.g., the occipital and temporal lobes) and motor (e.g., the frontal lobe) systems used to perceive and use the physical instantiation of the concept (e.g., an actual wrench; Barsalou, 1999; Martin, 2007). Because this theory does not attempt to separate conceptual and perceptual processors it does not suffer from drawbacks to the category-specific theory noted above. Indeed, proponents of this distributed theory argue that category-specific deficits are the result of lesions affecting perceptual or motor information related to the inherent properties needed to categorize and distinguish an object (Martin, 2007). The strongest evidence for the distributed theory of neural conceptual representation comes in the form of fMRI studies showing that the neural systems involved in perceiving or using an object are active when people *think* of the object (Chao & Martin, 1999; Creem-Regehr & Lee, 2005; Goldberg et al., 2006; Hauk et al., 2004; Simmons et al., 2007; in monkeys, Jeannerod et al., 1995).

The distributed theory of the cortical basis of concepts is not without its own drawbacks. The most important is based in the effects of semantic dementia on general conceptual processing. Because conceptual representations are spread across the

cortical regions responsible for perceiving and using particular objects, the distributed model predicts that concept-general deficits (e.g., deficits for processing both *WRENCH* and *ROBIN*) should not occur as a result of focal lesions. Yet, in the case of semantic dementia we observe impairments to conceptual processes that apply across all sensory modalities and for all types of concepts (Adlam et al., 2006; Bozeat et al., 2002; Snowden et al., 1996). The cortical degeneration responsible for semantic dementia is nearly always restricted to the bilateral anterior temporal lobes (BA38 and the anterior portions of BAs 21, 20, and 22; Desranges et al., 2007; Diehl et al., 2004; Nestor, Fryer, & Hodges, 2006). These symptoms are likely not a result of co-morbid cognitive and neurological complications unique to individuals predisposed to semantic dementia. Transcranial magnetic stimulation—a way of creating temporary and focused lesions—of the anterior temporal lobes in normal participants causes the same deficits seen in semantic dementia patients (Lambon Ralph Pobric, & Jeffries, 2009; Pobric, Jeffries, Lambon Ralph, 2007). The general deleterious effect of semantic dementia on conceptual processing and the focused cortical regions it degenerates discredit the distributed theory.

These semantic dementia results have led to the rise of a third theory regarding concepts and the brain: the distributed-plus-hub model (Patterson, Nestor, & Rogers, 2007). This model acknowledges the necessity—and strong evidence supporting—distributed representations of conceptual knowledge, but also seeks to explain the general effects of semantic dementia on conceptual processing. Patterson and colleagues suggest that the anterior temporal lobes act as conceptual hubs (2007). These hubs receive information from the distributed conceptual network, and are

responsible for integrating and processing high-level modality-independent representations of concepts. The inclusion of these hubs in the distributed model allows for effortless generalization across concepts that have very little perceptual or functional similarity. For example, the hubs permit the inclusion of a sweepstakes check and an oversized teddy bear into the *PRIZE* concept. These hubs also allow the differentiation of perceptually-similar/conceptually-dissimilar concepts (e.g., *LIGHT BULB* and *PEAR*). Further evidence for the distributed-plus-hub model comes from fMRI studies that show activation of the anterior temporal lobes for conceptual tasks across multiple sensory modalities and concept types (Noppeney & Price, 2002; Mummery, Shallice, & Price, 1999; Tsukiura, Mochizuki-Kawai, & Fujii, 2006).

The distributed-plus-hub model of cortical conceptual representation does a wonderful job of integrating aspects of previous theories while providing remedies for their shortcomings. As a result it is generally well accepted (though see also, Simmons, Reddish, Bellgowan, and Martin, 2010). It is worth noting that the results of my research may inform the debate between a distributed-only and a distributed-plus-hub model of conceptual representation. Observing conceptual combination for multiple concept types in a single cortical region would provide evidence for the distributed-plus-hub model. The observation of multiple loci of conceptual combination would provide better evidence for the distributed-only model.

Cortical Regions Likely To Be Involved in Conceptual Combination

Though no neuroimaging studies have directly examined the cortical basis of conceptual combination, previous research may hold some clues as to possible loci of compositionality. Such regions would likely meet two general criteria. First, because

conceptual combination is a foundational aspect of conceptual processing, regions responsible for it should be seen across neuroimaging research utilizing many types of conceptual tasks. Second, these regions should show increased activation to tasks that require some semantic composition (e.g., processing complex sentences). When reviewing the current literature, two candidate regions emerge: the left inferior frontal gyrus (IFG) and the left anterior temporal lobes (ATL).

The left lateral frontal cortex—most commonly regions on or around the inferior frontal gyrus (IFG)—is consistently activated in tasks requiring the retrieval of semantic knowledge (Thompson-Schill et al., 1998; Wagner et al., 2001). Patients suffering from degeneration of this region have marked deficiencies in expressing knowledge about familiar objects, vocabulary loss, inability to generate exemplars from semantic categories, recognition deficits for subordinate-level categories, and marked deficiencies in reading fluency (Hodges et al., 1992; Snowden, Neary, & Mann, 1996). These semantic deficits are positively correlated with the severity of cortical damage (Noppeney et al., 2007). The left IFG also shows activation to stimuli requiring semantic composition, responding more to complete sentences than to words, and more to ambiguous than to unambiguous sentences (Snijders et al., 2009).

As previously discussed, the left ATL appears in many studies examining conceptual processes (Lambon Ralph et al., 2009; Patterson et al., 2007; Visser et al., 2009). It serves as the conceptual hub in the distributed-plus-hub model of cortical conceptual representation (Patterson et al., 2007). There is strong evidence that the amount of degeneration in left ATL is directly correlated with the severity of the conceptual deficits seen in semantic dementia (Mummery et al., 2000). Like the left

IFG, left ATL shows increased activation to sentences compared to unintelligible speech (Spitsyna et al., 2006) and to stimuli of increasing semantic complexity (Dronkers et al., 2004; Humphries et al., 2006; Rogalsky & Hickock, 2009).

These findings have led researchers to suggest that the left IFG and ATL are the loci of semantic unification (a process wherein multilexemic samples of language are bound into complex and coherent ideas; Hagoort et al., 2009; Rogalsky & Hickock, 2009) and, potentially, conceptual combination (Hickok & Poeppel, 2007). Consequently, in the research presented here, it would be unsurprising to observe conceptual combination in either left ATL or IFG.

Overview of Dissertation Studies

The following work is, to the best of my knowledge, the first set of fMRI research to directly examine the neural basis of conceptual combination. In Study 1, I elicited neural representations for the concepts: *YOUNG*, *OLD*, *MAN*, *WOMAN*, *YOUNG WOMAN*, *YOUNG MAN*, *OLD WOMAN*, and *OLD MAN* from ten participants. In subsequent analyses, I determined the presence of combinatorial processes in functional regions of interest (fROIs) via multi-voxel pattern analysis (MVPA) classification. In this MVPA analysis, a region was considered to show evidence of conceptual combination if the neural representation of complex concepts (e.g., *YOUNG MAN*) was significantly approximated by the combination of the representations of appropriate constituents (e.g., *YOUNG* and *MAN*, when elicited separately). Study 2 built upon the general methodologies used in study 1; however, it corrected for the potential of phonological confounds. Any conceptual combination seen in study 1 could have been the result of actual compositionality or it could have

been caused by phonological composition—after all, *YOUNG MAN* is constructed from the same phonemes present in *YOUNG* and *MAN*. Thus, in Study 2, I examined the neural representations for the phonologically-independent concepts: *MALE*, *FEMALE*, *ADULT*, *CHILD*, *BOY*, *GIRL*, *MAN*, and *WOMAN*. In this study, a spherical searchlight (SL) analysis was used to locate brain regions where significant conceptual combination occurred. Again, a region showed evidence of compositionality when the neural representation of the complex concepts (e.g., *BOY*) was significantly approximated by the combination of appropriate constituents (e.g., *MALE* and *CHILD*). In a final study, I utilized the same methodologies and analyses from Study 2, but examined compositionality for non-social concepts. In Study 3, neural conceptual combination was evaluated from the concepts: *WILD*, *FARM*, *MAMMAL*, *BIRD*, *EAGLE*, *CHICKEN*, *LION*, and *COW*. Across all three studies, regions within the left anterior lobe showed evidence of significant conceptual combination.

The consistency of the results suggests that the left anterior temporal lobe plays an important role in conceptual combination. In this region, the representation of a complex concept can be approximated by the combination of its constituents. This is true for both social and non-social concepts. Taken together, these results provide further evidence for the supremacy of the distributed-plus-hub model (Patterson et al., 2007). Further discussion of my work's scientific implications, as well as the exact methodologies, analyses, and results of each study follow below.

Study 1: Compositionality of Simple Social Concepts

(Adapted from: Baron, Thompson-Schill, Weber, & Osherson, 2010)

Because of the exploratory nature of this initial study, I chose to focus on simple adjective-noun combinations. In such combinations, a modifier (e.g., *YOUNG*) is applied to a substantive concept (e.g., *MAN*). These types of conceptual combinations were chosen because they occur commonly in language and are well characterized within cognitive psychology (specifically the SMM of Smith et al., 1988). In this experiment, participants considered the following concepts: *YOUNG*, *OLD*, *MAN*, *WOMAN*, *YOUNG MAN*, *YOUNG WOMAN*, *OLD MAN*, and *OLD WOMAN*. I attempted to identify the neural regions that implement the first steps in the combinatorial process. In these first steps, I expect the meaning of each constituent to be represented in the meaning of the combination. As a result, multiplication was used as the combinatorial function. Thus, cortical regions were sought that represented the voxel-wise activations associated with complex concepts (e.g., *YOUNG MAN*) as the product of the activations of appropriate constituents (e.g., *YOUNG* and *MAN*).

Multiplication was chosen as the combinatorial function because it reveals regions where the representation of complex concepts depends on the interaction of constituent concepts—satisfying cognitive theories of composition (Gagne & Shoben, 1997; Hampton, 1988; Murphy, 1988; Smith et al., 1988; Wisniewski, 1996). The use of multiplication as a combinatorial function is also supported by literature proposing functions capable of facilitating the combination of constituent representations (Gougen, 1969; Osherson & Smith, 1982; Peng, Kandel, & Wang, 1991).

Method

Participants

Twelve Princeton University undergraduate students (8 female) participated in a preliminary behavioral study. A different group of ten graduate and undergraduate students (all female) participated in the same behavioral paradigm followed by an fMRI study.

Stimuli

The experiment was based on four simple and four complex concepts, namely, *YOUNG*, *OLD*, *MAN*, *WOMAN* and *YOUNG MAN*, *YOUNG WOMAN*, *OLD MAN*, *OLD WOMAN*. *FaceGen Modeller 3.1* (Singular Inversions, 2006; Todorov, Baron, & Oosterhof, 2008) was used to generate 112 faces, 28 per complex concept (see Figure 1). Seventy-two of the faces were used to create six sequences of 12 (no repeated faces). In a given sequence, each of the four complex concepts was satisfied by three faces. These six sequences will be termed “targets.” Twenty-four different faces from the original set of 112 were set-aside as “fillers.” The remaining 16 faces were called “hash mark faces;” each sported a small, randomly placed hash mark (#). Twelve randomly selected target faces were also chosen to sport an arbitrarily placed hash mark, and were then added to the hash mark faces. These faces, without hash marks, also remained within their respective target sequences.

Participants confronted these stimuli in a behavioral task and an fMRI task. The purpose of the behavioral task was to ensure that complex concepts were unitized (each processed as a single concept rather than a serial process of each constituent concept). I describe it first, followed by the fMRI task.



Figure 1. Examples of the four categories of faces used as stimuli and one example of a face containing a hash-mark. From left to right: *YOUNG MAN*, *OLD MAN*, *OLD WOMAN*, *YOUNG WOMAN*, and *YOUNG MAN* with a hash-mark.

Behavioral task

The 72 faces composing the target sequences and the 24 filler faces were employed. On a given trial, one of the eight concepts was written on screen followed by the 96 faces in random order in a self-paced serial presentation. For each face, the subject indicated “yes” or “no” as fast as possible according to whether the face satisfied the search category (inputs were collected via keyboard). Our measure of interest was the response time (RT) to categorize each face. Each of the eight concepts served as search category in one trial (768 faces classified in all); the order of the eight concepts was individually randomized.

fMRI task

The fMRI task was divided into four types of trial. A given trial consisted of a randomized sequence of faces, with each face presented for 850 ms followed by a 400 ms fixation cross. Preceding each trial, participants were shown a written display (lasting five seconds) of one of the eight concepts or the words “hash mark”. If shown a concept, subjects were to decide whether each face belonged to the given concept category. If shown ‘hash mark’, participants were to decide whether each face contained a hash mark (the presence of a hash mark on a given face was determined

randomly). Question marks occasionally appeared within the sequence of faces. When a question mark appeared, subjects were to respond on the basis of the face preceding it, e.g., affirming that a face was a young woman or that it held a hash mark, depending on the written display and the character of the face preceding the question mark. I now describe the four types of trial.

Target trials consisted of a target sequence lasting 15 seconds (12 faces). A question mark never appeared during target trials.

Catch trials consisted of a sequence of between one and 11 faces, followed by a three second question mark, then a fixation cross bringing the trial to 15 seconds. The presented faces consisted of filler and up to four randomly selected target faces. The purpose of the catch trials was to ensure vigilance in the target trials, obliging subjects to maintain the concept in mind throughout. Subjects had no way of distinguishing target from catch trials prior to appearance of the question mark.

Hash mark trials consisted of a presentation of 12 faces drawn from the filler and hash mark faces. A question mark never appeared during hash mark trials.

Hash mark catch trials consisted of a presentation of one to eleven faces drawn from the filler and hash mark faces, followed by a three second question mark, then a fixation cross bringing the trial to 15 seconds.

Faces from the target sequences were included in each of the four trial types to keep subject unaware of the differences between each type. I note that the same target sequences were presented for each of the eight concepts during target trials. Thus, in target trials, different concepts were maintained in mind while viewing the same sets of faces. Therefore any difference in neural activation between concepts was the result of

their mental representation rather than the stimuli themselves. Because faces were presented in random order, no participant noticed that the same target face appeared across different fMRI runs.

fMRI procedure

A scanning session consisted of an anatomical image scan followed by eight data acquisition runs. Each run was composed of six target, two catch, five hash mark, and two hash mark catch trials. Each of the eight concepts (four simple, four complex) was the search category in exactly one of the eight concept trials (six target or two catch trials). These eight trials were interleaved with the seven hash mark and hash mark catch trials. The order of concept-targets within a run was pseudo-randomized so that every concept preceded or followed every other concept. Over all eight runs, each concept was searched for in a target trial six times and in a catch trial two times.

