

3.09 Structural Basis of Semantic Memory[☆]

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3.09.1 What Is Semantic Memory?

Semantic memory refers broadly to an individual's acquired knowledge of the world. This vast store of information encompasses our knowledge of objects and their attributes, other people's traits and intentions (as well as our own), historical events and facts, and the meanings and interrelations of words (Tulving, 1972). Implicit among these is our knowledge of concepts and categories. Here we coarsely define concepts as amodal mental representations referring to classes of phenomena in the world, but refer the reader to more detailed treatments of this topic (Fodor, 1975; Margolis and Laurence, 2015; Murphy, 2004; Smith and Medin, 1981). Concepts provide a means for both categorizing specific experiences into more general classes and expressing relations among these classes; that is, conceptual knowledge provides us with "a taxonomy of things in the world" (Smith and Medin, 1981, p.7). This capacity for representing the world in a semantically organized fashion is critical for both perception and action and is a keystone of language and human cognition more generally. For humans, the acquisition of semantic memory is tightly interwoven with personal experience, social interaction, and cultural knowledge.

The scope of semantic memory may seem worryingly inclusive, so it is useful to highlight some of the theoretical distinctions made between semantic and other memory systems. Semantic memory is classically differentiated from episodic memory (Tulving, 1972). While in episodic memory an autobiographical experience of the remembered event is reconstructed often with rich perceptual and affective context, semantic knowledge is abstracted away from any particular context or experiential factors at play when the knowledge was acquired. In the broader taxonomy of memory systems, semantic memory is typically situated as a branch of declarative or explicit memory, separate from, e.g., procedural memory (Squire, 2004). These functionally distinct systems are thought to rely on partially dissociable, though overlapping, and interacting anatomical substrates. Semantic memory is typically thought to precede episodic memory in both ontogeny and phylogeny (Tulving, 1984), and may be geared toward certain environmental demands that render it ineffective in coping with environmental challenges for which other memory systems are well suited (i.e., functional incompatibility; Sherry and Schacter, 1987). Although the distinctions between these systems are theoretically valuable, memory is only adaptive in service of guiding forthcoming behavior, and our ability to navigate everyday situations relies on the orchestrated function of multiple systems (Klein et al., 2002).

The information represented in semantic memory is to some extent hierarchically organized (Collins and Quillian, 1969; Miller et al., 1990; Quillian, 1967), and recent feature-based approaches (e.g., McRae et al., 1997) represent each entry (e.g., word, concept) as a vector in a semantic space where more semantically similar entries are nearer to each other (Landauer and Dumais, 1997; Lund and Burgess, 1996; Turney and Pantel, 2010). Accessing or activating a particular semantic representation typically propagates activation to nearby items in the semantic representational space (i.e., spreading activation; Collins and Loftus, 1975). Furthermore, semantic memory also makes fairly direct contact with perception; that is, semantic representations are not

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invoked exclusively by explicit or deliberate retrieval tasks. During perceptual processing, semantic memory is deployed rapidly to assign semantic features to a sensory stimulus (Greene and Oliva, 2009; Potter and Faulconer, 1975; Thorpe et al., 1996). For example, the gist of a complex, naturalistic scene can be extracted within 200 ms (Oliva and Torralba, 2006), and the semantic context of a scene can rapidly facilitate target identification (Auckland et al., 2007; Biederman et al., 1982) and guide eye movements (Henderson, 2003). This sort of semantic deployment during perception is automatic and obligatory (at least for certain types of stimuli, e.g., words, faces) and cannot be strategically suppressed even when it undermines behavioral goals (Banaji and Hardin, 1996; MacLeod, 1991; Neely, 1991). Relatedly, semantic information has been shown to influence behavior with minimal consciousness in masked priming paradigms (Dehaene et al., 1998; Dell'Acqua and Grainger, 1999; Kouider and Dehaene, 2007; Naccache et al., 2001), during the attentional blink (Luck et al., 1996), and in cases of neglect (Làdavas et al., 1993; McGlinchey-Berroth et al., 1993).

In the following, we provide an overview of the structural basis of semantic memory with a special focus on how neural systems encode semantic information. We start with insights gained from the behavioral deficits of neuropsychological patients, then discuss the role of neuroimaging in localizing critical structural substrates, and finally highlight recent efforts to decode neural representations of semantic information. Our overall goal is to provide a high-altitude overview of the relevant work, with an emphasis on pivotal findings and pointers to more in-depth reviews. We take the previous edition of this chapter (Martin and Simmons, 2008) as a guide and encourage the reader to consult this and similar works by other authors (e.g., Yee et al., 2013) for different perspectives on what are still controversial issues. Understanding how the brain manages to acquire, retain, and organize semantic knowledge is not only critical to unraveling the mechanisms of learning and memory-related disease (e.g., semantic dementia), but is also becoming increasingly relevant in computer science. Neurally inspired computational models (e.g., deep convolutional neural networks) have become the dominant method for extracting semantic content from images and speech (LeCun et al., 2015), as well as for organizing the wealth of human knowledge on the Internet (e.g., Google's Knowledge Vault; Dong et al., 2014). These computational implementations are directly related to brain's own implementation of semantic memory and cross talk between fields will continue to prove fruitful for both parties.

3.09.2 Gross Functional Anatomy

3.09.2.1 The Medial Temporal Lobe

The acquisition of semantic knowledge relies on the medial temporal lobe (MTL). For example, in the famous case of patient H.M., the acquisition of both semantic and episodic memory was dramatically impaired after bilateral MTL excision, while some semantic memories acquired prior to the operation were preserved (Gabrieli et al., 1988). In fact, H.M. was reported to have acquired semantic knowledge after the operation (e.g., knowledge of people who had become famous postoperatively; O'Kane et al., 2004); however, this knowledge was limited and acquisition was abnormally laborious. There is some debate as to whether acquisition relies on the hippocampus proper (Squire and Zola, 1998) or whether the adjacent neocortex is more critical (Mishkin et al., 1998). Furthermore, it may be that hippocampal damage sustained in adulthood impairs acquisition (Manns et al., 2003) more so than damage sustained early in life (Vargha-Khadem et al., 1997).

The MTL also plays a role in the retrieval of semantic information. Cases of retrograde amnesia suggest that the necessity of MTL for semantic retrieval is temporally graded such that more recent memories (i.e., closer to the onset of amnesia) are more vulnerable while distant memories may be spared (Kapur and Brooks, 1999; Manns et al., 2003; Scoville and Milner, 1957; Zola-Morgan and Squire, 1990). Interestingly, the duration to which retrograde amnesia for semantic information extends into the premorbid period ranges from years to decades based on part on the location and severity of MTL tissue damage (Squire and Bayley, 2007). Critically, in cases where damage extends to neocortex (e.g., lateral temporal cortex), impairment is not temporally graded (i.e., flat retrograde amnesia; Bayley et al., 2005; Bright et al., 2006). These findings have led to the view that the MTL plays a critical initial role in supporting the context-rich experiential content of memory, but that the semantic information spanning many such events is eventually distilled and consolidated in the neocortex (Buzsáki, 1996; Eichenbaum, 2000, 2004; McClelland et al., 1995; Moscovitch et al., 2005).

In summary, MTL structures such as the hippocampus likely contribute to both the acquisition and retrieval of semantic knowledge under normal circumstances. Nonetheless, alternate routes for acquisition and retrieval may allow for limited function in cases where MTL damage is not overly severe.

3.09.2.2 The Neocortex

It is generally accepted that semantic knowledge is stored throughout the neocortex (Binder and Desai, 2011; Martin, 2007; Patterson et al., 2007). These representations are likely encoded in a distributed fashion across populations of cortical neurons (Hinton et al., 1986; McClelland and Rogers, 2003). Both the hippocampus and neocortex are thought to initially encode experiential content, but subsequent hippocampal reactivation serves to gradually incorporate memory traces into cortical circuitry, strengthening the corticocortical connections supporting the memory trace, and eventually rendering hippocampal involvement unnecessary (Frankland and Bontempi, 2005). To account for the temporally graded preservation of semantic knowledge in retrograde amnesia, the multiple trace theory suggests that the hippocampus is required to encode and retrieve detailed contextual information, but the cortex is sufficient for retrieving semantic content (Moscovitch et al., 2005; Nadel and Moscovitch, 1997).

Passive hippocampal reactivation of the memory trace is thought to sculpt and stabilize cortical representations of semantic content over time (McClelland et al., 1995; Squire and Alvarez, 1995). Work in animal models has revealed coordinated reactivation of distributed cortical memory representations at rest, providing compelling evidence for this theory of cortical consolidation (Squire and Alvarez, 1995). While changes in hippocampal–cortical connectivity supporting initial encoding may occur rapidly (and rapidly decay), the reorganization of corticocortical connections supporting semantic memory is both slower and more persistent. In mice, experimentally induced abnormalities in synaptic plasticity affecting cortex but sparing the hippocampus selectively impair the consolidation of remote memories thought to rely on cortical networks (Frankland et al., 2001; Hayashi et al., 2004). This cortical plasticity likely involves both adjusting synaptic weights among existing neurons as well as more dramatic structural plasticity (Chklovskii et al., 2004). Cortical reorganization results in observable functional changes in distributed cortical networks that are critical to remote memory retrieval (Bontempi et al., 1999; Maviel et al., 2004). In parallel, neuroimaging work in humans who have acquired expertise in particular domains (e.g., object categories such as birds or cars) suggests that learning nuanced semantic relationships is associated with alterations in cortical function (Folstein et al., 2013; Gauthier et al., 2000).