Image Acquisition

Blood oxygen level-dependent (BOLD) activation was used as a measure of neural activation. Echo planar images (EPI) were acquired (TR= 2 s, TE=30ms, FA= 80°, matrix size 64x64) using a Siemens 3.0 Tesla Allegra Scanner (Siemens, Erlangen, Germany) with a ‘bird-cage’ head coil. Whole brain coverage was achieved via 33 interleaved 3 mm axial slices (1 mm inter-slice gap). A high-resolution anatomical image (T1-MPRAGE, TR= 2.5 s, TE= 4.3ms, FA= 8°, matrix size= 256x256) was acquired for functional data registration and cross-subject spatial normalization.

Image Analysis

All fMRI data were treated with *Analysis of Functional Neuro-Images* software (AFNI; Cox, 1996). For each participant, motion was corrected using a six-parameter 3D motion correction algorithm following slice scan-time correction. All data were

spatially smoothed with a 6 mm full width at half maximum Gaussian kernel. Data were then low-pass filtered with a frequency cut-off of 0.1 Hz. Finally, signal was normalized to percent difference from the mean.

For each participant, voxel-wise multiple regression was used to generate parameter estimates. Nine regressors of interest (eight concepts and hash marks) were convolved with a canonical hemodynamic response function and entered into a general linear model. Motion estimates and all catch trials were included as regressors of no interest. The subsequent parameter maps for each concept and hashmark were projected into Talairach space (Talairach & Tournoux, 1988) and averaged across all participants.

Results

Behavioral Results

The behavioral portion of the experiment was meant to determine if complex concepts were processed as single conceptual units. Unitization implies that RTs associated with complex concepts are no longer than RTs for simple concepts. If such unitization was observed, concerns about serial activation of constituents would be obviated (i.e., compositionality could not be explained by phonological coactivation of constituents).

Across all subjects, 13 responses lasting longer than 5,000 ms were counted as outliers and removed from the full dataset. Consistent with unitization, average RT for simple concept categorizations (*YOUNG*, *OLD*, *MAN*, *WOMAN*) was 643 ms ($SD = 145$) whereas it was 594 ms ($SD = 119$) for complex concept categorizations (*YOUNG MAN*, *YOUNG WOMAN*, *OLD MAN*, *OLD WOMAN*). This RT difference is significant by t -test ($t(11) = 2.23$, $p < 0.05$, $d = 0.64$). Error rates were negligible for both simple

and complex concept categorization (2.26% and 1.26% respectively).

Prior to taking part in the fMRI study, participants completed the behavioral task. This version of the task contained a single random order of trials, and I compared the last trial of each type of concept. Again, evidence of unitization emerged: the RT for simple concepts was 617 ms ($SD = 282$) compared to 546 ms ($SD = 248$) for complex concepts, significantly different via t -test ($t(8) = 3.62, p < 0.05, d = 1.25$). As before, error rates were negligible for both simple and complex concept categorization (2.1% and 3.8% respectively). (One subject's data were not included due to data loss). In any case, if a true difference exists at all, reaction times for complex concepts are *faster* than those for simple concepts.

fMRI Results

Theories concerning the neurophysiological basis of conceptual knowledge have implicated both perceptual (i.e., the distributed model; Barsalou, 1999) and amodal systems (i.e., the distributed-plus-hub model; Patterson, Nestor, & Rogers, 2007). Consequently, functional regions of interest (fROIs) were defined using a contrast that would be sensitive both to perceptual and high-level cognitive representations of faces: A group-level contrast (t -test) for hash mark versus target trials was used to isolate the fROIs that were queried in subsequent analyses. Significant clusters were defined as contiguous voxels with $p < 0.01$, $t(9) > 3.25$, and a minimum volume of 2000 mm³. One cluster spanning aspects of right temporal and parietal lobe via the lateral sulcus was split along the sulcus into two anatomically meaningful clusters. The resulting fROIs are listed in Table 1.

Table 1. *Largest Voxel Clusters From the Contrast of Hash Marks vs. Target Trials*

Region	Center of Mass (x, y, z)	Size (3mm ³ voxels)	Peak <i>t</i> -value	Dependent correlation <i>t</i> -test performance
R. Precuneus	33, -66, 34	1,791	9.54	5/12
L. Parietal/Occipital	-38, -64, 31	1,518	9.66	7/12
R. Precentral Gyrus*	61, -20, 23	211	4.04	6/12
L. Precentral Gyrus	-55, -18, 37	182	6.44	5/12
R. Fusiform Gyrus	28, -50, -10	173	9.55	2/12
L. Fusiform Gyrus	-27, -41, -11	170	6.14	7/12
R. Temporal Pole	53, 16, -28	119	7.25	2/12
R. Medial Frontal Gyrus	7, 56, 37	110	7.10	5/12
R. Superior Temporal Gyrus*	63, -30, 6	108	3.91	6/12
L. Medial Frontal Gyrus	-8, 58, 5	96	6.22	2/12
L. Superior Temporal Gyrus (IALT)	-62, -5, 2	87	8.53	8/12

Notes: “Region” refers to the anatomical location of the center of mass. “Peak *t*-value” is the voxel with the greatest activation within the cluster. *fROI split along the lateral sulcus.

In each fROI, the average neural activations for simple and complex concepts were normalized from 0 to 1. The product of simple concepts were then used form conceptual combinations (CCs) to estimate neural representations for complex concepts in a given fROI. For example, the voxel-wise neural representation for *YOUNG* was multiplied by *MAN* ($YOUNG \times MAN$) to form the CC for *YOUNG MAN*. All CCs were then normalized from 0 to 1. I relied on Williams test of dependent correlations (Steiger, 1980), to determine whether a spurious CC ($YOUNG \times WOMAN$) was better correlated than an appropriate CC ($YOUNG \times MAN$) with a given complex concept (*YOUNG MAN*). Specifically, each complex concept (e.g., *YOUNG MAN*) was

correlated with the four CCs. One of the four CCs was appropriate (*YOUNG* × *MAN*). The remaining three CCs were spurious. One of the spurious CCs matched the target concept just in head noun (*OLD* × *MAN*), another matched just in modifier (*YOUNG* × *WOMAN*), and the third matched neither (*OLD* × *WOMAN*). The three spurious correlations were compared to the appropriate CC correlation via three Williams tests. This was done for all four of the complex concepts. In a given fROI, there were thus 12 opportunities for appropriate CCs to be better correlated than spurious CCs with their complex concepts.

Table 2. *Median correlations in lALT of appropriate and spurious CCs with each complex concept*

Complex Concept	Appropriate CC	Head Match	Modifier Match	No Match
Young Man	0.689	0.625	0.502	0.334
Young Woman	0.684	0.570	0.710	0.638
Old Man	0.671	0.490	0.549	0.641
Old Woman	0.757	0.441	0.467	0.086
Mean	0.700	0.532	0.557	0.425

Notes: “Complex Concept” refers to the target complex concept (e.g., *YOUNG MAN*). “Appropriate CC” is the calculated CC that correctly corresponds complex concept (*YOUNG* × *MAN* for *YOUNG MAN*). “Head match” is the CC that only contains the correct head concept constituent of the complex concept (*OLD* × *MAN* for *YOUNG MAN*). “Modifier match” is the CC that only contains the correct modifier concept constituent of the complex concept (*YOUNG* × *WOMAN* for *YOUNG MAN*). “No match” is the CC that contains no constituents that match with the complex concept (*OLD* × *WOMAN* for *YOUNG MAN*).

I tallied the number of correlations that were significantly stronger for appropriate versus spurious CCs. The last column of Table 1 reports the performance of each fROI. An area of left anterolateral temporal lobe (lALT) emerged as the fROI

with highest performance (see Table 1 & Panel A of Figure 2). Indeed, eight of the possible 12 comparisons for IALT were significantly in favor of the appropriate CCs; moreover, the correlation between appropriate CCs and their complex concepts was higher than for spurious CCs in 11 of 12 cases (Table 2). The product of activation for simple concepts to form the CC for the associated complex concept is illustrated in Panels B-E of Figure 2.

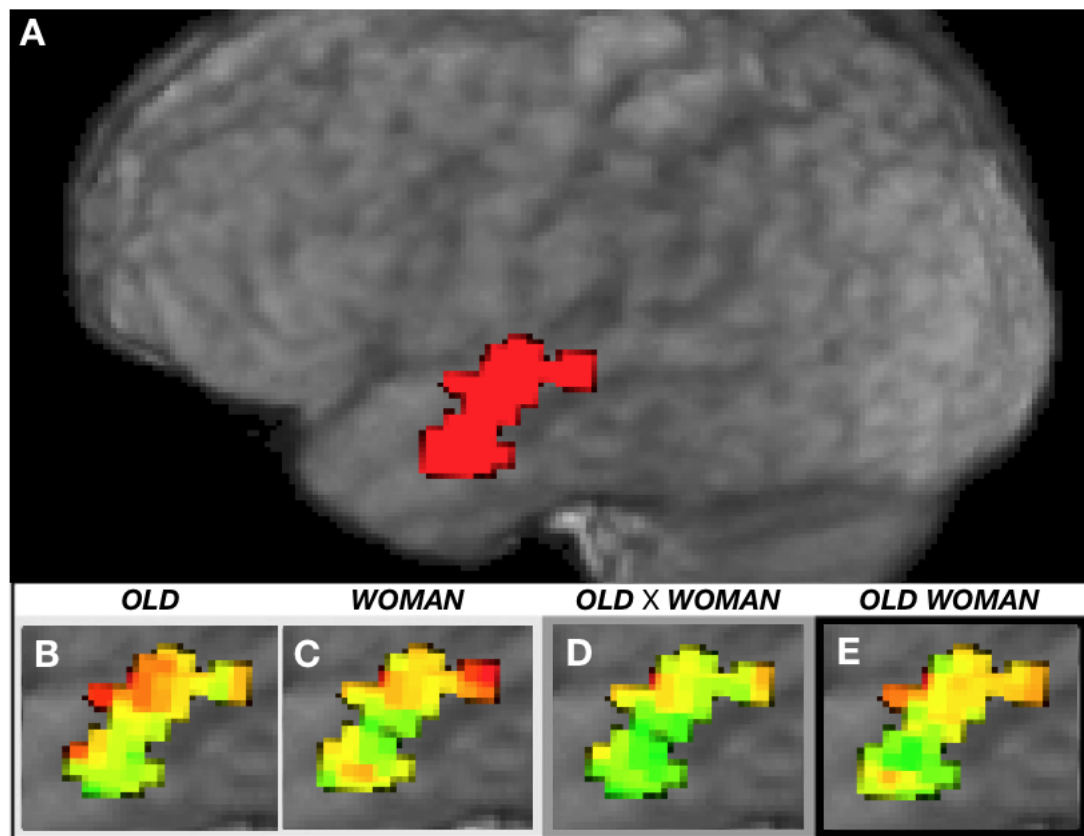


Figure 2. Left anterolateral temporal lobe fROI (IALT) and an example of addition of a CC ($OLD \times WOMAN$) via surface renderings of average neural response patterns to concepts. (A) IALT. (B) *OLD*. (C) *WOMAN*. (D) The calculation of the complex concept *OLD WOMAN* from a normalized product of old and woman. (E) The actual neural representation of *OLD WOMAN*.

I also performed the following permutation test on IALT. Each of the four simple concepts figured in six trials (see Methods). I randomly permuted the labels of these 24 trials and tallied the number of correlations in which a given complex concept

was correlated most strongly with its appropriate CC versus spurious CCs. As before, there are 12 such comparisons. Only 224 of 10,000 permutations produced tallies of 11, suggesting that the tally of 11 for the unpermuted data from IALT is not due to chance.

Discussion

The IALT fROI allows activations associated with complex concepts (e.g., *YOUNG MAN*) to be predicted from the sum of the activations associated with their simple constituents (e.g., *YOUNG* $\times$ *MAN*). No other fROI performed nearly as well. The localization of compositionality to IALT is consistent with previous reports of the role of the temporal lobe in conceptual knowledge (Mahon & Caramazza, 2009), specifically, regions overlapping IALT (Leveroni et al., 2000; Zahn et al., 2007). The same regions have also been implicated in processing complex semantics, for which conceptual combination is obviously essential (Rogalsky & Hickok, 2009; Vandenberghe, Nobre, & Price, 2002).

IALT is largely confined to the anterior temporal lobe. As previously discussed, the anterior temporal lobe appears to underlie semantic and conceptual processing in both healthy (Pobric, et al., 2007) and patient populations (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004). The region is amodal in the sense that it responds equally to semantic information presented via speech, written words, or pictures (Visser et al., 2009). Such amodality is likely the result of extensive reciprocal connections from prefrontal cortex, visual and auditory association cortices, and the limbic system (Markowitsch, Emmans, Irle, Streicher, & Preilowski, 1985; Patterson et al., 2007). This cortical interconnectivity and the region's amodal response to

conceptual information has led some researchers to propose that the anterior portion of the temporal lobe acts as a semantic hub: a region responsible for the cross-modal binding and high-level processing of conceptual knowledge (Patterson et al., 2007). Taken together, our findings and the previous literature concerning IALT, suggest that it is a likely candidate region responsible for conceptual combination.

Other than IALT, a parietal/occipital lobe fROI was the only one other region where appropriate CCs were better correlated with complex concepts than were spurious CCs more than half of the time (see Table 1). This fROI was quite large, extending from the lateral to the medial aspects of the left parietal and occipital lobes. In the anterior-to-posterior direction the fROI extended from the posterior aspect of the lateral sulcus to the anterior aspect of primary visual cortex (see Fig. 3).

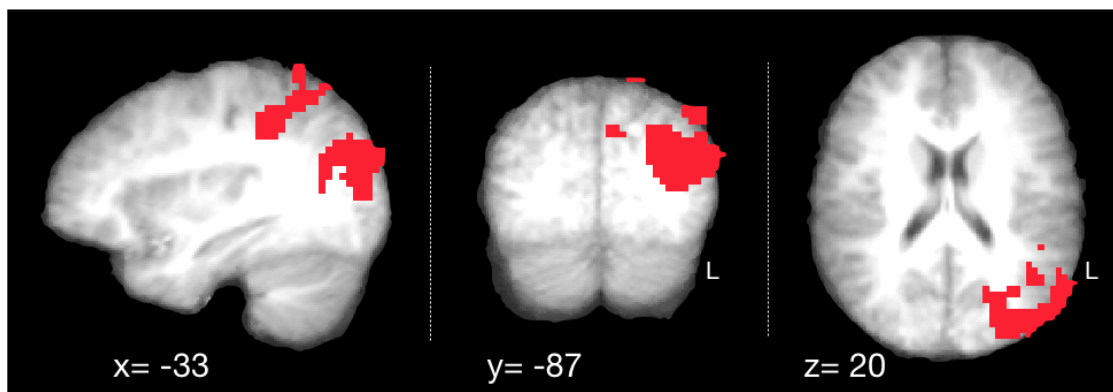


Figure 3. Left parietal/occipital lobe fROI. This region showed evidence of significant multiplicative on 7 of 12 possible comparisons between appropriate and spurious CCs.