The deliberate retrieval of cortical memories is thought to be mediated by the prefrontal cortex (Bookheimer, 2002; Miyashita, 2004; Petersen et al., 1988; Tomita et al., 1999). In fact, prefrontal cortex may perform the dual role of both reenacting cortical memory representations and inhibiting potentially interfering hippocampal activity (Frankland and Bontempi, 2005). Neuroimaging work has suggested that ventrolateral prefrontal cortices may guide controlled semantic retrieval processes (Badre and Wagner, 2007; Poldrack et al., 1999; Wagner et al., 2001) or select from among competing semantic representations (Thompson-Schill, 2003; Thompson-Schill et al., 1997). As we discuss in more depth later, although these retrieved semantic representations are stored throughout cortex, there is considerable debate about the extent to which they rely on sensorimotor machinery and the reenactment of sensorimotor representations (Barsalou, 2008; Mahon and Caramazza, 2008). However, from either perspective there is strong convergent evidence that the cerebral cortex encodes semantic information in an organized manner, and the following sections will focus on unpacking this organization.

3.09.3 Deficits in Semantic Memory

Our current understanding of semantic representation is grounded in a rich history of neuropsychological research. Although a variety of neurological conditions can result in impairments to semantic cognition (e.g., Alzheimer's disease, herpes simplex virus encephalitis, stroke), semantic dementia (Hodges et al., 1992; Hodges and Patterson, 2007; Snowden et al., 1989) has been particularly illuminating in revealing the organization of conceptual knowledge (Lambon Ralph, 2014; Patterson et al., 2007). Semantic dementia is traditionally characterized by deficits in the conceptual knowledge of objects, including their names, category membership, and defining properties (e.g., shape, color, usage; Hodges and Patterson, 2007). Critically, in certain cases the deficit is not specific to any particular stimulus or response modality, but generalizes to any task requiring the participant to retrieve conceptual knowledge of the probe (Lambon Ralph, 2014). When probed for a particular object, patients with semantic dementia may respond with an incorrect object within the same superordinate category, commensurate with hierarchical category membership and suggesting that more specific (subordinate) categories are more vulnerable than superordinate categories (Rogers and Patterson, 2007). It is critical here to maintain the distinction between semantic representation and the control systems mediating retrieval (Lambon Ralph, 2014). In fact, certain deficits, such as semantic aphasia, may result from abnormalities in this control system, rather than in semantic representation per se (Jefferies and Lambon Ralph, 2006). Furthermore, although the foundational neuropsychological work on semantic impairment has focused on object concepts, there is considerable evidence that other domains of semantic knowledge, such as action concepts, may be similarly affected (Buxbaum and Saffran, 2002; De Renzi and Lucchelli, 1988; Dumont et al., 2000; Heilman et al., 1997; Hodges et al., 2000; Johnson-Frey, 2004; Ochipa et al., 1992; Saygin et al., 2004; Tranel et al., 2003). In the following we focus on semantic deficits limited to particular categories and associated with a stereotyped set of neuroanatomical abnormalities.

3.09.3.1 Category-Specific Semantic Deficits

Patients with deficits limited to particular object categories have been critical in unraveling principle dimensions of semantic representation (Caramazza and Mahon, 2003; Mahon and Caramazza, 2009; Martin and Caramazza, 2003; Warrington, 1975; Warrington and McCarthy, 1987; Warrington and Shallice, 1984). These patients are selectively impaired for a specific domain of knowledge in semantic tasks such as picture naming and picture–word matching. Several category-specific deficits have been observed (Capitani et al., 2003). Deficits in the conceptual knowledge of living, animate objects (e.g., animals) with preserved knowledge of nonliving objects (e.g., tools, vehicles) have been observed (Blundo et al., 2006; Caramazza and Shelton, 1998). Several patients have also presented with selectively impaired conceptual knowledge of conspecifics, without perceptual deficits such as prosopagnosia (Ellis et al., 1989; Miceli et al., 2000). Selective impairments of artifacts (inanimate, artificial objects) have been observed as well (Sacchetti and Humphreys, 1992), though considerably less frequently. Knowledge of inanimate biological objects (e.g., fruits and vegetables; Hart et al., 1985) may also be subject to selective impairment or preservation. Taken together, these findings suggest that dimensions such as animate–inanimate and natural–artificial are central to the organization of human semantic knowledge. The extent to which these behavioral dissociations map onto continuous dimensions or discrete distinctions in terms of neural representation is currently debated (e.g., Sha et al., 2015).

Several models have been proposed to account for the organizational principles we can infer from these deficits. From one perspective, conceptual knowledge is organized according to the sensorimotor systems most directly relevant to particular objects; for example, our conceptual knowledge of artificial tools relies on the motor systems critical for using tools, while our knowledge of, e.g., animals relies more on systems processing visual form (Humphreys and Forde, 2001; Martin et al., 2000). In this property- or feature-based account (also referred to as the sensory/motor or sensory/functional model), damage to areas supporting a particular domain of sensorimotor processing will preferentially affect concepts relying primarily on features processed by that sensorimotor system. This model predicts that deficits specific to certain categories should be accompanied by deficits specific to knowledge of sensory or motor/functional features most related to the impaired category. However, deficits dissociating categories thought to rely on similar sensory/functional systems (e.g., fruits/vegetables and animals) exist, and there is disagreement as to whether category-specific deficits in fact cooccur with deficits in corresponding sensory/motor knowledge (Capitani et al., 2003; Caramazza and Mahon, 2003). This model is closely related to the notion of embodied conceptual knowledge that we discuss at length later.

An alternative model proposes that conceptual knowledge is organized in a domain-specific way (Caramazza and Mahon, 2003; Caramazza and Shelton, 1998). That is, evolutionary pressures have organized the brain into a collection of modules specialized to efficiently process particular types of information (e.g., animals, tools, conspecifics); category-specific deficits are predicted to adhere to the boundaries of domain-specific processing modules. This also puts an upper limit on the observable category-specific deficits, as only a subset of categories having particular adaptive value is associated with modular processing (Caramazza and Mahon, 2003).

A third class of models suggests that categories are represented according to their properties or features in a unitary semantic system (Caramazza et al., 1990; Riddoch et al., 1988), where features are encoded in a distributed fashion across cortex (Devlin et al., 1998; Tyler and Moss, 2001). This model accommodates the oftentimes diffuse cortical lesions resulting in category-specific deficits and provides a framework for interpreting fine-grained differences in impairment within a given domain of knowledge. Furthermore, this approach resonates with current theories of distributed neural representation (Haxby et al., 2014) and vector space models of semantic representation (Turney and Pantel, 2010). Semantic deficits resulting from damage to this system depend on what features define a particular category and to what extent these features are intercorrelated.

To summarize, each of these models accounts for some portion of variance in the observed semantic deficits. Critically, these models are not mutually exclusive and contribute at different levels to our understanding of how semantic knowledge is organized in the brain (Mahon and Caramazza, 2009). Although conceptual representations are likely encoded in a distributed fashion (McClelland and Rogers, 2003; Tyler and Moss, 2001), these features are not randomly organized, resulting in a nonuniform semantic space. Denser regions of the semantic space may approximate the observed category- or domain-specific organization (Caramazza et al., 1990). Furthermore, particular features or dimensions of the semantic space capturing sensory and motoric information may very well map onto the cortex in a way that abuts the neural systems mediating these sensorimotor processes (Martin, 2007). These organizational principles of representation may be multiplexed or superimposed at different spatial scales in the functional topography of a cortical field (Grill-Spector and Weiner, 2014; Haxby et al., 2014).

3.09.3.2 Neuroanatomy of Semantic Deficits

The diffuse and variable nature of cortical lesions resulting in semantic deficits limits us to only general inferences about the underlying functional neuroanatomy. As mentioned before, in cases of temporally graded semantic deficits in retrograde amnesia, damage typically extends beyond the hippocampus to frontal, temporal, and occipital cortices (Bayley et al., 2005; Bright et al., 2006). Early attempts to map category-specific semantic deficits to localized cortical lesions suggested that deficits for living things are typically associated with damage in ventral temporal cortex (Vandenbulcke et al., 2006), while impaired knowledge of tools and actions was associated with left-lateralized frontoparietal damage (Gainotti, 2000) and posterior middle temporal damage (Kalénine et al., 2010), respectively. Convergent structural abnormalities across several etiologies suggest that the anterior temporal lobe (ATL) may be a central substrate for semantic knowledge (Patterson et al., 2007). These findings have inspired a model where the ATL serves as a semantic “hub,” supporting amodal or transmodal representations of conceptual knowledge, which interfaces with a distributed network of more peripheral modality-specific “spoke” systems (Lambon Ralph, 2014; Patterson et al., 2007; Rogers et al., 2004). Modern approaches to mapping cortical lesions to semantic deficits are culminating in efforts to fully integrate this body of work with neuroimaging and other experimental modalities (Jefferies, 2013).

3.09.4 Localizing Semantic Knowledge

Functional neuroimaging in humans has been instrumental in revealing the fine-grained localization of semantic memory throughout the cortex (Binder and Desai, 2011; Binder et al., 2009; Bookheimer, 2002; Price, 2010). In the following, we summarize evidence for the structural bases of both modality-specific and supramodal components of semantic representation.

3.09.4.1 Cortical Basis of Modality-Specific Representation

Numerous neuroimaging studies have provided evidence that cortices typically associated with a particular modality of sensory or motor processing are recruited during tasks probing semantic knowledge related to these modalities (Martin, 2007; Pulvermüller,

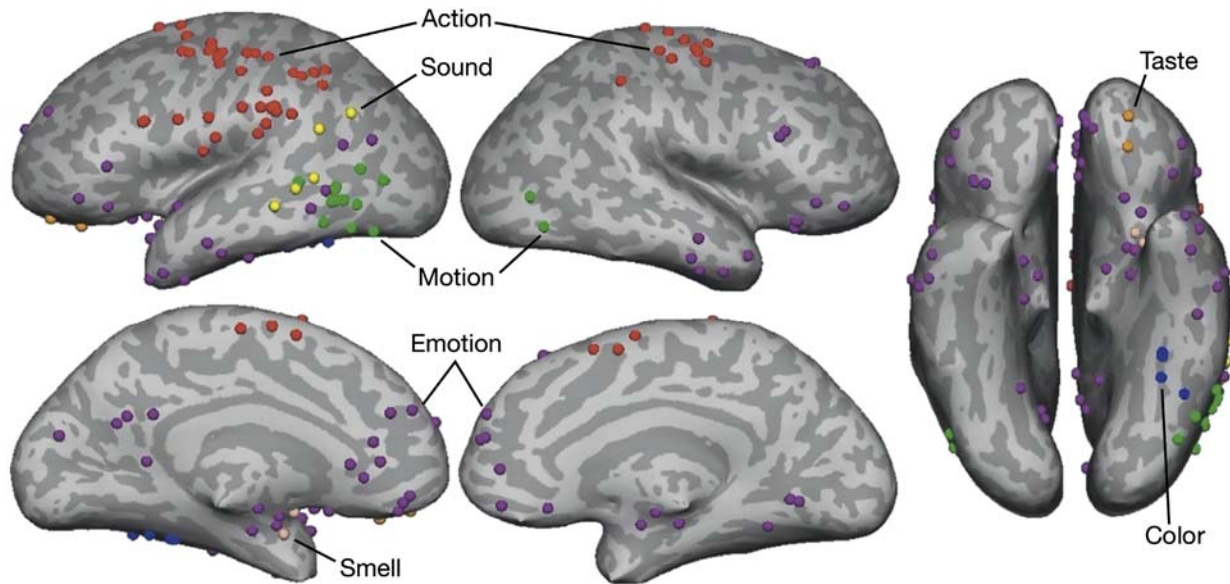


Figure 1 Metaanalysis of peak responses for language comprehension tasks eliciting the retrieval of modality-specific semantic information. Retrieving modality-specific semantic content evokes activity in modality-specific sensorimotor cortices. Retrieving action knowledge (red) elicits responses in posterior frontal and anterior parietal somatomotor cortices (e.g., [Martin et al., 1995](#)). Although retrieving motion knowledge (green) evokes activity in inferolateral occipitotemporal cortex (near visual motion area MT+; e.g., [Saygin et al., 2010](#)), similar stimuli (e.g., action verbs) are often used to probe action and motion knowledge, resulting in overlapping activations. Tool knowledge is associated with similar areas (e.g., [Martin et al., 1996](#)). Color knowledge (blue) is associated with activity in ventral temporal cortex anterior to color-processing regions (e.g., [Simmons et al., 2007](#)). Retrieving auditory information (yellow) evokes activity in superior temporal and temporoparietal auditory association areas (e.g., [Kiefer et al., 2008](#)). Retrieving gustatory knowledge (orange) evokes activity in orbitofrontal cortex ([Goldberg et al., 2006b](#)), while olfactory knowledge (pink) is associated with amygdalar and prepiriform activation ([González et al., 2006](#)). Emotion knowledge is associated with a widespread network including medial prefrontal, anterior temporal, and posterior cingulate cortices, as well as the amygdala (e.g., [Cunningham et al., 2003](#); [Lewis et al., 2007](#)). Adapted from Binder, J.R., Desai, R.H., 2011. The neurobiology of semantic memory. *Trends Cogn. Sci.* 15, 527–536.

2005). In the case of object concepts, requiring participants to retrieve the color canonically associated with a particular object has been shown to recruit an area of occipitotemporal cortex just anterior to and partially overlapping with the cortical area activated during color perception ([Simmons et al., 2007](#)). Studies following a similar logic have suggested that the semantic retrieval of object properties such as size, sound, touch, and taste recruit cortical areas matching or adjacent to the respective modality-specific sensory systems ([Chao et al., 1999](#); [Goldberg et al., 2006a,b](#); [Kellenbach et al., 2001](#); [Simmons et al., 2005](#)). Furthermore, certain objects such as tools afford particular actions or usage; e.g., retrieving semantic knowledge of a tool's use recruits motion- and motor-related cortical areas ([Chao and Martin, 2000](#)).

More generally, retrieving semantic representations of actions recruits cortical areas involved in both action recognition and execution ([Johnson-Frey, 2004](#); [Noppeney, 2008](#)). This includes the posterior middle temporal gyrus, intraparietal sulcus, and premotor cortex (e.g., [Kellenbach et al., 2003](#)), all of which are members of the putative human mirror neuron system ([Oosterhof et al., 2013](#)). These motor areas are thought to be recruited rapidly (within 200 ms), even in the case of action word stimuli ([Pulvermüller et al., 2005](#)). Most dramatically, well-matched word stimuli associated with actions requiring different body parts have been shown to recruit different motor areas roughly reflecting the somatotopic organization of motor cortex ([Hauk et al., 2004](#)). Despite reports of motor and premotor recruitment, a recent metaanalysis suggests that posterior middle temporal areas typically associated with action recognition are most reliably recruited during the retrieval of action concepts ([Watson et al., 2013](#)).

Finally, in an extensive metaanalysis, [Binder et al. \(2009\)](#) collated loci of activation from over 100 functional neuroimaging studies [both functional magnetic resonance imaging (fMRI) and positron emission tomography (PET)] using linguistic stimuli to probe semantic knowledge. This analysis revealed widespread recruitment of modality-specific cortices in semantic retrieval. Results from 38 imaging studies probing language comprehension suggest that the retrieval of modality-specific semantic content (e.g., color, motion, sound) recruits the modality-specific sensorimotor cortices typically associated with processing that type of information ([Fig. 1](#)). This body of work is typically taken to support the hypothesis that conceptual knowledge is grounded in sensorimotor representations (e.g., [Barsalou, 2008](#); [Pulvermüller, 2005](#)), a claim we will discuss in greater detail later.

3.09.4.2 Cortical Basis of Supramodal Representation

In contrast to the modality-specific systems contributing to semantic knowledge, many models of the semantic system also posit a role for a supramodal hub (alternatively referred to as amodal, transmodal, heteromodal, or a convergence zone; [Binder et al.,](#)

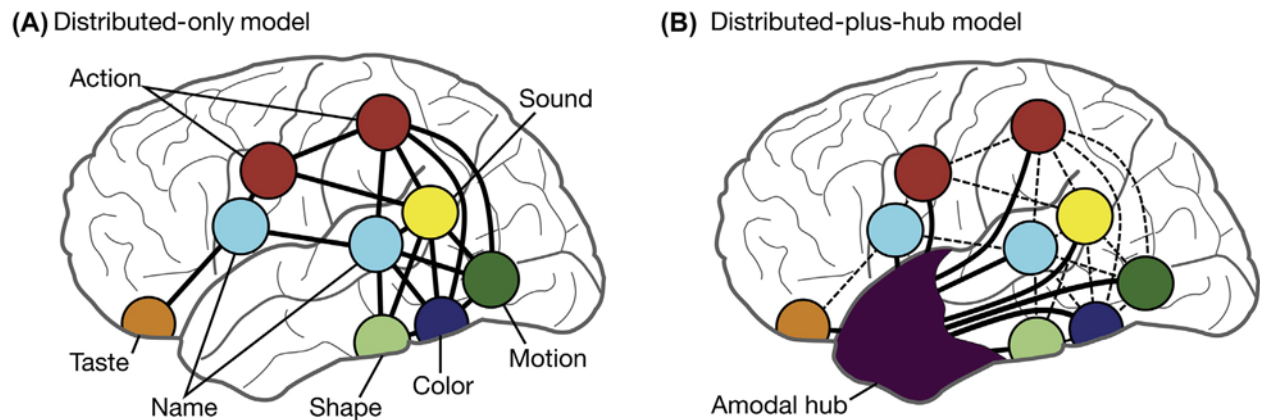


Figure 2 Distributed-only and distributed-plus-hub (hub-and-spoke) models of the cortical semantic system. (A) In the distributed-only model (e.g., Allport, 1985; Damasio, 1989; Martin, 2007), the semantic system comprises a network of widespread sensorimotor systems. Semantic relationships are encoded in the interconnections among these systems (*black lines*), and activation is gated to particular systems based on task demands. (B) The distributed-plus-hub model adopts this distributed sensorimotor network (*dotted lines*), but posits an additional amodal or transmodal hub in the anterior temporal lobes, where signals from modality-specific sensorimotor systems converge (*bold black lines*; Lambon Ralph, 2014; Patterson et al., 2007). This hub supports abstract conceptual associations and higher-order generalization across concepts that are semantically similar but differ in their sensorimotor attributes. Adapted from Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987.

2009; Damasio, 1989; Lambon Ralph, 2014; Patterson et al., 2007) responsible for storing amodal conceptual representations or integrating information across modalities (cf. Allport, 1985). Generally, these association cortices are adjacent to late-stage perceptual areas and run laterally from the intraparietal sulcus to the ATL. One candidate structure thought to play a supramodal role in semantic representation is the angular gyrus (AG) of the inferior parietal lobule, which responds across modalities in lexical decision tasks (Bonner et al., 2013) and indexes concept concreteness (Wang et al., 2010). However, the AG responds differentially in a variety of tasks and contexts, making its role in semantic cognition unclear (Seghier et al., 2010).

The ATL is the presumptive site of supramodal semantic representation (Lambon Ralph, 2014; Patterson et al., 2007). From a neuropsychological perspective, semantic deficits associated with the circumscribed bilateral deterioration of the anterior lobe are remarkably selective and amodal (Patterson et al., 2007). Although there is disagreement in the neuroimaging literature as to the role of the ATL in semantic cognition, this may be in some part due to methodological issues, and there is convergent evidence that the ATL is activated by semantic tasks in a modality-independent fashion (Visser et al., 2010). Interestingly, fMRI studies of semantic memory may underestimate the involvement of the ATL due to susceptibility artifacts near the sinuses; PET may in fact have an advantage in resolving signal in the ATL (Devlin et al., 2000). Furthermore, transcranial magnetic stimulation (TMS) applied to the ATL induces amodal semantic deficits reminiscent of semantic dementia (e.g., Pobric et al., 2007). Overall, these studies provide compelling evidence for the ATL as a supramodal convergence zone, and current studies are now teasing apart the roles of different regions of the ATL in supporting conceptual knowledge (Binney et al., 2010; Clarke and Tyler, 2015).