This fROI extends across regions of cortex responsible for myriad cognitive and perceptual functions. This includes occipital and parietal regions responsible for primary and secondary visual processes (Kandel, Schwartz, & Jessell, 2000), as well as regions thought to mediate the experience of self-consciousness and attention (Cavanna & Trimble, 2006; Cusack, Mitchell, & Duncan, 2010). It is worth noting that

regions within this fROI do appeared to preferentially respond to some conceptualization tasks (Binder et al., 2009); however, these regions do not show any preference for semantically complex tasks/stimuli (Spitsyna et al., 2006; Rogalsky & Hickock, 2009). The wide variety of functions attributed to regions circumscribed by the parietal/occipital fROI, and the lack of evidence showing its preference for semantically complex stimuli, make it an unlikely site of conceptual combination.

Table 3. *Median correlations in the left parietal/occipital lobe fROI of appropriate and spurious CCs with each complex concept*

Complex Concept	Appropriate CC	Head Match	Modifier Match	No Match
Young Man	0.925	0.904	0.923	0.905
Young Woman	0.916	0.899	0.918	0.898
Old Man	0.883	0.883	0.880	0.879
Old Woman	0.942	0.916	0.933	0.910
Mean	0.917	0.901	0.914	0.898

Notes: “Complex Concept” refers to the target complex concept (e.g., *YOUNG MAN*). “Appropriate CC” is the calculated CC that correctly corresponds complex concept (*YOUNG* × *MAN* for *YOUNG MAN*). “Head match” is the CC that only contains the correct head concept constituent of the complex concept (*OLD* × *MAN* for *YOUNG MAN*). “Modifier match” is the CC that only contains the correct modifier concept constituent of the complex concept (*YOUNG* × *WOMAN* for *YOUNG MAN*). “No match” is the CC that contains no constituents that match with the complex concept (*OLD* × *WOMAN* for *YOUNG MAN*).

When considering the correlations of CCs with complex concepts, IALT shows a better pattern of results than the parietal/occipital fROI does. In both regions appropriate CCs are better correlated with complex concepts than are spurious CCs for 11 out of 12 opportunities (see Table 2 & 3). Closer inspection reveals that within IALT the average difference between these correlations (e.g., how much greater the

correlation between *YOUNG* × *MAN* and *YOUNG MAN* is than *YOUNG* × *WOMAN* and *YOUNG MAN*) is significantly greater (mean difference in $r = 0.20$, $SD = 0.19$) than within the parietal/occipital fROI (mean difference in $r = 0.013$, $SD = 0.011$, $t(11) = 3.44$, $p = 0.0055$).

Why was there no evidence of conceptual combination within the left IFG? Perhaps left IFG processes conceptual combinations at a later stage of the compositional process. Indeed, Hagoort and colleagues have suggested that it may have such a function (2009). Specifically, they argue that the left IFG is responsible for semantic unification (the combination of multi-sentence discourse into coherent ideas; Hagoort et al., 2009). It could be that the combination observed in IALT is just an early stage of compositional processing. In this stage, the representations of simple concepts are combined so that regions like the left IFG can use them for more elaborate analyses. Within left IFG, emergent qualities of particular combinations might be revealed (e.g., the bright colors and size of a *BEACH TOWEL*), and larger arrays of concepts may be combined (as in speech). If this is true, then left IFG may not respond to the basic composition seen in IALT.

Critical Concerns from Study 1 and Motivation for Studies 2 & 3

In the study reported above I was left with two major concerns. First, the results may reflect sub-vocal repetition (e.g., repeating *YOUNG* and *MAN* while conceptualizing *YOUNG MAN*) rather than pure conceptual combination. In this instance, we would simply be observing the serial activation of phonological representations shared by constituent and complex concepts. To some extent this concern was obviated by the fact that we found significant unification of complex concepts. This suggests that participants did not process the complex concepts used in Study 1 by activating phonological constituents. Further, most research examining the correlates of verbal working memory and phonological processing do not implicate the left anterior temporal lobe. Instead, such research has revealed regions of the inferior lateral frontal lobes as well as parietal lobes (Awh et al., 1996; Shivde & Thompson-Schill, 2004). While there are reasons to believe that the compositionality seen in IALT does not reflect phonological processing, this cannot be confirmed without further experimental replication.

The second concern from the pilot study comes as a result of the nature of the concepts I used. As previously noted, the distributed-only model of the cortical representation of concepts posits that different types of concepts (e.g., living-things and artifacts) may activate very different regions of cortex (Martin, 2007). It follows that compositionality in the distributed-only model would occur in different places for different concepts (Barsalou, 1999). Because only social concepts were used in Study 1, we are unable to know with certainty that IALT is a locus of general conceptual combination. It remains that IALT may only combine social concepts. While there is

strong evidence to suggesting that IALT processes both social and non-social concepts (e.g., Snowden et al., 1996), it is impossible to make any general claims about compositionality within the left anterior temporal lobe without assessing the composition of other types of concepts.

In the studies that follow, I attempted to address both of these concerns. Study 2 examined conceptual combination with phonologically distinct social concepts, namely: *GIRL*, *BOY*, *MAN*, *WOMAN*, *CHILD*, *ADULT*, *FEMALE*, and *MALE*. Here, I sought to replicate the results of the first study, but with non-phonologically dependent concepts. In the third study I evaluated the cortical basis of compositionality using non-social concepts: *WILD*, *FARM*, *MAMMAL*, *BIRD*, *EAGLE*, *CHICKEN*, *LION*, and *COW*. Again, I was attempting to replicate the first study, but with non-social and phonologically distinct concepts. Across both Studies 2 and 3, the goal was to test the importance of the left anterior temporal lobe in conceptual combination.

Methodologies and Analyses Common to Studies 2 & 3

Since Studies 2 and 3 share essentially the same methodologies and analyses, these will be described once fully in this section. In fact, much of the methodology described below is highly similar to the methods used in Study 1. Completely novel methods and analyses begin in the section entitled “Searchlight Analysis.” Please note that I will typically only refer to the constituent (i.e., *MALE*, *FEMALE*, *ADULT*, and *CHILD*) and complex (i.e., *MAN*, *WOMAN*, *BOY*, and *GIRL*) concepts used in Study 2. This is done for the sake of brevity, and the reader should know that the methodologies and analyses were also applied to the constituent (i.e., *WILD*, *FARM*, *MAMMAL*, and *BIRD*) and complex (i.e., *LION*, *EAGLE*, *COW*, and *CHICKEN*) concepts of Study 3.

As in Study 1, I hypothesized that in conceptual areas, the product of voxel-wise activations elicited by a given concept (e.g., *GIRL*) would be better correlated with the product of the activations elicited by its semantic constituents (e.g., *CHILD* × *FEMALE*) than with spurious combinations (e.g., *ADULT* × *MALE*). These concepts were presented to participants for classification during functional magnetic resonance imaging, and whole brain neural representations for each concept were acquired. As in Study 1, neural representations were gathered while participants viewed identical stimuli (e.g., stimuli seen while categorizing *MALE* were the same as when categorizing *CHILD*). *Thus, any differences in representation were strictly due to conceptualization.*

Stimuli

In each experiment I examined eight concepts (e.g., *FEMALE*, *MALE*, *ADULT*, *CHILD*, *WOMAN*, *MAN*, *GIRL*, and *BOY*). One hundred and twelve images

were collected, 28 for each of the complex concepts (e.g., *WOMAN*, *MAN*, *BOY*, and *GIRL*). All images were collected via Internet image searches, and were converted to grayscale and rescaled to approximately the same size. Masking removed most aspects of the source image background.

Seventy-two of the stimuli (18 for each complex concept) were used to create six sequences of 12 (no image repeated). These sequences will henceforth be referred to as “target” sequences and the images that make them up “target” images. Within every target sequence complex concepts were instantiated three times; thus, each of the constituent concepts were instantiated six times. Of the remaining 40 stimuli, 16 were used as “hash mark images.” Superimposed on each of these hash mark images was a single, randomly placed black hash mark (#). Twelve images (four each of the complex concepts) were also randomly selected from the target sequences to become hash mark images (these 12 images remained in their respective target sequences). The remaining 24 stimuli were used as “filler” images.

fMRI task

Prior to the fMRI experiment, participants would be shown all of the images used in the experiment. They were also shown randomly selected examples of hash mark images. Participants were not allowed to begin the experiment until they were comfortable classifying each type of stimulus as either a member or nonmember of our eight concepts. When asked if any image was an ambiguous or poor member of their specific concept, all participants stated that concept membership was always clear.

The fMRI task consisted of four different trial types. All trials consisted of a randomized sequence of images — each presented for 850 ms followed by a 400 ms fixation cross. At trial onset participants were presented with a written display (for

5000 ms) of one of the eight concepts or the words “hash mark.” If the trial was preceded by a concept label (e.g., “BOY”), the participant had to decide the membership of each image in the given concept category. If prompted with “hash mark,” participants were required to determine for each image whether it contained a hash mark; in these “hash mark” trials the presence or absence of a hash mark on a given image was randomly determined. Question marks would occasionally appear for 3000 ms within a sequence of images. Upon encountering a question mark while classifying images, participants would press one button with their index finger (confirming concept membership or presence of a hash mark) or another button with their middle finger (rejecting concept membership or indicating the absence of a hash mark) in reference to the last image they had seen.

Target trials were composed of a target sequence (12 images), and lasted a total of 15 seconds. During these trials a question mark never appeared.

Catch trials consisted of a random sequence of one to 11 images, followed by a question mark, and then a fixation cross. The fixation cross was presented for varying amounts of time, and was used to bring the total trial length to 15 seconds. These catch trials were composed of filler and up to four randomly selected target images. We used catch trials to ensure participants’ attention during target trials; participants had no way of distinguishing a catch trial from a target trial prior to the presentation of a question mark.

Hash mark trials consisted of a sequence of 12 images taken from the filler and hash mark images. During these trials a question mark never appeared. Like the target trials, hash mark trials lasted a total of 15 seconds.

Finally, *hash mark catch trials* were composed of one to eleven images taken from the filler and hash mark images, followed by a question mark, and then a fixation cross. As with the catch trials, the fixation cross brought the total trial length to 15 seconds. Hash mark and hash mark catch trials were used to separate verification of one concept (e.g., *MAN*) from the next concept (e.g., *WOMAN*). In this way, the hash mark trials “cleared” the neural representation of concepts that preceded them. I also note that by including target images in each of the trial types I prevented participants from distinguishing trials on the basis of images shown.

fMRI procedure

Each participant completed an anatomical image scan followed by eight data acquisition runs. Each acquisition run consisted of six target, two catch, five hash mark, and two hash mark catch trials. Participants verified concept membership for each of the eight concepts once per run (during the six target and two catch trials). These verification trials were interleaved with seven hash mark and hash mark catch trials. The order of the concepts verified in each run was pseudo-randomized such that each concept preceded or followed every other concept across the entirety of the experiment. Catch and hash mark trials occurred randomly within acquisition runs. Across all eight runs, each concept was verified within a target trial six times (and in a catch trial twice).

An important characteristic of my design, shared with Study 1, is that the same six target sequences were used for concept verification for each of the eight concepts. This means that during target trials, different concepts were represented in the mind while viewing the same set of images. Therefore any differences in neural activation

between concepts must be the result of mental representation rather than the stimuli themselves. For any given target sequence, images were presented in random order. This was done to prevent participants from recognizing when a target sequence was occurring. (Since no response was elicited during such sequences participants could have simply ignored them and attended only to catch trials.) In fact, no participant indicated knowledge of stimulus differences between target and catch trials when asked at the conclusion of the experiment.

Image acquisition

A high-resolution anatomical image (T1-MPRAGE, TR = 2500 ms, TE = 4.3 ms, FA = 8°, matrix size = 256×256) was acquired for functional data registration and cross-participant spatial normalization. I used blood oxygen level-dependent (BOLD) response as a measure of neural activation. Using a Siemens 3.0 Tesla Allegra Scanner (Siemens, Erlangen, Germany) with a standard “bird-cage” head coil, I acquired echo planar images (EPI; TR = 2000 ms, TE = 30 ms, FA = 80°, matrix size 64×64). Via 33 interleaved 3 mm axial slices (1 mm inter-slice gap) whole brain coverage was achieved.

Image analysis

All fMRI data were processed using Analysis of Functional Neuro-Images software (AFNI; Cox, 1996). Each participant’s motion was corrected using a six-parameter 3D motion correction algorithm following slice scan-time correction. All data were then spatially smoothed using a 6 mm full width at half maximum Gaussian kernel. Data were then low-pass filtered with a frequency cut-off of 0.1 Hz. Signal was then normalized to percent difference from the mean. Each participant’s EPI data were then masked so that only brain regions contributing signal were kept.

Next, multiple regression was used to generate parameter estimates for each participant. Nine regressors of interest—hash marks and the eight concepts—were convolved with a canonical hemodynamic response function and entered into a general linear model. These regressors were specific to the 15 second target and hash mark trials. As mentioned above, during these trials participants were presented with every type of image; here I am modeling the entire span of each trial rather than responses to just the type of image being searched for. There were six target trials per concept and 40 hash mark trials across the entire experiment. All catch trials, motion estimates, and estimates of time-dependent linear and quadratic trends caused by scanner drift were included as regressors of no interest. The resultant parameter maps (in percent signal change) for each concept along with hash marks were projected into Talairach space (Talairach & Tournoux, 1988). These average voxel-wise neural representations were used in subsequent analyses.

Searchlight analysis

Because I was able to validate the use of multiplication as a combinatorial rule in the first study, I utilized a much more hypothesis driven approach to isolating regions showing evidence of the sort of conceptual combination (multiplicative) that was hypothesized. Thus, in both Studies 2 and 3 I used spherical searchlight (SL; Kriegeskorte et al, 2006) analysis to isolate fROIs. These SL analyses were carried out on each participant's data using the AFNI Matlab library and Matlab (R2009b; Mathworks Inc, 2009).