Overall, the structural basis of semantic memory emerging from the imaging literature converges with and expands on evidence from neuropsychology. Controlled retrieval and selection processes are associated with the prefrontal areas, in particular the left ventrolateral prefrontal cortex (Thompson-Schill, 2003; Wagner et al., 2001). Components of conceptual knowledge associated with, e.g., object color and usage are associated with the corresponding modality-specific sensory and motor cortices. Certain models of semantic knowledge might stop here (Allport, 1985; Barsalou, 2008; Martin, 2007; Pulvermüller, 2005). These distributed-only models suggest that this network of modality-specific subsystems is sufficient for conceptual knowledge; that is, concepts are fully specified as the sum total of their sensorimotor components. However, there is compelling evidence for supramodal convergence zones where truly amodal representations integrating across their sensorimotor constituents are encoded (Hodges and Patterson, 2007; Lambon Ralph, 2014). This hub-and-spoke model of the semantic system adopts the distributed network of sensorimotor areas (the spokes), but places the ATLs (the hub) at its center (Fig. 2). However, neuroimaging is correlational and cannot speak to the necessity of particular regions for semantic cognition. In the next section we touch on the debate as to whether modality-specific systems are necessary for conceptual representation.

3.09.5 Embodiment and Conceptual Knowledge

One of the central debates in the literature on semantic memory revolves around the extent to which conceptual knowledge is grounded in sensory and motor systems. At one end of this spectrum, concepts are abstract mental representations referring symbolically to phenomena in the world (Fodor, 1975; Pylyshyn, 1986). At the other end of the spectrum, concepts can be reduced to the

concerted reenactment of the sensory and motor representations at play when they were acquired (Allport, 1985; Barsalou, 2008; Gallese and Lakoff, 2005; Pulvermüller, 2005). This latter perspective is an extension of the sensory/motor model of semantic memory discussed earlier (Martin, 2007) and falls under the umbrella term of embodied cognition. Other current theories of conceptual knowledge (e.g., Mahon and Caramazza, 2009; Patterson et al., 2007) occupy a middle ground between these two extremes.

The embodied view is empirically motivated by neuroimaging work demonstrating that linguistic and semantic retrieval tasks recruit sensory and motor areas corresponding to the modality of the retrieved information (Martin, 2007; Pulvermüller, 2005). For example, words depicting actions associated with particular body parts evoke somatotopically organized activation in motor cortex (Hauk et al., 2004). Similarly, object words associated with a canonical color evoke activity in posterior temporal cortices also activated during color perception (Simmons et al., 2007). Proponents of the embodied view interpret these findings to indicate that conceptual knowledge relies on the sensory and motor machinery used in perception and action. That is, conceptual knowledge relies on simulation or the reenactment of sensorimotor representations. An outstanding example of this view is the mirror neuron theory of action understanding, which claims that action understanding is instantiated in the simulation of motor execution programs corresponding to the observed action (Rizzolatti and Sinigaglia, 2010).

However, as Mahon and Caramazza (2008) point out, these findings are not sufficient to support strong claims of embodiment. That is, correlative measures such as functional neuroimaging do not provide evidence that activity in a particular sensory or motor area is necessary for conceptual knowledge – the observed activation could be epiphenomenal or reflect activation propagating downward from structures encoding higher-order or supramodal conceptual representations. In fact, these neuroimaging findings are equally compatible with nonembodied theories of conceptual knowledge and are not sufficient to adjudicate between the two interpretations. This argument extends to the electrophysiological recordings in nonhuman primates typically referenced in support of the mirror neuron theory (Caramazza et al., 2014; Hickok, 2009). Studies using TMS to disrupt premotor cortex during action recognition in an attempt demonstrate causality have met with mixed results (Papeo et al., 2013). In the case of action recognition, there is compelling evidence that applying TMS to the posterior middle temporal gyrus—not considered a central component of the mirror neuron system—robustly disrupts action recognition (Papeo et al., 2015).

Overall, it remains unclear to what extent conceptual knowledge relies on the activation of sensorimotor representations. Despite relatively polemical work on this topic, the reality is likely a compromise between the two theoretical extremes. Conceptual knowledge is represented in highly distributed fashion, and conceptual representations may directly interface with sensorimotor machinery, particularly if lower-level features are demanded by the retrieval task. On the other hand, there is not yet compelling evidence for such strong embodiment as to completely rule out amodal or supramodal conceptual representation.

3.09.6 Distributed Semantic Representations

Computational approaches to semantic memory and natural language processing have converged on a general framework in which semantic representations are encoded in a distributed fashion as points in a high-dimensional, continuous vector space (Bengio et al., 2003; Mikolov et al., 2013; Turney and Pantel, 2010). The organization of this semantic space is typically derived from word cooccurrence statistics in large corpora of text (Landauer and Dumais, 1997; Lund and Burgess, 1996). This framework resonates with psychological models of semantic knowledge appealing to distributed representation (Hinton et al., 1986; McClelland and Rogers, 2003; Tyler and Moss, 2001). In these models, similar concepts are encoded nearer to each other in a psychological semantic space than are dissimilar concepts (Edelman, 1998; Shepard and Chipman, 1970). This complex semantic space is presumably encoded in the neural activity of the human brain, but how? Can we leverage computational models of semantic representation to decode the brain's vast store of conceptual knowledge?

3.09.6.1 Decoding Semantic Representations

Methodological advances in cognitive neuroscience have directly applied this computational framework to neuroimaging data, providing a foothold for decoding complex neural representations (Haxby et al., 2014; Norman et al., 2006; Tong and Pratte, 2012). Here we use the word “decode” in a particular sense. Semantic representations are embedded or “encoded” in a high-dimensional neural representational space where each dimension of the space corresponds to the measured activity of a single neural variable (i.e., a neuron or voxel; Haxby et al., 2014). Concepts or semantic representations can be visualized as points in this neural representational space (Fig. 3). Each point in this space corresponds to a unique pattern of activity across a distributed neural population. This distributed strategy for representation may not yield an intuitive mapping between neural activity and semantic content, but has the capacity to encode vast amounts of information with striking fidelity using a neurally inspired architecture (Hinton et al., 1986). Simply put, there is a very complex code mapping semantic information to patterns of brain activity. The overarching goal then is to unravel this code – that is, to develop algorithms that can “decode” the mapping between neural activity and the semantic content encoded therein.

A simple approach is to construct a linear classification algorithm that can differentiate between two or more object categories based on the distributed patterns of activation associated with these categories (Norman et al., 2006). In early applications of this approach, human participants were presented with object images comprising several categories (e.g., faces, houses, tools, etc.), and a classifier was trained to discriminate the resulting neural response patterns (Cox and Savoy, 2003; Haxby et al., 2001). Although

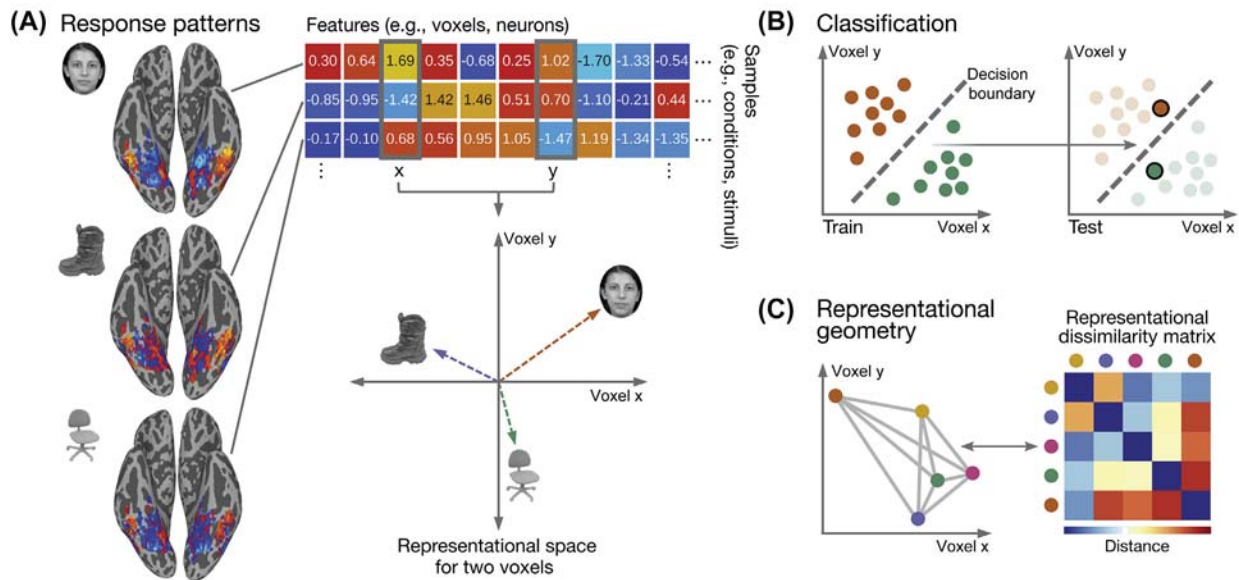


Figure 3 Decoding neural representations of semantic knowledge. (A) Distributed neural responses to stimuli such as object images (e.g., faces, shoes, chairs) are collated into a matrix where each column corresponds to a measured neural variable (i.e., features, such as voxels or neurons) and each row corresponds to an observation (i.e., samples, such as conditions, stimuli, or time points). Here, each row is a distributed pattern of activation across a set of voxels. Each sample or condition can be represented as a vector in a representational space where each dimension corresponds to a particular voxel response. In this case, the three objects are encoded in a two-voxel neural representational space. If the brain region encodes semantic information, responses patterns for semantically similar stimuli will be more similar (nearer to each other) in the neural representational space (Haxby et al., 2014). (B) One approach to decoding semantic information is to construct a classifier to discriminate stimulus classes. In this example, a decision boundary is constructed to discriminate response patterns for two classes of stimuli, e.g., faces and chairs (orange and green, respectively). Several samples from each class are used to train the classifier, then the resulting decision boundary is applied to previously unseen test samples (outlined in black) to evaluate generalization and ensure the classifier has not overfit the training data (Norman et al., 2006). (C) Rather than discriminating between two or more classes of stimuli, representational similarity analysis (RSA) quantifies the pairwise distances between each condition or stimulus (Kriegeskorte and Kievit, 2013; Kriegeskorte et al., 2008a). These pairwise distances are collated into a representational dissimilarity matrix (RDM) characterizing the representational geometry of a given brain area, which can then be compared to RDMs derived from computational models or human behavior.