Within the SL analysis, every voxel in the brain was analyzed as the center of a 3-voxel radius sphere (the maximum number of voxels included in such a sphere was

121 —fewer when the center voxel was near an edge of the brain. In each sphere, the voxel-wise neural representation of each concept was linearly scaled to run from zero to one. Then, appropriate conceptual combinations (CCs) for each of our four complex concepts were created. For Study 2, these appropriate CCs were as follows: *BOY* = *CHILD* × *MALE*; *GIRL* = *CHILD* × *FEMALE*; *MAN* = *ADULT* × *MALE*; *WOMAN* = *ADULT* × *FEMALE*. For Study 3, these appropriate CCs were as follows: *LION* = *WILD* × *MAMMAL*; *EAGLE* = *WILD* × *BIRD*; *COW* = *FARM* × *MAMMAL*; *CHICKEN* = *FARM* × *BIRD*. For each appropriate CC, the neural representations for the constituent concepts (e.g., *BOY* and *GIRL*, for *CHILD*) were multiplied. Within the sphere, spurious CCs were also created (three for each concept). These spurious CCs were as follows. For Study 2, *BOY*: *CHILD* × *FEMALE*, *ADULT* × *MALE*, and *ADULT* × *FEMALE*; for *GIRL*: *CHILD* × *MALE*, *ADULT* × *FEMALE*, and *ADULT* × *MALE*; for *MAN*: *ADULT* × *FEMALE*, *CHILD* × *MALE*, and *CHILD* × *FEMALE*; for *WOMAN*: *ADULT* × *MALE*, *CHILD* × *FEMALE*, and *CHILD* × *MALE*. For study 3, *LION*: *WILD* × *BIRD*, *FARM* × *MAMMAL*, and *FARM* × *BIRD*; for *EAGLE*: *WILD* × *MAMMAL*, *FARM* × *BIRD*, and *FARM* × *MAMMAL*; for *COW*: *FARM* × *BIRD*, *WILD* × *MAMMAL*, and *WILD* × *BIRD*; for *CHICKEN*: *FARM* × *MAMMAL*, *WILD* × *BIRD*, and *WILD* × *MAMMAL*. Williams test of dependent correlation (Steiger, 1980) was used to determine whether a given concept was significantly better correlated with its appropriate CC (e.g., *CHILD* × *MALE* for *BOY*) than with one of its spurious CCs (e.g., *CHILD* × *FEMALE* for *BOY*). Each concept's appropriate CC could be significantly better than three spurious CCs. Hence, up to 12 times (four concepts × three spurious CCs) a given concept could be significantly better correlated to its

appropriate CC than to its spurious CCs. Consequently, my measure of performance—that is, the value attributed to the center voxel of each sphere—was a number between zero and 12. I assigned the score of zero to any SL sphere with less than ten voxels, and also to any sphere with ten voxels of the same value. For each participant, the SL analysis resulted in a brain map showing SL performance across the entire cortex. Thus the resultant brain maps would reveal cortical regions where multiplicative compositionality occurred most significantly.

Group analysis

In Study 2 and 3, I identified brain regions that showed conceptual combination across participants. This was achieved by averaging the SL analysis brain maps for all participants. This average brain map was then masked to exclude voxels that were absent from the cortex of any participant's data. The group level threshold for significance was determined through a label-shuffle test. For each shuffle iteration, one randomly permuted order of labels for the eight concepts was generated, the same SL analysis described above was completed for each participant, and the results were averaged to create a group level brain map.

A total of 600 label permutations were completed for each study. Once an acceptable voxel-wise α -level was identified, group level brain maps were thresholded according to this value and significant clusters were isolated. It is important to note that these shuffle tests act as a family-wise correction for multiple comparisons because they reveal the probability of attaining a given mean voxel value across the entire brain-space. The results of these permutation tests and voxel-wise α -levels for each study are reported in each study's analysis section below.

Study 2: Compositionality of Phonologically Independent Social Concepts

(Adapted from: Baron & Osherson, 2011)

The results of Study 1 suggest that the left anterior temporal lobe is involved in conceptual combination, yet there remains a concern about the phonological dependence of the concepts used. In Study 2, I sought to replicate the general findings of Study 1, but with the use of the phonologically independent social concepts: *MALE*, *FEMALE*, *ADULT*, *CHILD*, *MAN*, *WOMAN*, *BOY*, and *GIRL*.

Method

Participants

Fifteen Princeton University graduate and undergraduate students (all female; 18-28 years old) participated in the fMRI study. Three participants' data were not included in subsequent analyses (one forgot the task, another fell asleep, and the third made excessive movements). All participants gave their written consent and were debriefed as required for studies approved by Princeton University's Institutional Review Board.

Stimuli

In the experiment I examined eight concepts: *FEMALE*, *MALE*, *ADULT*, *CHILD*, *WOMAN*, *MAN*, *GIRL*, and *BOY*. To instantiate them, faces were gathered from images posted on flickr.com (each designated as “noncommercial” or unclassified). One hundred and twelve images were collected, 28 for each of *WOMAN*, *MAN*, *BOY*, and *GIRL*. The face stimuli for each concept consisted of approximately the same number of happy versus neutral expressions — no faces expressed negative emotions. *MAN* and *WOMAN* (i.e., *ADULT*) faces were restricted to images of adults who were approximately 25-45 years of age. *BOY* and *GIRL* (i.e., *CHILD*) faces were

restricted to images of children who were approximately 4-11 years of age. All images were converted to grayscale and rescaled to approximately the same size. Circular masking removed most aspects of the source image background. No participant recognized the identity of any of the face stimuli when queried at the conclusion of the experiment. See Fig. 4.



Figure 4. Examples of the four categories of faces used as stimuli and one example of a face containing a hash-mark. From left to right: *MAN*, *BOY*, *GIRL*, *WOMAN*, and *BOY* with a hash-mark.

Results

Regions showing conceptual combination across all participants

The label shuffle test revealed that the likelihood of finding a group level voxel with a mean SL analysis value greater than 4.83 corresponded to a voxel-wise α -level of $p < 0.01$. I therefore thresholded the group average brain at 4.83, and defined fROIs as clusters containing more than twenty contiguous voxels. In this group analysis, 12 fROIs showed evidence of significant conceptual combination (See Table 4).

The best performing fROI was a 97-voxel cluster located in the left anterior temporal lobe (ATL). Across participants, the average number of times (out of 12) that an appropriate CC was better correlated with a complex concept than were any spurious CCs within this left ATL fROI was 6.25 (See Table 4 & Fig. 5).

Table 4. *Voxel clusters from the Study 2 group level searchlight analysis*

Region	Peak Voxel (x,y,z)	Cluster Size (3x3x4mm) Voxels	Mean SL-value (0-12)
R. Precentral Gyrus	43.5, -7.5, 32	103	6.08
R. Claustrum	25.5, 22.5, 16	101	5.75
L. Anterior Temporal Lobe	-40.5, 13.5, -24	97	6.25
L. Parahippocampal Gyrus	-19, -16, -16	80	5.50
L. Sup. Parietal Lobule	-19, -50, 60	72	5.75
L. Inf. Parietal Lobule	-52.5, -31, 36	69	5.83
R. Precentral Gyrus	58.5, 1.5, 12	58	5.67
R. Precuneus	7.5, -64, 52	42	5.93
R. Cingulate Gyrus	7.5, 16.5, 40	39	5.50
L. Putamen	-19.5, 13.5, 4	32	5.42
R. Middle Temporal Gyrus	58.5, -4.5, -12	26	5.58
R. Superior Frontal Gyrus	22.5, 46.5, 20	25	5.42

Notes: “Region” refers to the anatomical location of the peak voxel. “Mean SL-value” is the voxel with the greatest mean SL value across participants within the cluster.

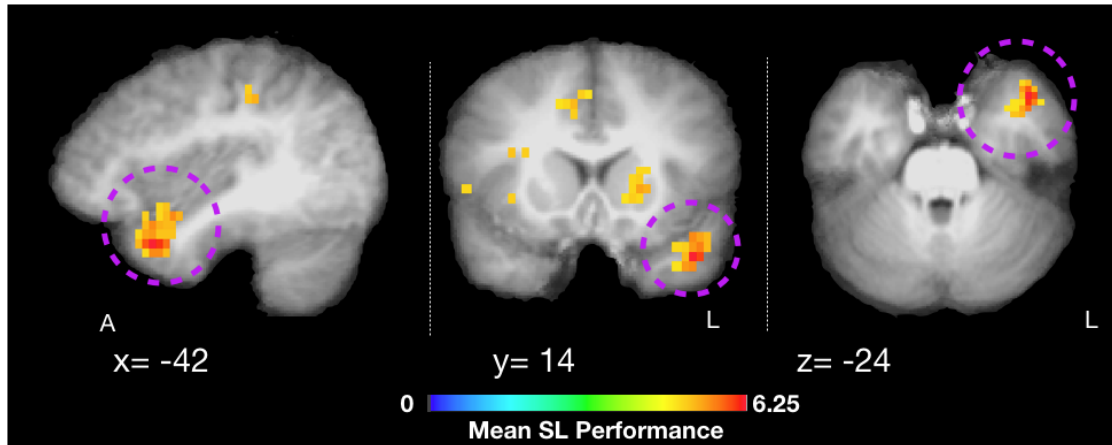


Figure 5. Left anterior temporal lobe fROI (circled) from Study 2. This region showed evidence of significant conceptual combination across participants (6.25, $p < 0.01$). These statistical maps show average results of the SL analyses performed on all 12 subjects.

Only one other cluster performed nearly as well as the left ATL fROI, a 103-voxel cluster located in the right precentral gyrus (See Table 4 & Fig. 6). Across participants, the average number of times (out of 12) that an appropriate CC with better correlated with a complex concept than were any spurious CCs within the right precentral gyrus fROI was 6.08.

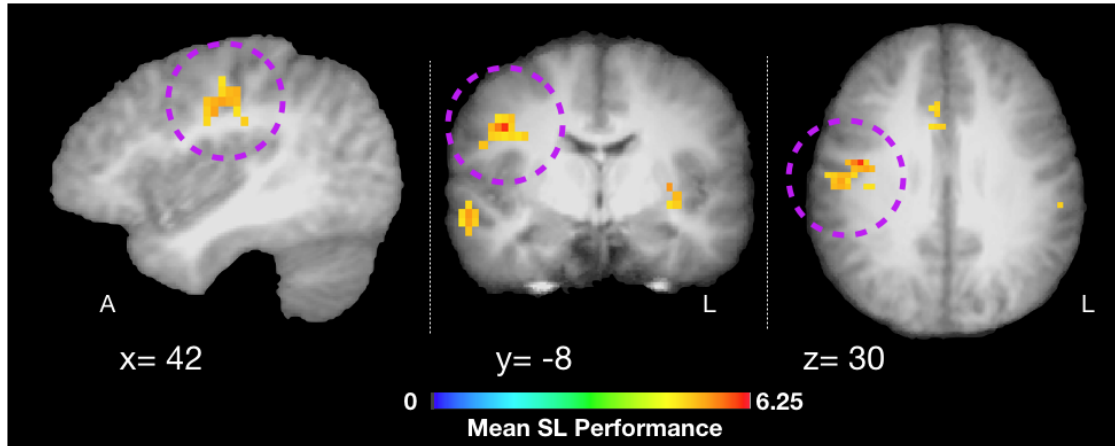


Figure 6. Right precentral gyrus fROI (circled) from Study 2. This region showed evidence of significant conceptual combination across participants (6.08, $p < 0.01$). These statistical maps show average results of the SL analyses performed on all 12 subjects.

fROI performance was also assessed by calculating the mean correlation across participants for each CC (both appropriate and spurious) with complex concepts. For the left ATL fROI, appropriate CCs were better correlated with complex concepts than were spurious concepts for ten out of 12 possible opportunities (see Table 5a). Within the right precentral gyrus fROI, appropriate CCs beat spurious CCs nine of 12 times (see Table 5b). However, the average difference between these correlations in the left ATL fROI (e.g., how much greater the correlation between *MALE* $\times$ *CHILD* and *BOY* is than *MALE* $\times$ *ADULT* and *BOY*) was *not* significantly greater (mean difference in $r = 0.057$, $SD = 0.053$) than within the right precentral gyrus fROI (mean difference in $r = 0.044$, $SD = 0.075$, $t(11) = 0.70$, $p = 0.49$).

Table 5a. Mean correlations in the left ATL fROI (Study 2) of appropriate and spurious CCs with each complex concept

Complex Concept	Appropriate CC	Spurious 1	Spurious 2	Spurious 3
Boy	0.576	0.505	0.517	0.411
Girl	0.493	0.423	0.458	0.450
Man	0.513	0.482	0.477	0.526
Woman	0.455	0.378	0.475	0.322
Mean	0.509	0.447	0.482	0.427

Table 5b. Mean correlations in the right precentral gyrus fROI (Study 2) of appropriate and spurious CCs with each complex concept

Complex Concept	Appropriate CC	Spurious 1	Spurious 2	Spurious 3
Boy	0.685	0.657	0.596	0.552
Girl	0.694	0.591	0.655	0.581
Man	0.511	0.519	0.601	0.596
Woman	0.656	0.633	0.579	0.544
Mean	0.637	0.600	0.608	0.568

Notes: “Complex Concept” refers to the target complex concept (e.g., *BOY*). “Appropriate CC” is the calculated CC that correctly corresponds complex concept (*MALE* × *CHILD* for *BOY*). “Spurious 1” is the CC that only contains the correct age concept constituent of the complex concept (*FEMALE* × *CHILD* for *BOY*). “Spurious 2” is the CC that only contains the correct gender concept constituent of the complex concept (*MALE* × *ADULT* for *BOY*). “No match” is the CC that contains no constituents that match with the complex concept (*FEMALE* × *ADULT* for *BOY*).

Discussion of Study 2

In Study 1, we observed conceptual combination in left ALT. However, the complex concepts used in that study (e.g., *YOUNG MAN*) were phonologically related to their constituents (*YOUNG* and *MAN*). In the current experiment, this confound was

addressed by using social concepts that were related on a purely semantic level (e.g., *BOY* versus *MALE* and *CHILD*).

The results of this study confirm the importance of the left ATL in conceptual combination, and also implicate a region of the right precentral gyrus in compositional processing. In these regions, the voxel-wise pattern of brain activity for a given concept was predicted by the product of activations for its constituents taken singly. The appearance of the right precentral gyrus fROI was unexpected, but it has been reported to respond to semantic information related to faces (Henke et al., 2003; Zysset, Huber, Ferstl, & von Cramon, 2002) as well as the retrieval of self-referential semantic information (Andreasen et al., 1995). This region is *not* seen in a recent 120-study meta-analysis of the neural correlates of conceptual processing (Binder et al., 2009). Perhaps the right precentral gyrus fROI only mediates conceptual representations for social concepts, and did not appear in the meta-analysis because Binder and colleagues collapsed across all conceptual domains (2009). In the present context, the compositionality observed within the right precentral gyrus fROI might reflect conceptual processing unique to social concepts—as would be expected in the distributed-only model of conceptual representation (Martin, 2007).

It is well established that the anterior temporal lobes play an important role in conceptual processing (Patterson et al., 2007; Visser et al., 2009). The pathological deterioration of ATL negatively affects conceptual knowledge quite broadly (Snowden et al., 1996). The effects of pathology have been reproduced in healthy participants through temporary lesions of bilateral ATL induced by transcranial magnetic stimulation (Lambon Ralph et al., 2009). Moreover, left ATL has been implicated in

tasks requiring semantic composition and processing (Humphries et al., 2006; Snijders et al., 2009; Spitsyna et al., 2006; Vandenberghe et al., 2002). That conceptual combination was observed within LATL is thus unsurprising, and provides more evidence for its importance in semantic processing.

All of the other regions that showed significant conceptual combination have appeared in previous studies of conceptual processing. Left hemisphere parahippocampal gyrus (Binder et al., 2009), putamen (Roskies et al., 2001), superior frontal gyrus (Devlin et al., 2002), and inferior (Assmus, Giessing, Weiss, & Fink, 2007) and superior parietal lobule (Zannino et al., 2010), are all found to respond to semantic tasks. The same is true for right hemisphere cingulate gyrus (Marques, Canessa, Siri, Catricala, & Cappa, 2008), superior frontal gyrus (Goldberg et al., 2007), middle temporal gyrus (Wible et al., 2006; Zannino et al., 2010), precuneus (Baker et al., 2001; Friederici et al., 2000; Zannino et al., 2010), and insula (Goldberg et al., 2007; Zannino et al., 2010). These regions may be part of the distributed network used to processes social concepts (though many of these regions overlap with non-social general conceptual regions, Binder et al., 2009), or they may be more generally involved in compositionality. Further evaluation of these fROIs—and comparisons between fROIs seen in both Study 2 and 3—is presented in the general dissertation discussion.

Study 3: Compositionality of Phonologically Independent Non-Social Concepts

Taken together, the results of Studies 1 and 2 show the importance of the left ATL in conceptual combination. However, in both experiments, compositionality was only observed for social concepts. It is possible that left ATL only combines social concepts. Though this seems unlikely given previous research showing that the left ATL responds to many different types of concepts (Mummery, Shallice, & Price, 1999; Noppeney & Price, 2002; Tsukiura, Mochizuki-Kawai, & Fujii, 2006), further experimentation was needed to implicate the left ATL in general compositionality. Thus, in Study 3, I attempted to replicate the results of my previous research, but with the non-social concepts: *WILD*, *FARM*, *MAMMAL*, *BIRD*, *LION*, *EAGLE*, *CHICKEN*, and *COW*.

Method

Participants

Twenty Princeton University graduate and undergraduate students (all female; 18-27 years old) participated in the fMRI study. Four participants' data were not included in subsequent analyses (one forgot the task, another fell asleep, and two made excessive movements). All participants gave their written consent and were debriefed as required for studies approved by Princeton University's Institutional Review Board.

Stimuli

In the experiment I examined eight concepts: *WILD*, *FARM*, *MAMMAL*, *BIRD*, *LION*, *EAGLE*, *CHICKEN*, and *COW*. To instantiate them, images of animals were gathered from online search-engine image searches. All images were converted to grayscale and rescaled to approximately the same size. Images showed roughly the same amount of each animal's body, and none of the images showed evidence of

human made artifacts in their background. See Fig. 7.



Figure 7. Examples of the four categories of animals used as stimuli and one example of an animal containing a hash-mark. From left to right: *CHICKEN*, *EAGLE*, *COW*, *LION*, and *EAGLE* with a hash-mark.

Results

Regions showing conceptual combination across all participants

The label shuffle test revealed that the likelihood of finding a group level voxel with a mean SL analysis value greater than 4.75 corresponded to a voxel-wise α -level of $p < 0.01$. I therefore thresholded the group average brain at 4.75, and defined fROIs as clusters containing more than twenty contiguous voxels. In this group analysis, 12 fROIs showed evidence of significant conceptual combination (See Table 6).

The best performing fROI was a 42-voxel cluster located in the left lateral anterior temporal lobe (ALT). Across participants, the average number of times (out of 12) that an appropriate CC with better correlated with a complex concept than were any spurious CCs within this left ALT fROI was 5.87 (See Table 6 & Fig. 8).

Table 6. *Voxel clusters from the Study 3 group level searchlight analysis*

Region	Peak Voxel (x,y,z)	Cluster Size (3x3x4mm) Voxels	Mean SL-value (0-12)
L. Cuneus	-10.5, -82.5, 28	111	5.62
R. Inf. Frontal Gyrus	40.5, 25.5, -4	57	5.5
R. Post. Cingulate Cortex	7.5, -49.5, 20	57	5.25
L. Anterior Temporal Lobe	-67.5, -7.5, -4	42	5.87
L. Precentral Gyrus	-16.5, -25.5, 67.9	42	5.69
R. Precuneus	16.5, -64.5, 59.9	36	5.50
L. Cuneus	28.5, -79.5, 28	27	5.06
Medial Premotor Cortex	4.5, 16.5, 59.9	27	5.37
L. Fusiform Gyrus	-43.5, -64.5, -15.9	25	5.24
L. Middle Frontal Gyrus	-31.5, 55.5, 0	24	5.44
L. Culmen	-13.5, -52.5, -4	24	5.44
R. Fusiform Gyrus	22.5, -88.5, -11.9	23	5.25

Notes: “Region” refers to the anatomical location of the peak voxel. “Mean SL-value” is the voxel with the greatest mean SL value across participants within the cluster.

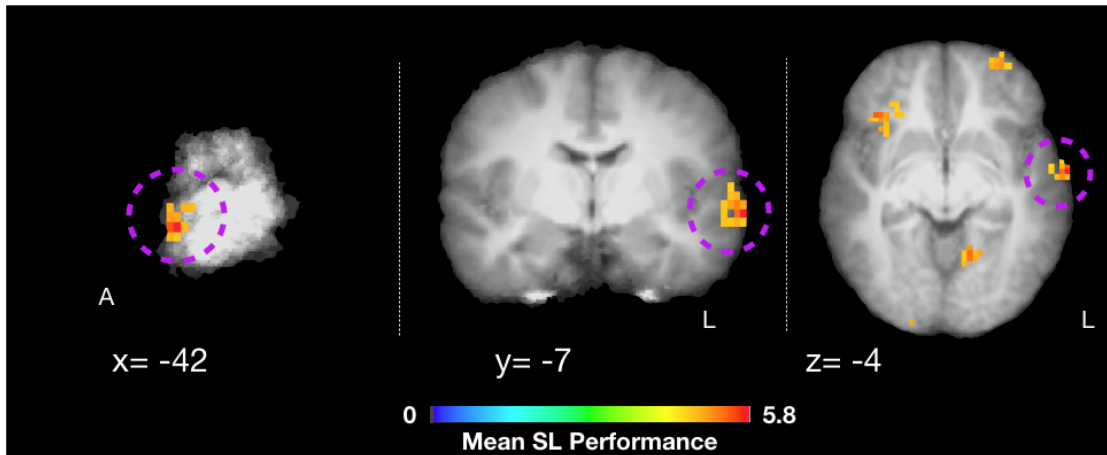


Figure 8. Left lateral anterior temporal lobe fROI (circled) from Study 3. This region showed evidence of significant conceptual combination across participants (5.87, $p < 0.01$). These statistical maps show average results of the SL analyses performed on all 16 subjects.

As in Study 2, the second best performing cluster was located within the precentral gyrus; however, in this instance, the fROI was in the left hemisphere (See Table 6 & Fig. 8). Across participants, the average number of times (out of 12) that an appropriate CC was better correlated with a complex concept than were any spurious CCs within this left precentral gyrus fROI was 5.69.

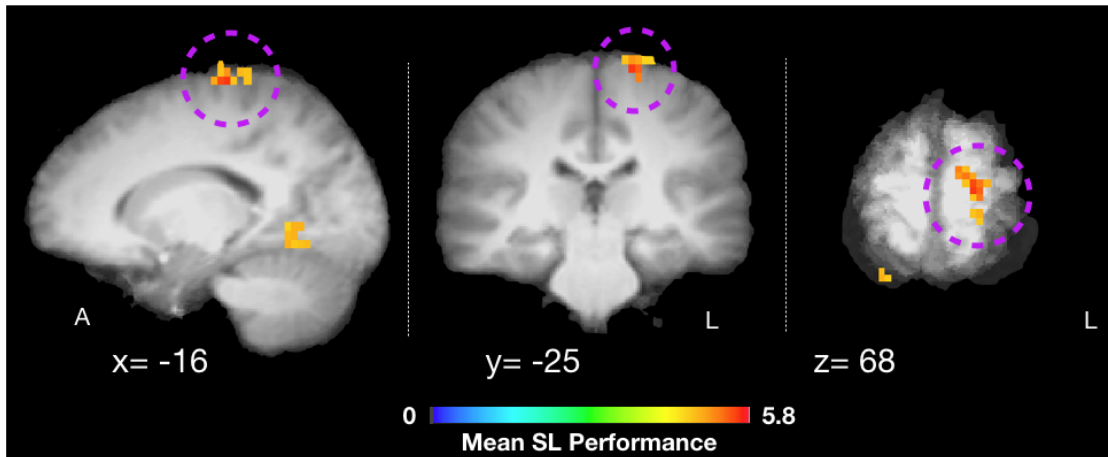


Figure 8. Left precentral gyrus fROI (circled) from Study 3. This region showed evidence of significant conceptual combination across participants (5.69, $p < 0.01$). These statistical maps show average results of the SL analyses performed on all 16 subjects.

Again, fROI performance was also assessed by calculating the mean correlation across participants for each CC (both appropriate and spurious) with complex concepts. For the left ALT fROI, appropriate CCs were better correlated with complex concepts than were spurious concepts for eight out of 12 possible opportunities (see Table 7a). Within the left precentral gyrus fROI, appropriate CCs outperformed spurious CCs eight of 12 times (see Table 7b). The average difference between these correlations in the left ALT fROI (e.g., how much greater the correlation between *WILD* $\times$ *BIRD* and *EAGLE* is than *WILD* $\times$ *MAMMAL* and *EAGLE*) was *not* significantly greater (mean difference in $r = 0.022$, $SD = 0.065$) than within the left precentral gyrus fROI (mean difference in $r = 0.015$, $SD = 0.029$, $t(11) = 0.43$, $p =$

0.68). None of the remaining fROIs had appropriate CCs outperform spurious CCs more than six of 12 times.

Table 7a. Mean correlations in the left ATL fROI (Study 3) of appropriate and spurious CCs with each complex concept

Complex Concept	Appropriate CC	Head Match	Modifier Match	No Match
Eagle	0.533	0.581	0.530	0.515
Chicken	0.687	0.596	0.646	0.496
Lion	0.594	0.578	0.592	0.634
Cow	0.503	0.506	0.526	0.490
Mean	0.580	0.565	0.574	0.559

Table 7b. Mean correlations in the left precentral gyrus fROI (Study 3) of appropriate and spurious CCs with each complex concept

Complex Concept	Appropriate CC	Head Match	Modifier Match	No Match
Eagle	0.549	0.562	0.528	0.483
Chicken	0.660	0.637	0.641	0.624
Lion	0.528	0.523	0.540	0.563
Cow	0.526	0.521	0.522	0.469
Mean	0.566	0.561	0.558	0.535

Notes: “Complex Concept” refers to the target complex concept (e.g., *EAGLE*). “Appropriate CC” is the calculated CC that correctly corresponds complex concept (*WILD* × *BIRD* for *EAGLE*). “Head match” is the CC that only contains the correct head concept constituent of the complex concept (*FARM* × *BIRD* for *EAGLE*). “Modifier match” is the CC that only contains the correct modifier concept constituent of the complex concept (*WILD* × *MAMMAL* for *EAGLE*). “No match” is the CC that contains no constituents that match with the complex concept (*FARM* × *MAMMAL* for *EAGLE*).

Discussion of Study 3

Again we observed evidence of significant conceptual combination within the left anterior temporal lobe; however, in this case compositionality was shown for non-social concepts. The IALT fROIs isolated in Studies 1 and 3 are startlingly similar (see Fig. 9). Nearly 36 percent of the Study 3 IALT fROI overlaps the Study 1 fROI (15 of 42 voxels). Given IATL's well-established role in conceptual processing (e.g., Humphries et al., 2006; Lambon Ralph et al., 2009; Spitsyna et al., 2006; Vandenberghe et al., 2002; Visser et al., 2009), its position within theoretical models of conceptual representation (i.e., the hub in the distributed-plus-hub model; Patterson et al., 2007), and my consistent observation of it in each of my studies, there is strong evidence to believe IATL may be the cortical locus of conceptual combination.

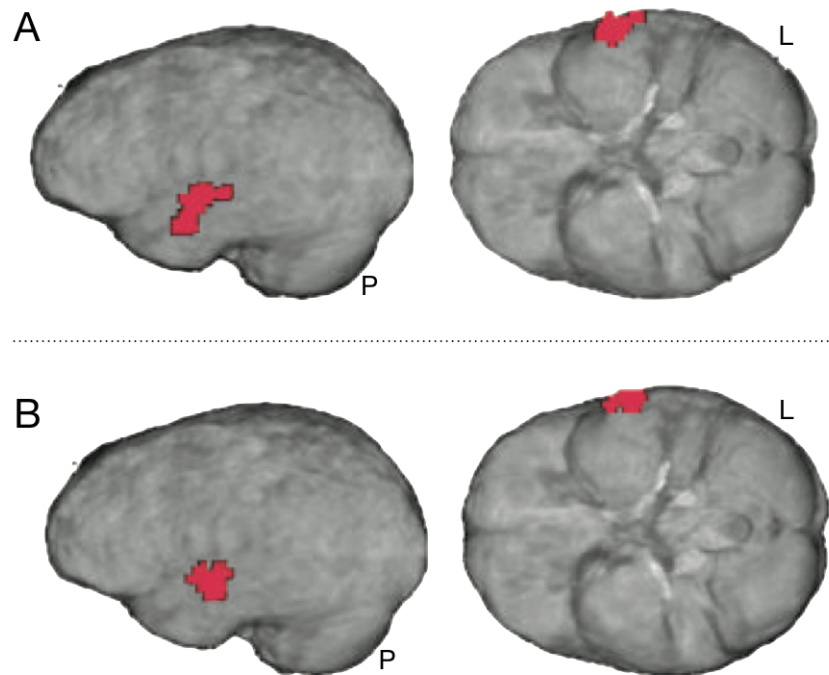


Figure 9. Glass-brain view: Left ALT fROIs from A) Study 1 (e.g., *YOUNG* $\times$ *MAN* for *YOUNG MAN*), and B) Study 3 (e.g., *WILD* $\times$ *BIRD* for *EAGLE*). These regions show evidence of significant conceptual combination. *Note.* A glass-brain view is meant to reveal the position of an fROI in three dimensions, by placing an opaque fROI within a transparent brain. Though the brain in this figure does not appear to be transparent, it is with respect to the fROIs.