this approach investigates perceptual processing and does not explicitly require semantic retrieval, there are nonetheless patterns in the classifier performance that may hint at semantic information; e.g., the classifier may confuse response patterns for human faces more with those for cats than for houses. Although this example is not sufficient to distinguish between semantic and perceptual contributions to classifier performance (Bracci and Op de Beeck, 2016), it serves to illustrate an important point. Multivariate pattern analysis is geared toward a fundamentally different question than that addressed by univariate neuroimaging analysis. Univariate analyses are best suited for localizing areas of the brain involved in a given process (usually by contrasting responses to two tasks differing along a particular dimension), while multivariate analysis are best suited for revealing information or representational content contained in the response topographies of a given area of the brain (Henson, 2005; Mur et al., 2009; Poldrack, 2011). Note that classification analyses can also be applied iteratively to small patches of cortex throughout the brain, a “searchlight analysis,” to approximately localize where information is represented (Kriegeskorte et al., 2006).

More recently, numerous studies using multivariate pattern analysis have begun decoding the neural representations supporting declarative memory (Rissman and Wagner, 2012). In a remarkable study on memory search, a classification algorithm was used to demonstrate that cortical response patterns associated with the category of a previously memorized stimulus reemerge during a free recall period (Polyn et al., 2005). Prior to a given item being verbally recalled, the authors were able to decode cortical response patterns most resembling those for the to-be-recalled item’s category (face, location, or object). Interestingly, category-specific cortical activity diagnostic of a soon-to-be-recalled item emerged several seconds before verbal recall. Furthermore, a sensitivity analysis revealed that a network of category-selective ventral temporal cortical areas, as well as medial temporal and medial prefrontal cortices contributed most to classifier performance. Restricting the classification analysis to highly responsive regions of interest negatively impacted performance, suggesting that memory retrieval relies on the coordinated activity of highly distributed cortical areas. This provides compelling evidence for the reenactment of cortical memory traces during recall and suggests that category-specific cortical activity recapitulated during recall may guide retrieval to items of that category.

Several studies have explored neural representations of semantic content evoked by word stimuli. Unlike pictures, where visual features can drive confounding perceptual representation, words are symbolic and obtain their representational content by making contact with our previously acquired semantic knowledge. Note, however, that reading words may still evoke ancillary imagery

and/or neural activity in modality-specific sensorimotor areas. In an early example of this approach, [Mitchell et al. \(2004\)](#) demonstrated that the semantic category of word stimuli (12 total categories) could be decoded from whole-brain response patterns with considerable accuracy. Other studies have taken the approach of decoding abstract versus concrete words ([Wang et al., 2010](#)) and lexical versus syntactic information ([Fedorenko et al., 2012](#)), implicating widespread association cortices. [Just et al. \(2010\)](#) demonstrated that the meaning of a wide variety of individual words (60 in total) can be decoded from response patterns extracted from a small subset of distributed cortical voxels.

In a clever approach where participants expected an object of a particular category to emerge from visual noise, category-specific conceptual content could be decoded from patterns of activation in the ATL even when no stimulus was actually present ([Coutanche and Thompson-Schill, 2015](#)). In line with this, [Peelen and Caramazza \(2012\)](#) demonstrated that, while more posterior temporal areas encode perceptual representations of objects, semantic associations, such as where an object is typically found or how it is typically used, are encoded in the ATL.

Recent work has extended the decoding methodology to magnetoencephalography (MEG), where the high temporal resolution can be leveraged to measure the emergence of semantic information over time ([Chan et al., 2011](#); [Sudre et al., 2012](#)). In a striking example of this capitalizing on the respective strengths of both fMRI and MEG, [Cichy et al. \(2014\)](#) demonstrated that, during visual object recognition, different types of category relationships emerge at several stages within the first 200 ms of processing.

The cross-validation procedure typical of classification analyses can be modified to construct a classifier that generalizes across modalities, a technique called multivariate cross-classification ([Kaplan et al., 2015](#); [Kriegeskorte, 2011](#); [Nastase et al., 2016b](#)). This approach is particularly well suited for decoding amodal or supramodal neural representations. In this approach, a classifier is trained on data from one modality and tested on data from the other modality, and vice versa; successful classification entails that the neural response patterns encode information that generalizes across modality. [Fairhall and Caramazza \(2013\)](#) presented participants with pictures and words referring to five semantic categories and used searchlight-based cross-classification to localize areas of the brain representing category distinctions that generalize across the two stimulus modalities. This fairly stringent test for supramodal neural representation revealed several left-lateralized association areas, including lateral and dorsomedial prefrontal cortex, posterior middle temporal cortex, the AG, precuneus, and ventral temporal cortex. [Shinkareva et al. \(2011\)](#) performed a related analysis and demonstrated that cross-modal classification performance generalizes across participants, while [Simanova et al. \(2014\)](#) extended this approach to the auditory modality (verbal words and natural sounds). In an ingenious experimental design, both [Buchweitz et al. \(2012\)](#) and [Correia et al. \(2014\)](#) used cross-language classification (with visually and verbally presented words, respectively) in bilingual participants to demonstrate that neural representations of the semantic content of a word generalize across languages. Finally, a similar approach has been applied to action representation, suggesting that lateral occipitotemporal and inferior parietal cortices encode supramodal action representations that generalize across observation (and viewpoint), execution, imagery, and the object acted upon ([Oosterhof et al., 2012a,b, 2010](#); [Wurm et al., 2016](#); see also [Wurm and Lingnau, 2015](#)).

3.09.6.2 Geometry of Semantic Representation

Most of the decoding methods mentioned earlier operate by learning a generic function that classifies neural responses patterns into two or more classes (i.e., experimental conditions, stimuli). Although this is a powerful method for determining whether response patterns contain information discriminating the classes, it is limited in the sense that it does not fully describe the relationships among responses patterns for the various conditions or stimuli. Classifiers are agnostic to what distinctions between the stimuli might be driving classifier performance. A related approach is to instead compute the pairwise distances between response patterns for each stimulus or condition—a technique called representational similarity analysis (RSA; [Kriegeskorte et al., 2008a](#)). These pairwise distances are typically collated in a representational dissimilarity matrix (RDM) and describe the geometry of representation in the multivariate response space ([Kriegeskorte and Kievit, 2013](#)). Once again, each response pattern evoked by a stimulus or experimental condition can be visualized as a point in a representational space where each dimension corresponds to a single voxel's (or neuron's) response magnitude. Response patterns for conditions that are represented similarly by a given brain region will be located nearer to each other in this neural representational space than conditions represented very distinctly ([Edelman, 1998](#)). This approach has at least two advantages over classification analyses: (1) it provides a more nuanced description of the representational space, particularly when a large and diverse set of stimuli are used and (2) because representational dissimilarity can be computed over any set of multivariate observations, it allows the investigator to test different (e.g., neural, behavioral, computational) models of the representational space ([Kriegeskorte, 2011](#)).

In the seminal application of this approach, [Kriegeskorte et al. \(2008b\)](#) demonstrated that distributed response patterns in ventral temporal cortex encode diverse category relationships among a large variety of object stimuli. Interestingly, the category structure revealed by RSA in human ventral temporal cortex using fMRI very closely resembled the representational geometry of a population of macaque inferotemporal neurons measured using single-unit electrophysiology ([Kiani et al., 2007](#)). This analysis revealed that ventral temporal cortex tightly clusters the representation of human faces, which are represented more similarly to human bodies and nonhuman animals than they are to inanimate objects. This rich representational geometry in the ventral visual pathway is likely driven by both perceptual properties of the stimulus and semantic knowledge. Importantly, this study also demonstrated that RSA can capture similarities in representation across very different systems and modalities (in this case, primate species and physiological measurements).

This versatility in comparing representational geometries also opens the door for testing computational models of representation. For example, Connolly et al. (2012) showed that a neurally inspired model of early visual processing (Serre et al., 2007) captured the geometry of neural responses in early visual cortex to visually presented images of animals. Importantly, in downstream temporal areas, the neural representation of animal taxonomy was not visually organized, but organized according to animacy; that is, primates were represented more similarly to birds than to insects (Fig. 4). Sha et al. (2015) expanded on this work, demonstrating that ventral temporal cortex encodes object stimuli along an “animacy continuum,” with humans at one end and inanimate objects such as tools at the other (Fig. 5). Responses to “low-animacy” animals, such as insects and fish, overlap with responses to inanimate objects. The animals at the “low” end of this animacy continuum are fully animate but differ from animals at the “high” end in terms of their similarity to humans and the complexity of internal states that motivate agentic behavior. This organization can be visualized as the first dimension using multidimensional scaling (Fig. 5B) and shows clearly that the animate–inanimate dichotomy is not the dominant principle for neural representation in ventral temporal cortex but, rather, is a special case of the animacy continuum. The animate–inanimate distinction reflects only the contrast of extreme examples at the ends of this continuum—mammals and birds versus objects—whereas fully animate animal concepts (insects and fish) are collocated at the “low” end of the continuum with inanimate objects.