Noteworthy compositionality was also observed within the left precentral gyrus. There is some evidence linking this region to conceptual tasks (Canessa, Borgo, Cappa, & Perani, 2008; Marques et al., 2008; Wiggs, Weisberg, & Martin, 1999); however, many studies of conceptual and semantic representation have failed to consistently observe left precentral gyrus (Binder et al., 2009). This precentral fROI typically responds in motor and sensory tasks related to the movement of limbs (Penfield & Rasmussen, 1950; Rizzolatti & Luppino, 2001; Yousry et al., 1997). In both the distributed-only and distributed-plus-hub models of cortical conceptual representation, motor and sensory regions are critically involved in conceptualization (Barsalou, 1999; Paterson et al., 2007). This region of precentral gyrus appears to be involved in processing semantic knowledge related to action (Canessa et al., 2008; Hauk, Johnsrude, & Pulvermuller, 2004). Perhaps, the compositionality observed in the precentral gyrus is the result of some sensory or motor simulation needed to represent the animal concepts used in this study. This is purely speculation, and will require further study.

All the other regions showing significant compositionality have been previously observed in studies of conceptualization. The left hemisphere fusiform gyrus (Baker et al., 2001; Binder et al., 2009; Denmonet et al., 1992), cuneus (Luke, Liu, Wai, Wan, & Tan, 2002; Sheldon & Moscovitch, 2011), middle frontal gyrus (Luke et al., 2002; Sheldon & Moscovitch, 2011), and culmen (Luke et al., 2002) prefer conceptual stimuli/tasks. Right hemisphere inferior frontal gyrus (Friederici et al., 2000), posterior cingulate gyrus (Binder et al., 2009), fusiform gyrus (Baker et al., 2001; Zannino et al., 2010), precuneus (Baker et al., 2001), and superior frontal gyrus

(Goldberg et al., 2007), also show prefer for semantic tasks. However, only one of these regions—right precuneus—was also observed in Study 2. Consequently, it seems likely that the regions not common to both Studies 2 and 3 are not used in general conceptual combination.

General Discussion

The Left Anterior Temporal Lobe and Conceptual Combination

Conceptual combination was consistently observed within the left anterior temporal lobe. In the left anterior temporal lobe fROIs, the voxel-wise representation of a concept (e.g., *BOY*) could be simulated by the product of the representations of its conceptual constituents (e.g., *MALE* and *CHILD*) considered separately. This was observed for social (e.g., *BOY* and *YOUNG MAN*) as well as non-social (e.g., *EAGLE*) concepts. The left anterior temporal lobe has been shown to play an important role in conceptual processing (Mummery, Shallice, & Price, 1999; Visser et al., 2009; Noppeney & Price, 2002; Patterson et al., 2007). It has also been implicated in tasks that require semantic composition and processing (Humphries et al., 2006; Snijders et al., 2009; Vandenberghe et al., 2002). Thus the conceptual combination observed within the left anterior temporal lobe was anticipated, and provides even more evidence for its importance to semantic processing.

The appearance of the left anterior temporal lobe as the locus of conceptual combination also informs the debate surrounding the distributed-only (Barsalou, 1999; Martin, 2007) and the distributed-plus-hub (Patterson et al., 2007) models of cortical conceptual representation. The distributed-only model predicts that conceptual combinations for different concept types (e.g., social and non-social) will occur in different concept-specific regions of cortex (Barsalou, 1999; Martin, 2007). We did not find evidence to support this.

For each of the studies presented in this dissertation, the highest level of compositional processing was *always* observed within the left anterior temporal lobe

(see Fig. 10). Had the distributed-only model been correct, compositionality of animal-specific concepts should have occurred in brain regions that preferentially process animals (i.e., the posterior temporal lobe; Chao, Weisberg, & Martin, 2002; Grossman et al., 2002). This was not the case, as 15 of 42 voxels in the Study 3 fROI overlapped with the Study 1 fROI. That such compositionality was observed within a single region of cortex, for different types of concepts, provides evidence for the distributed-plus-hub model of conceptual representation (Patterson et al., 2007). That this region is the actual hub proposed by Patterson and colleagues further supports their theory while adding validity to our results (2007).

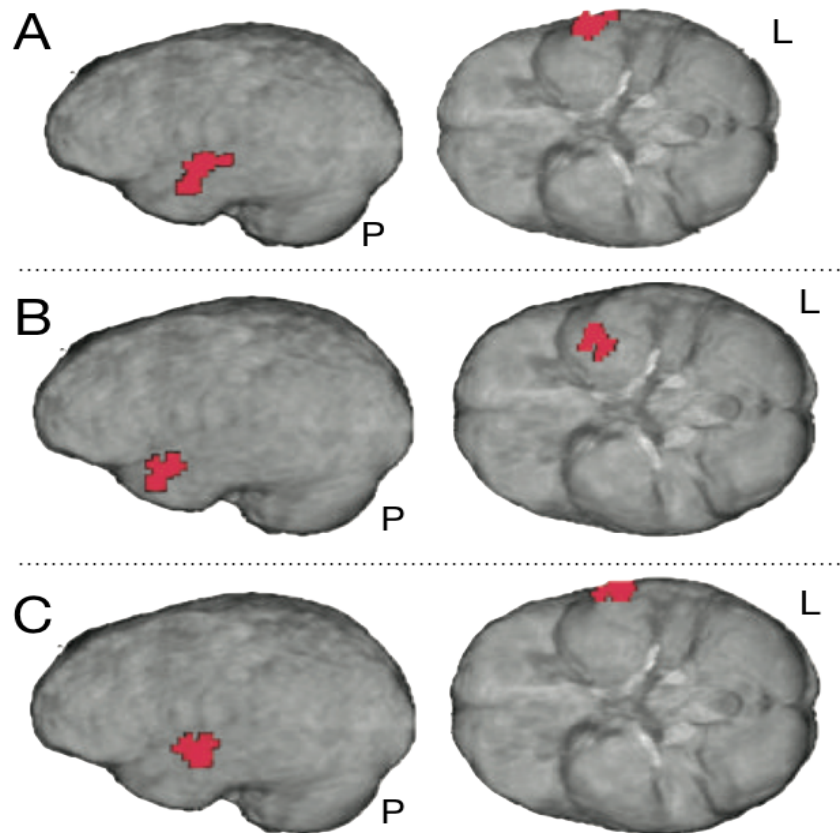


Figure 10. Glass-brain view: Left ALT fROIs from A) Study 1 (e.g., *YOUNG* × *MAN* for *YOUNG MAN*); B) Study 2 (e.g., *MALE* × *CHILD* for *BOY*); and Study 3 (e.g., *WILD* × *BIRD* for *EAGLE*). These regions showed strongest conceptual combination in their respective study.

What allows the anterior temporal lobes to serve as the hubs of the distributed-plus-hub model, and—in the case of the left anterior temporal lobe—the locus of conceptual combination? The most logical explanation is the impressive interconnectivity the anterior temporal lobes share with sensory and prefrontal cortices. They are connected to higher order auditory, visual, olfactory, and somatosensory processing areas (Kondo, Saleem, & Prince, 2003; Markowitsch et al., 1985). These connections to sensory cortex—where distributed sensory-dependant representations of concepts originate (e.g., Barsalou, 1999)—could allow for the creation of high-level amodal conceptual representations within the anterior temporal lobes.

The anterior temporal lobes are also connected to the orbitofrontal, medial prefrontal, and the lateral prefrontal cortices (Jones & Powell, 1970; Markowitsch et al., 1985; Moran, Mufson, & Mesulam, 1987; Kondo et al., 2003). These prefrontal connections, in agreement with theories of prefrontal function (e.g., Miller & Cohen, 2001; McClelland, McNaughton & O'Reilly, 1995), could guide the processing of the anterior temporal lobes according to task relevant cognitive and attentional demands. Such prefrontal “guidance” would facilitate the conceptual combination of amodal conceptual representations, while the prefrontal cortex (e.g., left IFG) could use the conceptual representations of the anterior temporal lobe for further evaluation (e.g., uncovering emergent features; Hampton, 1995) and greater semantic unification (e.g., Hagoort, 2009).

It is worth noting that the aforementioned connectivity studies were completed in non-human primates using transneuronal tracer methodologies (Loewy, 1998). Because these studies reveal neural connections via the transmission of viral infections

across the cortex, such experiments are typically not done in humans. In humans, connectivity is usually assessed through post-mortem fiber tract dissections and fMRI correlation analyses. While these methodologies do not reveal connectivity with the same level of certainty as transneuronal tracer studies, both fMRI connectivity and post-mortem cortical evaluations suggest that the connections reported above are in humans as well (Chabardes et al., 2002; Croxson et al., 2005; Damoiseaux et al., 2007; Simmons et al., 2010).

The Role of the Precentral Gyrus in Conceptual Combination

In Study 2 and 3 we observed that regions of the precentral gyrus were the second best performing fROIs with regard to compositionality (see Fig. 11). The observation of conceptual combination in this region of cortex was unexpected, as neither fROI is located in an area of the brain typically active during tasks relying on conceptual manipulation (Binder et al., 2009). These fROI are also located in extremely dissimilar portions of the precentral gyrus (see Fig. 11). Specifically, the fROI observed in Study 2 is located in the right hemisphere while the Study 3 fROI was found in the left. The Study 2 fROI is also in a more lateral and anterior region of cortex than the Study 3 fROI.

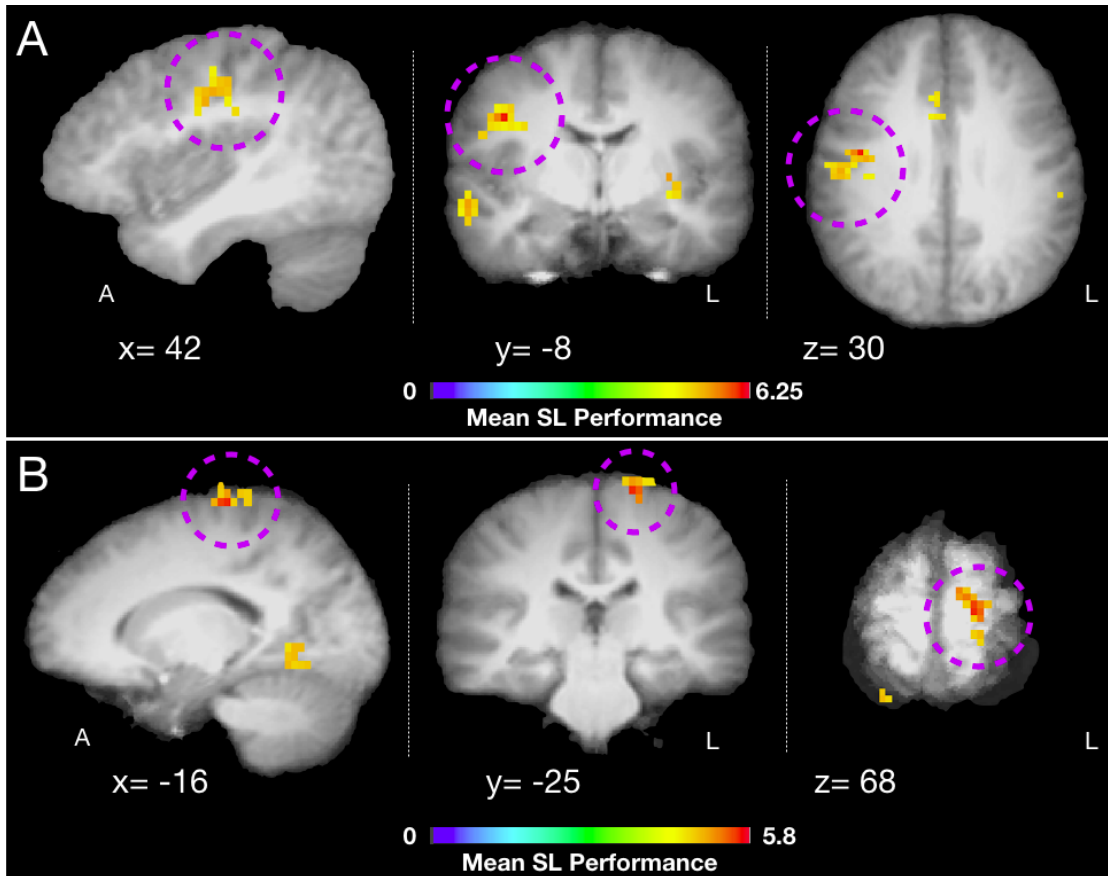


Figure 11. Precentral gyrus fROIs (circled) from: A) Study 2 (e.g., *MALE* $\times$ *CHILD* for *BOY*) located in the right hemisphere, and B) Study 3 (e.g., *WILD* $\times$ *BIRD* for *EAGLE*) located in the left hemisphere.

Why do we see the precentral gyrus—a region typically implicated in motor and somatosensory processing—involved in conceptual combination? Perhaps the answer lies in the sensory-perceptual representations of these concepts. The Study 2 fROI is located near the neural regions responsible for sensation and movement of the face (Leslie, Johnson-Frey, & Grafton, 2004; Penfield & Rasmussen, 1950). While the Study 3 fROI is located in a region of cortex responsible for the motor and somatosensory processing of our limbs (Penfield & Rasmussen, 1950; Rizzolatti & Luppino, 2001; Yousry et al., 1997). Both of these regions show significant activation when people view others moving, or when people move their own, limbs and face (Leslie et al., 2004; Montgomery & Haxby, 2008). This suggests that these regions are

important for facilitating self-movement/sensation and for understanding the actions of others (Rizzolatti & Craighero, 2004). It may be that within these sensory-motor regions there exist representations related to processing or interacting with the concepts used in Studies 2 and 3. For example, there might be specific voxel-wise representations for face related constituents (e.g., *MALE* and *CHILD*) within face-specific motor and sensory cortex, and within these regions the representations of complex face concepts (e.g., *BOY*) are created via the interaction of constituents. The same could be true for the limb regions of motor and sensory cortex with respect to the animal concepts of Study 3. These concept-specific processing units would be part of the extended network of the distributed-plus-hub model (Patterson et al., 2007). In this case, their activity would facilitate the amodal conceptual combination seen in the left anterior temporal lobe.

Other Cortical Regions Common to Studies 2 & 3

It is unlikely that the compositionality observed in the Study 1 ALT fROI is the result of phonological confounds. For, significant conceptual combination was observed in the left anterior temporal lobe for two other studies utilizing phonologically independent concepts. Yet, the use of the sort of SL analysis completed in Studies 2 and 3 on the data from Study 1 would be unadvisable. The resultant brain map would be difficult to interpret, as it would reveal neural regions displaying phonological composition, conceptual composition, or some combination of both. Consequently, I will only discuss compositional regions found in both Studies 2 and 3. I ignore fROIs found in only one of the studies, because these regions may simply

reflect concept-specific compositional processing. While such compositionality is interesting, these regions would not be able to facilitate the type of general conceptual combination that left anterior temporal lobe does.

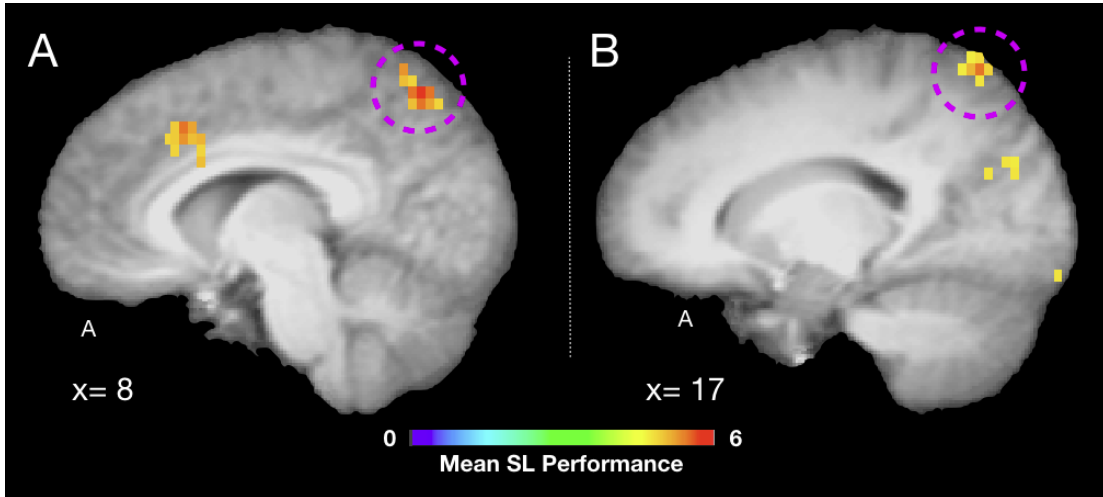


Figure 11. Right precuneus fROIs (circled) from: A) Study 2 (e.g., *MALE* × *CHILD* for *BOY*) and B) Study 3 (e.g., *WILD* × *BIRD* for *EAGLE*).

Only the right precuneus showed evidence of significant conceptual combination in both Studies 2 and 3 (see Fig. 12). Though this region consistently showed weaker compositionality than left anterior temporal lobe fROIs (see Tables 4 & 6), its potential role in conceptual combination is worth exploring.

The precuneus is one of the most commonly reported brain regions across the human neuroimaging literature, and a number of possible functions have been attributed to it (Cavanna & Trimble, 2006). It seems to play a role in mental imagery (Fletcher et al., 1995), multi-sensory memory retrieval (Krause et al., 1999; Shallice et al., 1994), and multimodal attentional control (Shomstein & Yantis, 2006). The precuneus also shows an interesting response profile to certain conceptual tasks. When presented with word-pairs (e.g., *JACKET-VEST* or *JACKET-BUTTON*), the precuneus responds more to those whose conceptual relationship is difficult to establish (Sachs et

al., 2008). This increased response may result from attentional demands required to evaluate difficult concept pairs, but it might also reflect some processing necessary in composition.

As described in the SMM (Smith et al., 1988), specific dimensions of substantive concepts (e.g., ‘color’ in *WAGON*) are selected and modified during conceptual combination (e.g., *RED WAGON*). Perhaps the precuneus facilitates the selection of dimensions to be modified. To do this, the precuneus would utilize its multi-sensory memory representations and attentional control to search for the substantive dimension(s) most likely to be adjusted by a modifier concept. In this case, the word-pair task results (Sachs et al., 2008) would reflect the processing demands of this search. The appearance of the precuneus in both Studies 2 and 3 suggests that it might complete its combinatorial functions in harmony with the left anterior temporal lobe. Clearly, further work exploring its contributions to compositionality is needed.

Directions for Future Research

In all of the studies reported here, I utilized concepts related to living-things. It may be that the appearance of left anterior temporal lobe is limited to the composition of such concepts. This does not appear to be the case, as human (Simmons et al., 2010) and animal (Chao, Weisberg, & Martin, 2002; Grossman et al., 2002) related concepts seem to be processed in different cortical regions. Further, as has been exhaustively discussed, the left ATL is involved in conceptual processing across a wide variety of concept-types (Mummery, Shallice, & Price, 1999; Noppeney & Price, 2002; Tsukiura, Mochizuki-Kawai, & Fujii, 2006). Despite this, concerns based on my use of living-

concepts cannot be dismissed based solely on related research. Thus, in a future experiment, it is necessary to replicate the findings presented in this dissertation by observing composition for non-living concepts within left anterior temporal lobe. Showing, for example, $FAST \times CAR \rightarrow CORVETTE$, in the left anterior temporal lobe would remove any concerns about concept-specific compositionality in my results.

The type of composition observed in the left anterior temporal lobe suggests a simple mechanism that allows for the representation of complex concepts in a non-redundant fashion. Rather than creating a unique cortical representation for a concept like *BOY* the brain would just rely on the integration of the representations of constituents (e.g., *MALE* and *CHILD*). This type of semantic architecture would preserve precious cortical space, and would allow for the near infinite conceptual productivity observed in human cognition (Fodor, 2008). However, such a model of representation brings a set of related questions. If concepts are represented via their constituents, is it possible that these constituents have their own constituents (e.g., is *CHILD* constructed from the some simpler concepts)? If so what are the atoms of concepts? Is there some expansive set of concept features (e.g., ‘color’, ‘shape’, ‘function’) stored within the left anterior temporal lobe? These are deep questions about conceptual representation that cannot be answered in one study; yet, they are critical to address if we hope to understand the neural basis of conceptual processing.

These are not the only questions left to address regarding conceptual combination and conceptual representation within the cortex. It is also necessary to explore other regions that may be part of some extended compositional network. For example, what exactly is the role of the precuneus in conceptual combination? Does

the left IFG actually mediate extended semantic unification, and if so, how might it utilize the left anterior temporal lobe? Where is the cortical origin of emergent features related conceptual combinations? Are metaphors processed within the left anterior temporal lobe, or do special regions of cortex processes this kind of compositionality? What about conceptual representation based in negation (e.g., *all sports that are not games*)? A career could be made attempting answer any one of these questions, and all touch on critical cognitive processes.

Final Comments

Across the three studies presented in this dissertation, we saw strong evidence that concepts are composed of their constituents (e.g., *YOUNG* × *MAN* → *YOUNG MAN*). Regardless of concept-type, the highest level of conceptual combination always occurred within the left anterior temporal lobe. The observation of the left anterior temporal lobe as a locus of conceptual combination fits well with the current literature exploring the neural basis of conceptual processing. The left anterior temporal lobe responds across many tasks requiring the manipulation of conceptual information and to many different types of concepts (Noppeney & Price, 2002; Visser, Jefferies, & Lambon Ralph, 2009; Zahn et al., 2007). It also shows a preference for semantically complex stimuli (Humphries et al., 2006; Snijders et al., 2009).

My results also fit well with the distributed-plus-hub model of cortical conceptual representation (Patterson et al., 2007). In this model, the anterior temporal lobes are hypothesized to act as amodal conceptual processing hubs used in high-level conceptual tasks. Our observation of the left anterior temporal lobe as the primary compositional locus across experiments relying on different concept types adds support to the distributed-plus-hub model while discrediting the distributed-only model (Barsalou, 1999; Martin, 2007).

There are many questions that remain regarding the neural basis of conceptual combination and conceptual representation. However, I believe that the experiments and results presented here add to the foundation of future research seeking to better delineate how compositional processes unfold within the cortex.

References

- Adlam, A.R., Patterson, K., Rogers, T., Nestor, P., Salmond, C., Acosta-Cabronero, J., & Hodges, J. (2006). Semantic dementia and fluent primary progressive aphasia: Two sides of the same coin? *Brain*, 129(11), 3066—3080.
- Andreasen, N., O’Leary, D., Cizadlo, T., Arndt, S., Rezai, K., Watkins, G., Boles Ponto, L., & Hichwa, R. (1995). PET studies of memory: Novel versus practiced free recall of word lists. *NeuroImage*, 2(4), 296—305.
- Armstrong, S.L., Gleitman, L.R., & Gleitman, H. (1983). What some concepts might not be. *Cognition*, 13, 263—308.
- Ashby, F., & Ell, S. (2001). The neurobiology of human category learning. *Trends in Cognitive Sciences*, 5, 204—210.
- Assmus, A., Giessing, C., Weiss, P., & Fink, G. (2007). Functional interactions during the retrieval of conceptual action knowledge: An fMRI study. *Journal of Cognitive Neuroscience*, 19(6), 1004—1012.
- Awh, E., Jonides, J., Smith, E., Schumacher, E., Koeppel, R., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from positron emission tomography. *Psychological Science*, 7(1), 25—31.
- Baker, J.T., Sanders, A.L., Maccotta, L., & Buckner, R.L. (2001). Neural correlates of verbal memory encoding during semantic and structural processing tasks. *Neuroreport*, 12(6), 1251—1256.
- Baron, S.G., Thompson-Schill, S., Weber, M., & Osherson, D. (2010). An early stage of conceptual combination: Superimposition of constituent concepts in left anterolateral temporal lobe. *Cogn Neurosci*, 1(1), 44—51.

- Baron, S.G., & Osherson, D. (2011). Evidence for conceptual combination in the left anterior temporal lobe. *NeuroImage*, (IN PRESS)
- Barsalou, L.W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22, 577—660.
- Binder, J.R., Desai, R.H., Graves, W.W., & Conant, L.L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*, 19, 2767—2796.
- Bozeat, S., Lambon Ralph, M., Patterson, K., & Hodges, J. (2002). When objects lose their meaning: What happens to their use? *Cognitive, Affective, & Behavioral Neurosciences*, 2(3), 236—251.
- Burianova, H., & Grady, C.L. (2007). Common and unique neural activations in autobiographical, episodic, and semantic retrieval. *J Cogn Neurosci*, 19(9), 1520—1534.
- Canessa, N., Borgo, F., Cappa, S., Perani, D., Falini, A., Buccino, G., Tettamanti, M., & Shallice, T. (2008). The different neural correlates of action and functional knowledge in semantic memory: An fMRI study. *Cerebral Cortex*, 18(4), 740—751.
- Caramazza, A., & Shelton, J. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience*, 10(1), 1—34.
- Cavanna, A.E., & Trimble, M.R. (2006). The precuneus: A review of its functional anatomy and behavioral correlates. *Brain*, 129, 564—584.

- Chabardes, S., Kahane, P., Minotti, L., Hoffmann, D., & Benabid, A. (2002). Anatomy of the temporal pole region. *Epileptic Disorders*, 4, 9—14.
- Chao, L., Martin, A., (1999). Cortical representation of perception, naming, and knowledge of color. *Journal of Cognitive Neuroscience*, 11, 25—35.
- Chao, L.L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex*, 12, 545—551.
- Cox, R. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 29, 162—173.
- Cohen, J., & Walter, W. (1966). The interaction of responses in the brain to semantic stimuli. *Psychophysiology*, 2(3), 187—196.
- Creem-Regehr, S., & Lee, J. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research*, 22(3), 457—469.
- Croxson, P., Johansen-Berg, H., Behrens, T., Robson, M., Pinski, M., Gross, C., Richter, W., Richter, M., Kastner, S., & Rushworth, M. (2005). Quantitative investigation of connections of the prefrontal cortex in the human and macaque using probabilistic diffusion tractography. *The Journal of Neuroscience*, 25(39), 8854—8866.
- Cusack, R., Mitchell, D., & Duncan, J. (2010). Discrete object representation, attention switching, and task difficulty in the parietal lobe. *Journal of Cognitive Neuroscience*, 22(1), 32—47.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, 92, 179—229.
- Damoiseaux, J.S., Beckmann, C.F., Sanz Arigita, E.J., Barkhof, F., Scheltens, P., Stam,

- C.J., Smith, S.M., & Rombouts, S. (2007). Reduced resting-state brain activity in the “default network” in normal aging. *Cerebral Cortex*, 18, 1856—1864.
- Demonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., Rascol, A., & Frackowiak, R.S.J. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, 115, 1753—1768.
- Demonet, J.-F., Price, C., Wise, R., & Frackowiak, R.S.J. (1994). Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron-emission tomography study in normal human subjects. *Neurosci Lett*, 182, 25—28.
- Desgranges, B., Matuszewski, V., Piolino, P., Chetelat, G., Mezenge, F., Landeau, B., Sayette, V., Belliard, S., & Eustache, F. (2007). Anatomical and functional alterations in semantic dementia: A voxel-based MRI and PET study. *Neurobiology of Aging*, 28(12), 1904—1913.
- Devlin, J.T., Russell, R.P., Davis, M.H., Price, C.J., Moss, H.E., Fadili, M.J., & Tyler, L.K. (2002). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia*, 40, 54—75.
- Diehl, J., Grimmer, T., Drzezga, A., Riemenscheider, M., Forstl, H., & Kurz, A. (2004). Cerebral metabolic patterns at early stages of frontotemporal dementia and semantic dementia. A PET study. *Neurobiology of Aging*, 25(8), 1051—1056.
- Dronkers, N., Wilkins, D., Van Valin Jr., R., Redfern, B., & Jaeger, J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, 92(1- 2), 145—177.

- Fletcher, P., Frith, C., Baker, S., Shallice, T., Frackowiak, R., & Dolan, R. (1995). The mind's eye—Precuneus activation in memory-related imagery. *NeuroImage*, 2(3), 195—200.
- Fodor, J. (2008). *LOT 2: The language of thought revisited*. USA: Oxford University Press.
- Fodor, J., & Lepore, E. (1996). The red herring and the pet fish. *Cognition*, 59(2), 246—262.
- Friederici, A.D., Opitz, B., & von Cramon, D.Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cereb Cortex*, 10(7), 698—705.
- Forde, E., Francis, D., Riddoch, M., Rumiati, R., & Humphreys, G. (1997). On the links between visual knowledge and naming: A single case study of a patient with a category specific impairment for living things. *Cognitive Neuropsychology*, 14, 403—458.
- Gagne, C., & Shoben, E., (1997). Influence of thematic relations on the comprehension of modifier-noun combinations. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23(1), 71—87.
- Gianotti, G., Silveri, M., Daniele, A., & Giustolisi, L. (1995). Neuroanatomical correlates of category-specific semantic disorders: A critical survey. *Memory*, 3(3-4), 247—263.
- Gianotti G., & Silveri, M. (1996). Cognitive and anatomical locus of lesion in a patient with a category-specific impairment for living beings. *Cognitive Neuropsychology*, 13, 357—389.