Recent studies have used RSA to characterize additional organizing features of object representation in ventral temporal cortex and elsewhere. Work by Konkle and colleagues (Konkle and Caramazza, 2013; Konkle and Oliva, 2012) demonstrates that real-world object size (but not animal size) is also an important dimension for the organization of semantic knowledge in ventral temporal cortex. Connolly et al. (2016) have also used this method to demonstrate that the degree to which an animal is perceived to be threatening (e.g., a wolf is more threatening than a deer) is encoded in the anterior superior temporal sulcus. Applying RSA to word stimuli reveals a widespread left-lateralized network encoding the semantic content of both pictures and words in lateral temporal cortex and inferior parietal cortex (Devereux et al., 2013). Going beyond the neural representation of category relationships in ventral temporal cortex, Tyler and colleagues (Clarke and Tyler, 2014, 2015; Tyler et al., 2013) have shown that the semantic relationships of individual objects are encoded in perirhinal cortex. These finer-grained distinctions likely emerge later (after 200 ms) than gross category relationships in the occipitotemporal processing hierarchy (Clarke et al., 2013). Current applications

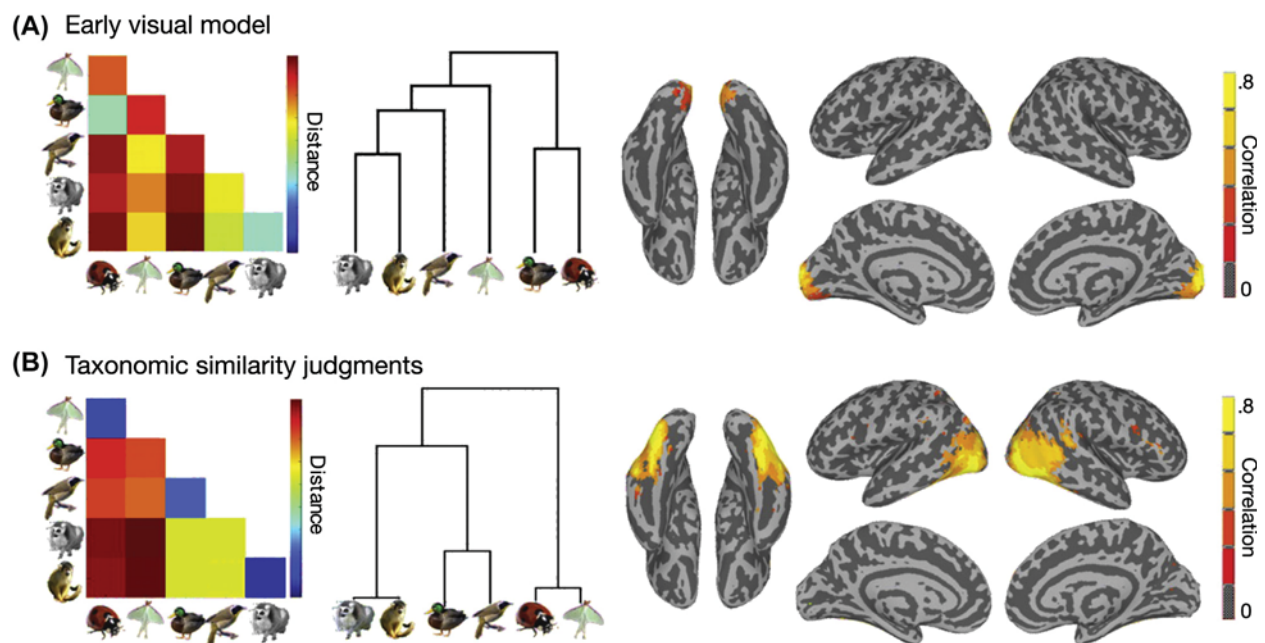


Figure 4 Neural representation of animal taxonomy. Representational similarity analysis (Kriegeskorte et al., 2008a) was used in conjunction with surface-based searchlights (Kriegeskorte et al., 2006; Oosterhof et al., 2011) to localize areas of the brain encoding animal stimuli according to either visual or semantic similarity. (A) A computational model of early visual processing (Serre et al., 2007) was used to construct a representational dissimilarity matrix (RDM) for images of six different animals (ladybird beetles, luna moths, common yellowthroat warblers, mallard ducks, ring-tailed lemurs, and squirrel monkeys). The RDM for this model, and the associated dendrogram, reflect visual similarities between the animals. The representational geometry for this model was then correlated with the representational geometries of searchlights throughout the brain, revealing that the model reflects representational geometry in early visual cortex at the occipital pole. (B) Participants made behavioral judgments of the biological similarity of the six animals, and these were used to construct a behavioral RDM. The dendrogram associated with this RDM clearly depicts the taxonomic organization of the animals. This behavioral RDM was then used to probe searchlight representational geometries, revealing that behavioral judgments of animal taxonomy are encoded in ventral temporal and lateral occipitotemporal cortices. Adapted from Connolly, A.C., Guntupalli, J.S., Gors, J., Hanke, M., Halchenko, Y.O., Wu, Y.-C., Abdi, H., Haxby, J.V., 2012. Ventral temporal cortex encodes fine-grained category relationships amongst animals. *J. Neurosci.* 32, 2608–2618.

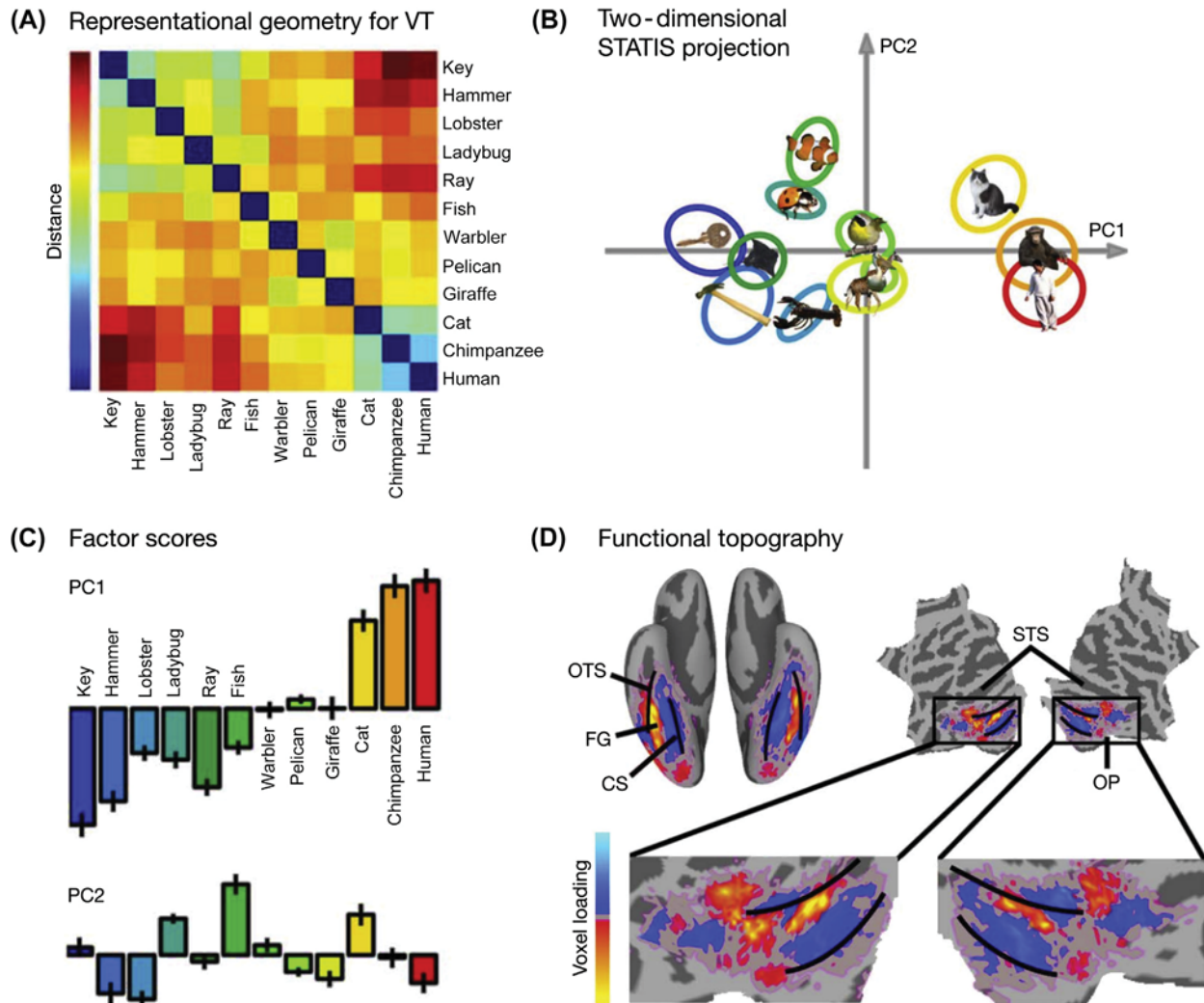


Figure 5 The animacy continuum in ventral temporal cortex (VT). (A) Representational dissimilarity matrix (RDM) comprising the pairwise distances between 12 visually presented objects (key, hammer, lobster, ladybug, ray, fish, warbler, pelican, giraffe, cat, chimpanzee, and human) for VT. Although participants draw a clear distinction between animate and inanimate (key, hammer) objects when making behavioral judgments of similarity, this is not reflected in the representational geometry of VT. (B) Response patterns for each object were projected from the high-dimensional voxel space to a low-dimensional subspace using STATIS, a variant of principal components analysis (PCA) for multiple data tables (Abdi et al., 2012). The first two principal components (PCs) are shown here. The first PC captures a gradient from the objects having the greatest “animacy” or human-like agency (e.g., humans, nonhuman primates) to the least animacy, including fish, invertebrates, and finally inanimate tools. This gradient is apparent even when only nonprimate animals, or alternatively only tools and primates, are used to derive the projection. Ellipses denote bootstrapped 95% confidence intervals around the mean location. (C) Factor scores for the first two PCs returned by STATIS. Note that there is a continuous gradient in animacy from primates and other mammals on one end to fish and invertebrates, which cluster nearer to tools at the other end. The first PC reflecting the animacy continuum accounts for 55% of the variance in these data. The next PC does not have such clear structure and accounts for only 10% of variance. Error bars denote the standard error of the mean factor score. (D) The functional topography of the first PC can be visualized by projecting the mean voxel loadings across participants onto the cortical surface. Here, *warm colors* indicate voxels responding more strongly to more animate stimuli, while *cool colors* indicate voxels responding more to low-animacy and inanimate stimuli. The functional topography of the animacy continuum in VT subsumes the topography resulting from coarser-grained animate–inanimate contrasts, with greater responses to animate stimuli in lateral fusiform gyrus and responses to inanimate stimuli occurring more medially (Chao et al., 1999; Mahon and Caramazza, 2009). CS, collateral sulcus; FG, fusiform gyrus; OP, occipital pole; OTS, occipitotemporal sulcus; STS, superior temporal sulcus. Adapted from Sha, L., Haxby, J.V., Abdi, H., Guntupalli, J.S., Oosterhof, N.N., Halchenko, Y.O., Connolly, A.C., 2015. The animacy continuum in the human ventral vision pathway. *J. Cogn. Neurosci.* 27, 665–678.