- Goldberg, R.F., Perfetti, C.A., Fiez, J.A., & Schneider, W. (2007). Selective retrieval of abstract semantic knowledge in left prefrontal cortex. *J Neurosci*, 27(14), 3790—3798.
- Gougen, J.,(1969). The logic of inexact concepts. *Synthese*, 19, 325—373.
- Grabowski, T.J., Damasio, H., Tranel, D., Boles Ponto, L.L., Hichwa, R.D., & Damasio, A.R. (2001). A role for left temporal pole in the retrieval of words for unique entities. *Human Brain Mapping*, 13, 199—212.
- Graves, W.W., Binder, J.R., Desai, Conant, L.L., & Seidenberg, M.S. (2010). Neural correlates of implicit and explicit combinatorial semantic processing. *Neuroimage*, 2, 638—646.
- Grossman, M., Koenig, P., DeVita, C., Glosser, G., Alsop, D., Detre, J., & Gee, J. (2002). The neural basis for category-specific knowledge: An fMRI study. *NeuroImage*, 15, 936—948.
- Hagoort, P., Baggio, G., Willems, R.M. (2009). Semantic unification. In M.S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (4th ed.) (pp. 819—836). Cambridge, MA: MIT Press.
- Hampton, J.A. (1979). Polymorphous concepts in semantic memory. *Journal of Verbal Learning & Verbal Behavior*, 18, 441—461.
- Hampton, J. (1988). Overextension of conjunctive concepts: Evidence for a unitary model of concept typicality and class inclusion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 14(1), 12—32.
- Hampton J. (1995). Emergent attributes in combined concepts. In *Conceptual*

- Structures and Processes: Emergence Discovery and Change*. Eds., T. Ward, S. Smith, & J. Viad. Washington DC: American Psychological Association.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41, 301—307.
- Henke, K., Mondadori, C., Treyer, V., Nitsch, R., Buck, A., & Hock, C. (2003). Nonconscious formation and reactivation of semantic associations by way of the medial temporal lobe. *Neuropsychologia*, 41(8), 863—876.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nat Rev Neurosci*, 8, 393—402.
- Hodges, J.R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia: Progressive fluent aphasia with temporal lobe atrophy. *Brain*, 115(6), 1783—1806.
- Hull, C.L. (1920). Quantitative aspects of the evolution of concepts. *Psychological Monographs*, XXVIII(1.123), 1—86.
- Humphries, C., Binder, J.R., Medler, D.A., & Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *J Cogn Neurosci*, 18(4), 665—679.
- Jeannerod, M., Arbib, M., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neurosciences*, 18(7), 314—320.
- Jones, E., & Powell, T. (1970). Connexions of the somatic sensory cortex of the rhesus monkey. *Brain*, 93, 37—56.
- Kandel, E., Schwartz, J., & Jessell, T. (2000). *Principles of neural science*. 4th ed, New

York: McGraw-Hill.

Medin, D., & Schaffer, M. (1978). Context theory of classification learning.

Psychological Review, 85(3), 207—238.

Kellenbach, M., 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.

Kiel, F. (1989). *Concepts, kinds and cognitive development*. Cambridge, MA: MIT Press.

Kondo, H., Saleem, K., & Prince, J. (2003). Differential connections of the temporal pole with the orbital and medial prefrontal networks in macaque monkeys. *Journal of Comparative Neurology*, 465, 499—523.

Krause, B., Schmidt, D., Mottaghy, F., Taylor, J., Halsband, U., Herzog, H., Tellman, L., & Muller-Gartner, H. (1999). Episodic retrieval activates the precuneus irrespective of the imagery content of word pair associates: A PET study. *Brain*, 122(2), 255—263.

Kreigeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proc Natl Acad Sci U S A*, 103(10), 3863—3868.

Lambon Ralph, M.A., Pobric, G., & Jeffries, E. (2009). Conceptual knowledge is underpinned by the temporal pole bilaterally: Convergent evidence from rTMS. *Cerebral Cortex*, 19(4), 832—838.

Leslie, K.R., Johnson-Frey, S.H., & Grafton, S.T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *NeuroImage*, 21, 601—607.

- Leveroni, C., Seidenberg, M., Mayer, A., Mead, L., Binder, J., & Rao, S. (2000). Neural systems underlying the recognition of familiar and newly learned faces. *Journal of Neuroscience*, 20(2), 878—886.
- Loewy, A.D. (1998). Viruses as transneuronal tracers for defining neural circuits. *Neuroscience & Biobehavioral Reviews*, 22(6), 679—684.
- Luke, K., Liu, H., Wai, Y., Wan, Y., & Tan, L. (2002). Functional anatomy of syntactic and semantic processing in language comprehension. *Human Brain Mapping*, 16, 133—145.
- Mahon, B., & Caramazza, A. (2003). Constraining questions about the organization and representation of conceptual knowledge. *Cognitive Neuropsychology*, 20, 433—450.
- Mahon, B.Z., & Caramazza, A. (2009). Concepts and categories: A cognitive neuropsychological perspective. *Annual Review of Psychology*, 60, 27—51.
- Markowitsch, H., Emmans, D., Irle, E., Streicher, M., & Preilowski, B. (1985). Cortical and subcortical afferent connections of the primate's temporal pole: A study of rhesus monkeys, squirrel monkeys, and marmosets. *The Journal of Comparative Neurology*, 242(3), 425—458.
- Marques, J., Canessa, N., Siri, S., Catricala, E., & Cappa, S. (2008). Conceptual knowledge in the brain: fMRI evidence for a featural organization. *Brain Research*, 11194, 90—99.
- Martin, A., & Chao, L. (2001). Semantic memory and the brain: structure and processes. *Current Opinion in Neurobiology*, 11(2), 194—201.
- Martin, A. (2007). The representation of object concepts in the brain. *Ann. Rev.*

Psychol. 58, 25—45.

MATLAB version 7.9.0.529(R2009b). Natick, Massachusetts: The MathWorks Inc., 2009.

McClelland, J., McNaughton, B., & O'Reilly, R. (1995) Why there are complementary learning systems in the hippocampus and neocortex: Insights from the success and failures of connectionist models of learning and memory. *Psychological Review*, 102, 419—457.

Medin, D.L. & Schaffer, M.M. (1978). Context theory of classification learning. *Psychological Review*, 85, 207—238.

Miller, E., & Cohen, J. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167—202.

Montgomery, K., & Haxby, J. (2008). Mirror neuron system differentially activated by facial expressions and social hand gestures: A functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 20(10), 1886—1897.

Moran, M., Mufson, E., & Mesulam, M. (1987). Neural inputs into the temporopolar cortex of the rhesus monkey. *The Journal of Comparative Neurology*, 256(1), 88—103.

Mummery, C., Patterson, K., Price, C., Ashburner, J., Frackowiak, R., & Hodges, J. (2000). A voxel-based morphometry study of semantic dementia: Relationship between temporal lobe atrophy and semantic memory. *Annals of Neurology*, 47, 36—45.

Mummery, C., Shallice, T., & Price, C. (1999). Dual-process model in semantic priming: A functional imaging perspective. *NeuroImage*, 9(5), 516—525.

- Murphy, G. (1988). Comprehending complex concepts. *Cognitive Science*, 12(4), 529—562.
- Murphy, G. (1990). Noun phrase interpretation and conceptual combination. *Journal of Memory and Language*, 29, 259—288.
- Murphy, G. (2004). *The big book of concepts*. Cambridge, MA: MIT Press.
- Nestor, P., Fryer, T., & Hodges, J. (2006). Declarative memory impairments in Alzheimer's disease and semantic dementia. *NeuroImage*, 30(3), 1010—1020.
- Noppeney, U., & Price, C. (2002). A PET study of stimulus- and task-induced semantic processing. *NeuroImage*, 14, 862—872.
- Noppeney, U., & Price, C.J. (2004). Retrieval of abstract semantics. *NeuroImage*, 22, 164—170.
- Noppeney, U., Patterson, K., Tyler, L.K., Moss, H., Stamatakis, E.A., Bright, P., Mummery, C., & Price, C.J. (2007). Temporal lobe lesions and semantic impairment: A comparison of herpes simplex virus encephalitis and semantic dementia. *Brain*, 130(4), 1138—1147.
- Osherson, D. & Smith, E. (1981). On the adequacy of prototype theory as a theory of concepts. *Cognition*, 9, 35—58.
- Osherson, D., & Smith, E. (1982). Gradedness and conceptual combination. *Cognition*, 12(3), 299—318.
- Patterson, K., Nestor, P., & Rogers, T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976—987.
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man; a clinical study of*

localization of function. Oxford, England: Macmillan.

Peng, X., Kandel, A., & Wang, P. (1991). Concepts, rules, and fuzzy reasoning: A factor space approach. *IEEE Transactions on Systems, Man and Cybernetics*, 21(1), 194—205.

Pexman, P.M., Hargreaves, I.S., Edwards, J.D., Henry, L.C., & Goodyear, B.G. (2007). Neural correlates of concreteness in semantic categorization. *J Cogn Neurosci*, 19(8), 1407—1419.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage*, 14(5), 1013—1026.

Pobric, G., Jefferies, E., & Lambon Ralph, M. (2007). Anterior temporal lobes mediate semantic representation: Mimicking semantic dementia by using rTMS in normal participants. *Proceedings of the National Academy of Sciences*, 104(50), 20137–20141.

Price, C.J., Wise, R.J.S., Watson, J.D.G., Patterson, K., Howard, D., & Frackowiak, R.S.J. (1994). Brain activity during reading: The effects of exposure duration and task. *Brain*, 117(6), 1255—1269.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169—192.

Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31(6), 889—901.

Rogalsky, C., & Hickok, G. (2009). Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex.

Cerebral Cortex, 19(4), 786—796.

Roskies, A.I., Fiez, J.A., Balota, D.A., Raichle, M.E., & Petersen, S.E. (2001). Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *J Cogn Neurosci*, 13(6), 829—843.

Sachs, O., Weis, S., Zellagui, N., Huber, W., Zvyagintsev, M., Mathiak, K., & Kircher, T. (2008). Automatic processing of semantic relations in fMRI: Neural activation during semantic priming of taxonomic and thematic categories. *Brain Research*, 1218, 194—205.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. *Brain*, 115, 15—36.

Shallice, T., Fletcher, P., Frith, C., Grasby, P., Frackowiak, R., & Dolan, R. (1994). Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature*, 368, 633—635.

Sheldon, S., & Moscovitch, M. (2011). The nature and time-course of medial temporal lobe contributions to semantic retrieval: An fMRI study on verbal fluency. *Hippocampus*, early online access.

Shivde, G., & Thompson-Schill, S. (2004). Dissociating semantic and phonological maintenance using fMRI. *Cognitive, Affective, & Behavioral Neuroscience*, 4(1), 10—19.

Shomstein, S. & Yantis, S. (2006). Parietal cortex mediates voluntary control of spatial and nonspatial auditory attention. *The Journal of Neuroscience*, 26(6), 435—439.

Simmons, W., Ramjee, V., Beauchamp, M., McRae, K., Martin, A., & Barsalou, L.

- (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, 45(12), 2802—2910.
- Simmons, W., Reddish, M., Bellgowan, S., & Martin, A. (2010). The selectivity and functional connectivity of the anterior temporal lobes. *Cerebral Cortex*, 20(4), 813—825.
- Singular Inversions (2006). FaceGen 2.1 Full SDK Documentations. <http://facegen.com> (last accessed 5 June 2007).
- Smith, E. E., Osherson, D., Rips, L., & Keane, M. (1988). Combining prototypes: A selective modification model. *Cognitive Sciences*, 12, 485—527.
- Snijders, T.M., Vosse, T., Kempen, G., Van Berkum, J.J.A., Petersson, K.M., & Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: An fMRI study using word-category ambiguity. *Cereb Cortex*, 19, 1493—1503.
- Snowden, J. S., Neary, D. & Mann, D. M. A. *Fronto-Temporal Lobar Degeneration: Fronto-Temporal Dementia, Progressive Aphasia, Semantic Dementia* (Churchill Livingstone, New York, 1996).
- Spitsyna, G., Warren, J.E., Scott, S.K., Turkheimer, F.E., & Wise, R.J.S. (2006). Converging language streams in the human temporal lobe. *J Neurosci*, 26(28), 7328—7336.
- Steiger, J. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, 87(2), 245—251.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme Medical Publishers.

- Thompson-Schill, S.L., Swick, D., Farah, M., D'Esposito, Kan, I.R., & Knight, R.T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proc Natl Acad Sci U S A*, 95, 15855—15860.
- Todorov, A., Baron, S.G., & Oosterhof, N. (2008). Evaluating face trustworthiness: A model based approach. *Social Cognitive and Affective Neuroscience*, 3(2), 119–127.
- Tranel, D., Damasio, H., & Damasio, A. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, 35(10), 1319—1327.
- Tsukiura, T., Mochizuki-Kawai, H., & Fujii, T. (2006). Dissociable roles of the bilateral anterior temporal lobe in face-name associations: An event-related fMRI study. *NeuroImage*, 30(2), 617—626.
- Vandenberghe, R., Nobre, A., & Price, C. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience*, 14(4), 550—560.
- Visser, M., Jefferies, E., Lambon Ralph, M.A. (2009). Semantic processing in the anterior temporal lobes: A meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience*, 21(3), 1—12.
- Wagner, A.D., Pare-Blagoev, E.J., Clark, J., & Poldrack, R.A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, 31, 329—338.
- Warrington, E.K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology*, 27, 635—657.
- Warrington, E. & Shallice, T. (1984). Category specific semantic impairments. *Brain*,

107(3), 829—853.

- Wible, C., Han, S., Spencer, M., Kubicki, M., Niznikiewicz, M., Jolesz, F., McCarley, R., & Nestor, P. (2006). Connectivity among semantic associates: An fMRI study of semantic priming. *Brain and Language*, 97(3), 294—305.
- Wiggs, C., Weisberg, J., & Martin, A. (1999). Neural correlates of semantic and episodic memory retrieval. *Neuropsychologia*, 37, 103—118.
- Wisniewski, E. (1996). Construal and similarity in conceptual combination. *Journal of Memory and Language*, 35(3), 434—453.
- Wisniewski, E.J. (1997). When concepts combine. *Psychonomic Bulletin and Review*, 4, 167—183.
- Yousry, T., Schmid, U., Alkadhi, H., Schmidt, D., Peraud, A., Buettner, A., & Winkler, P. (1997). Localization of the motor hand area to a knob on the precentral gyrus. A new landmark. *Brain*, 120(1), 141—157.
- Zahn, R., Moll, J., Krueger, F., Huey, E., Garrido, G., & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Sciences*, 104(15), 6430—6435.
- Zannino, G.D., Buccione, I., Perri, R., Macaluso, E., Lo Gerfo, E., Catagirone, C., & Carlesimo, G.A. (2009). Visual and semantic processing of living things and artifacts: An fMRI study. *J Cogn Neurosci*, 22(3), 554—570.
- Zysset, S., Huber, O., Ferstl, E., & Yves von Cramon, D. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *NeuroImage*, 15(4), 983—991.