of RSA continue to test more sophisticated computational models of neural representation to tease apart how semantic information is extracted from visual stimuli (Khaligh-Razavi and Kriegeskorte 2014). Finally, recent work suggests that these neural representational spaces may not be static, but are actively shaped by behavioral goals (Çukur et al., 2013; Nastase et al., 2016a).

3.09.6.3 Forward Encoding Models

The previously described decoding methods assume an implicit mapping or intermediate feature space relating neural response patterns and the stimuli evoking them (e.g., words, pictures). However, recently developed approaches using forward encoding models (also referred to as voxel or population receptive field models) aim to map stimuli to neural responses via an explicit feature space (Kriegeskorte, 2011; Naselaris et al., 2011). In a particularly relevant example of this, Mitchell et al. (2008) implemented a computational model of semantic knowledge based on cooccurrence statistics for a variety of words. Based on this model, linear regression was used to predict the hemodynamic responses to nouns (picture–word pair stimuli) for each voxel in the brain (Fig. 6). For certain voxels, this semantic encoding model will capture a considerable amount of response variance evoked by the stimuli. In voxels that are well-predicted by this model, certain model parameters (semantic features) will be more heavily weighted than others, suggesting that these voxels encode something similar to those semantic features. The result is that each voxel is assigned a semantic tuning function. This approach has the benefit that, if the encoding model captures meaningful features of the representational space, it will generalize to novel stimuli. Mitchell and colleagues were able to show that, when supplied with novel nouns on which it was not previously trained, the model was able to predict distributed patterns of brain activity that resembled the actual patterns of brain activity evoked by those nouns. The authors also demonstrated that when all nouns of a given category were removed from the training set, the model was still able to accurately predict response patterns for nouns from the left-out category, suggesting the semantic model was rich enough to extrapolate to novel categories. Recent work by Pereira et al. (2011, 2016) expands this approach by demonstrating that semantically related words can be reconstructed from neural responses to word stimuli (text).

In a similar vein, Huth et al. (2012) used naturalistic movie stimuli to map semantic representation across the cortex. The movies were annotated to indicate the presence of over a thousand different objects and actions (nouns and verbs), and category relationships were assigned based on the WordNet hierarchy (Miller et al., 1990). Using these semantic features, they then estimated coefficients to predict hemodynamic responses to the movie for each voxel (using regularized regression due to the considerable number of model parameters). To test the validity of the model, voxel time courses were predicted for a novel movie stimulus.

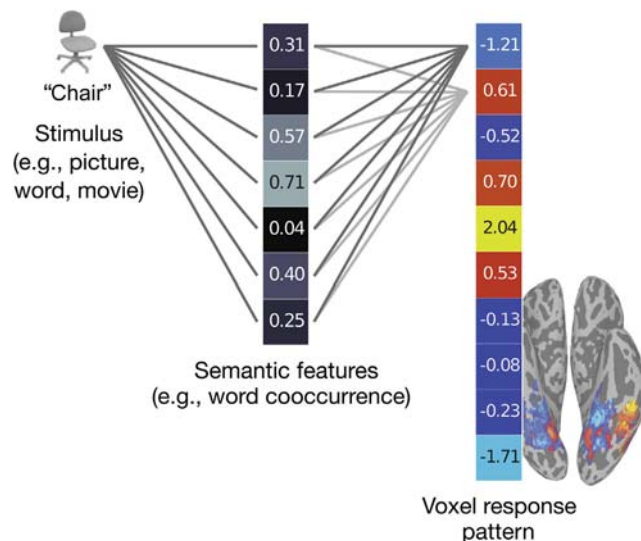


Figure 6 The forward encoding model maps a stimulus to neural responses via an intermediate representational space intended to capture certain features critical to the neural representation of the stimulus. In the case of a semantic encoding model, each stimulus (e.g., picture, word) is encoded as a distributed semantic representation (i.e., a semantic vector or word embedding) across a set of features derived from, e.g., word cooccurrence statistics extracted from a large text corpus. Stimuli that are semantically similar (i.e., tend to cooccur with a shared set of words) will be embedded nearer to each other in this feature space (i.e., they will have correlated semantic vectors). A regularized linear regression model is then estimated to predict each voxel's response from the intermediate semantic features (Huth et al., 2012, 2016). Note that in this visualization the response pattern is transposed with respect to Fig. 3. Overall, the predicted brain image is a weighted sum of basis images associated with each feature of the semantic encoding model (Mitchell et al., 2008; Pereira et al., 2011, 2016). Critically, novel stimuli can be supplied to the forward model to generate predicted brain images. If the predicted images resemble the actual brain images associated with these test stimuli, the model captures important features of neural representation. Finally, given brain images for novel stimuli, the model can be inverted to decode semantic vectors for each stimulus (Naselaris et al., 2011; Pereira et al., 2011, 2016).

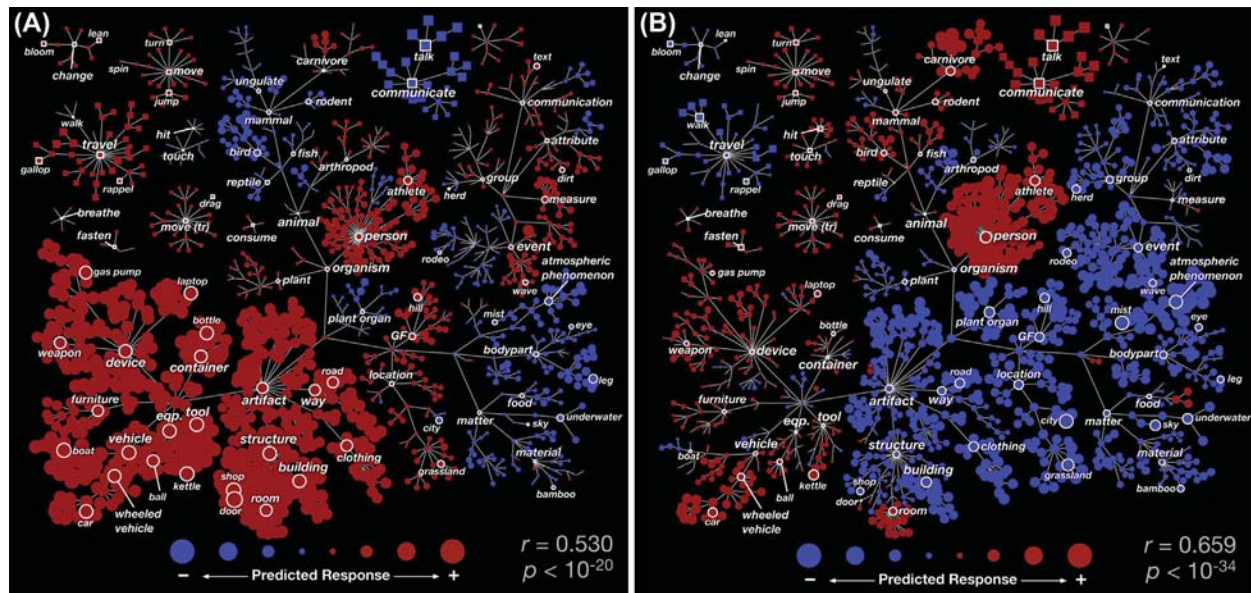


Figure 7 Semantic selectivity for two example voxels. For each voxel, estimated coefficients for each parameter of the semantic model are organized according to the graphical structure of WordNet. *Red markers* reflect positive predicted responses for a given category, *blue markers* reflect a negative response, and marker size indicates the magnitude of response. Correlations between the predicted and actual voxel responses are displayed in the bottom right corners. (A) Semantic selectivity for a voxel in the left parahippocampal place area. Coefficients depicted in red indicate that the model predicts positive responses for this voxel when, e.g., buildings or vehicles are present in the movie, consistent with the literature on this brain area (Epstein and Kanwisher, 1998). (B) Semantic selectivity for a voxel in the right precuneus reflecting positive predicted responses to people and social interaction. Adapted from Huth, A.G., Nishimoto, S., Vu, A.T., Gallant, J.L., 2012. A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron* 76, 1210–1224.

The model provided a good fit for widespread cortical voxels. Each voxel is characterized by the coefficients estimated for each parameter of the semantic model (see Fig. 7 for two example voxels). The authors then applied dimensionality reduction to these coefficients across cortex to find a low-dimensional semantic space that generalized well across participants. The dimensions accounting for the most variance in this neural representational space captured such semantic qualities as mobile–immobile, animate–inanimate, social–nonsocial, and natural–artificial. The authors then projected these dimensions back onto the cortical surface, revealing organized gradients of cortical representation for different semantic features (Fig. 8).

Recently, Huth et al. (2016) extended this approach to modeling the responses to the semantic content of individual words in auditory narratives. Participants listened to over 2 h of stories and a computational model capturing semantic features of the stories was used to predict brain activity. Again, the semantic model captured the response tuning of widespread cortical voxels. The authors then used these voxelwise semantic tuning functions to parcellate the cortex into areas primarily representing particular semantic features. In related work, Wehbe et al. (2014) applied a forward encoding model combining visual, syntactic, semantic, and discourse-level features to fMRI data collected while participants read a chapter from a novel. The authors were able to decode which 8-s passage the participant was reading from the entire chapter with 74% accuracy based on the response patterns predicted by the forward model. Overall, these studies highlight the utility of using sophisticated computational models to characterize voxelwise tuning. They demonstrate that semantic information is encoded robustly throughout much of cortex while certain dimensions of the semantic space preferentially map onto particular cortical areas.

3.09.6.4 Commonality of Semantic Representation

With some notable exceptions (e.g., Just et al., 2010; Shinkareva et al., 2011), most of the previously mentioned studies do not report neural representations of semantic knowledge that generalize across individual brains, instead relying on separate models constructed to fit each participant's functional anatomy. Although the forward encoding approach (e.g., Huth et al., 2012, 2016; Mitchell et al., 2008) assumes a common semantic model across individuals (e.g., based on word cooccurrence statistics in text), this model is fit differentially to each voxel in each individual's brain. The critical benchmark of common neural representation is to train an encoding or decoding model on a group of participants and test this model on a novel, left-out participant (Clithero et al., 2011; Mourão-Miranda et al., 2005). Although this may sound overly stringent, it is the de facto standard required for predictive models to provide diagnostic information in individual people (Dubois and Adolphs, 2016; Poldrack, 2011). Unfortunately, previous attempts at this have typically resulted in dismal generalization performance, particularly for representational content encoded in fine-grained response patterns. Recent work suggests that measurements of neural representational geometry can capture

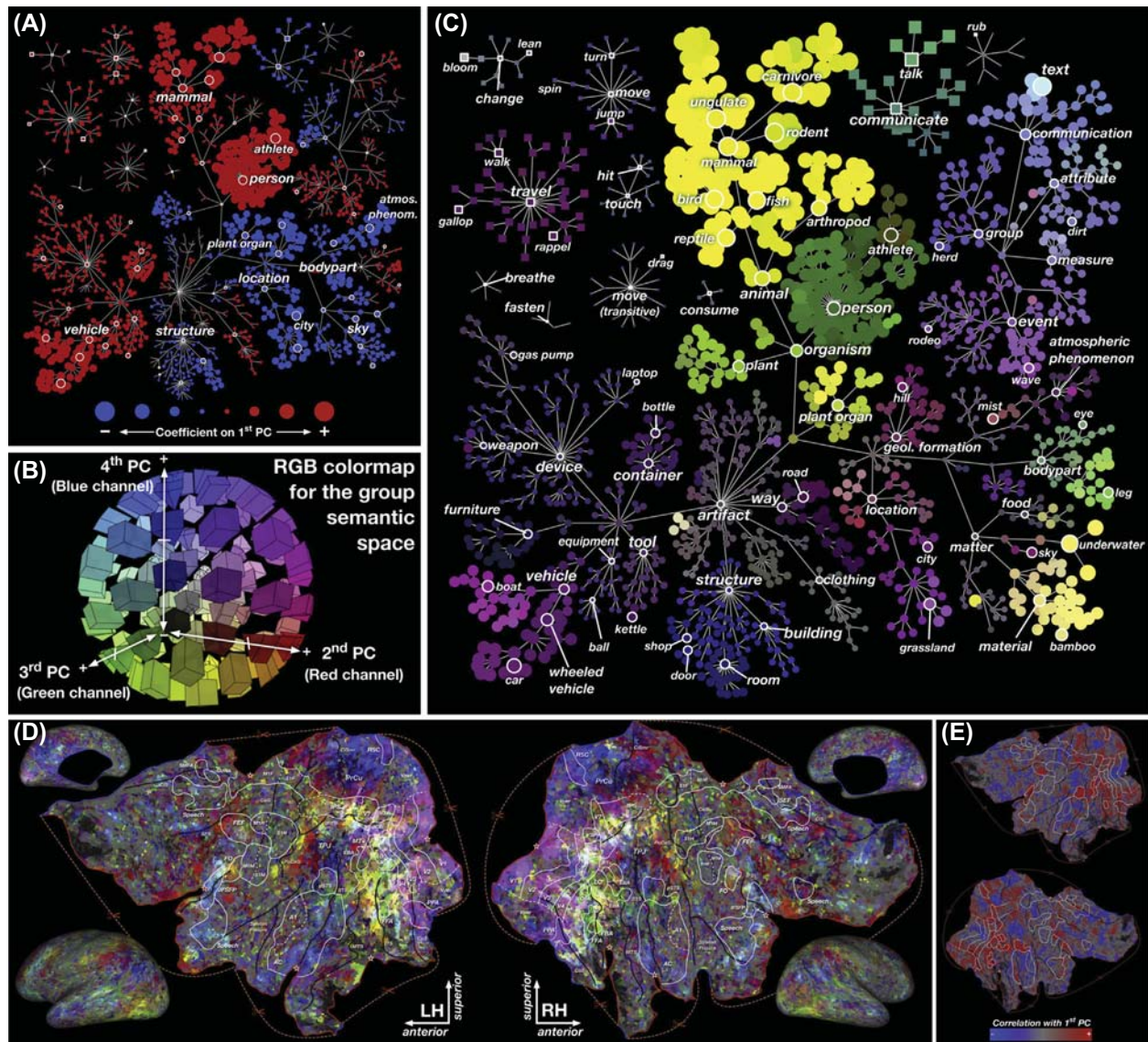


Figure 8 Gradients of semantic representation throughout human cortex. Participants were presented with naturalistic movie stimuli, and a forward encoding model capturing the semantic content of the movies was used to predict neural responses. Principal components analysis was used to recover four dimensions of semantic representation shared across participants. (A) Coefficients for the first principal component (PC1) organized according to the graphical structure of WordNet distinguish high- and low-motion energy categories. Marker size reflects the magnitude of the coefficient. (B) Three-dimensional color map for PCs 2–4. (C) Coefficients for PCs 2–4 indicate that semantically related categories (according to WordNet) are represented similarly in the brain. (D) Semantic model weights for each cortical voxel are projected onto PCs 2–4 and colored accordingly. Continuous gradients of semantic selectivity span much of cortex. (E) Projection of model weights for each voxel onto PC1 visualized on the cortical surface. Adapted from Huth, A.G., Nishimoto, S., Vu, A.T., Gallant, J.L., 2012. A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron* 76, 1210–1224.

an individual's unique perceptual judgments (Charest et al., 2014). What drives these individual differences? This is a particularly difficult question for the neural representation of high-level semantic knowledge and word meanings, as these are acquired through varying individual experiences. Presumably these differences in experience drive cortical plasticity toward subtle differences in functional topography. However, even for lower-level perceptual areas, this functional–anatomical mapping varies considerably across participants (Aine et al., 1996; Duncan et al., 2009; Frost and Goebel, 2012; Tootell et al., 1995; Watson et al., 1993). This poses a general problem: How can we construct a common model (i.e., an atlas or template) of the neural representation of semantic knowledge if functional topography varies idiosyncratically across brains? Put differently, how can we translate between two individuals' unique neural representation spaces?

An important clue comes from work demonstrating a striking correspondence in neural activity across participants during naturalistic perception and social interaction (Hasson et al., 2004, 2010, 2012). This suggests that rich, dynamic stimuli drive individual

functional responses in a similar way, even if the underlying anatomy is not exactly in register. Haxby et al. (2011) capitalized on this commonality of functional responses evoked by naturalistic stimuli to derive a mapping between the representational spaces of individual brains based on function rather than anatomy. Neural activity was measured with fMRI while participants freely viewed a 2-h Hollywood movie (*Raiders of the Lost Ark*). Cortical response patterns within a region of interest were then analyzed as vectors in a high-dimensional neural representational space, rather than in a two- or three-dimensional cortical topography. The trajectory of functional responses driven by the movie in each individual's representational space could then be rotated to best match the trajectories of other participants. For each individual participant, a transformation matrix was estimated using the Procrustes transformation to translate that participant's functional responses into a common model space, or into any other participant's idiosyncratic anatomy. This transformation is invertible and data from many individuals can be projected into a single individual's anatomical space, allowing investigators to leverage more data for prediction than any single participant could provide. When applied to ventral temporal cortex, this boosts decoding accuracies for between-participant pattern classification to levels that match or exceed within-participant pattern classification accuracies. Recent developments have extended this approach to the whole brain using a searchlight algorithm and demonstrated that it translates fine-grained functional topographies across individual brains (Guntupalli et al., 2016). Another variation on this method factorizes participants' response patterns into a low-dimensional shared response model and participant-specific bases, effectively suppressing participant-specific noise in the shared template (Chen et al., 2015). More broadly, these developments suggest that functional commonalities derived from naturalistic stimuli provide a rich description of the representational space that captures elements of semantic knowledge such as relationships between categories, as well as finer within-category relationships.

Developing this sort of functional atlas is critical for generalizing across individuals, but it also provides an anchor point for exploring finer-grained individual differences in functional anatomy (Dubois and Adolphs, 2016). If in the future we hope to provide diagnostic solutions for individual patients or pinpoint unique functional abnormalities, we need models that can both generalize across brains and preserve functional-anatomical idiosyncrasies. Rich, naturalistic stimuli and sophisticated models of cortical representation promise to provide increasingly better descriptions of the neural bases of semantic knowledge. These models should be general enough to capture commonalities across brains, but faithfully preserve the knowledge and expertise unique to an individual's personal experiences.

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