Semantic Memory

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Glossary

Amygdala It is responsible for processing of emotion (e.g., fear, disgust, happiness).

Association areas These are regions of the neocortex beyond the primary sensory processing cortex and cortical areas processing information before the primary motor cortex. Unimodal association areas surround primary sensory and primary motor areas, and multimodal association areas lie beyond these, that is, in between unimodal sensorimotor association areas.

Cingulate cortex It lies immediately superior to the corpus callosum, which is the white matter axonal fiber bundle that connects the cerebral hemispheres. Cingulate cortex is included in the limbic system implicated in emotion and motivation and continues posteriorly as the parahippocampal gyrus in the temporal lobe, which provides input to the hippocampus, consistent with a role in episodic memory.

Embodied (grounded) cognition This is a long-standing framework for cognitive science that proposes that processing of modal information (i.e., sensory, motor action, and mental state) has a necessary role in cognition, including semantic memory. Largely neglected until recently, this framework opposes the standard framework of cognition that states that an amodal symbol system exists apart from the modal systems and represents meaning in semantic memory. Embodied (grounded) cognition accounts vary according to whether embodied (grounded) cognition alone can explain all knowledge or embodied knowledge represents concepts alongside an amodal system. The latter hybrid frameworks vary further according to how much embodied and amodal systems each contribute to cognition.

Frontal lobe It extends from the anterior-most part of the brain to the central sulcus where the primary motor cortex ends. The frontal lobe contains motor areas and lateral and medial prefrontal regions and anterior cingulate regions implicated in cognitive control, working memory, and selective attention.

Lexicon This is the set of all words and expressions in a language (i.e., the vocabulary).

Linguistic This refers to perceptual cues (i.e., words) and actions involved in natural language, including semantics, grammar, and phonetics.

Mental state This is a state of brain activity related to introspection, that is, a state accompanied by a subjective quality of conscious experience (or qualia, e.g., feeling a headache, taste of food, your experience of the colors in a rainbow). Mirror neuron circuits, in which neurons involved in manipulating objects are also involved in perceiving another animate agent perform that action, may underlie social simulations for embodied cognition.

Occipital lobe It is the most posterior part of the neocortex. It includes the primary visual area (V1) in striate cortex and extrastriate visual cortex that lies anterior to V1, as well as association areas that are object-sensitive, responding more strongly to intact images of objects than scrambled versions with no coherent object structure. This lobe is retinotopically organized such that adjacent neurons receive input from nearby parts of the visual field (and corresponding retinal location). Neurons adjacent but displaced laterally from each other across the cortex represent adjacent but likewise displaced visual field (and retinal) locations. Consequently, this cortex effectively represents an orderly image of light hitting the retina, though distorted to magnify central over peripheral retina. Extrastriate visual areas contribute to semantic memory based on an embodied cognition account.

Parietal lobe This lies in the dorsal posterior part of the cerebral cortex. It includes the angular gyrus region in the lateral inferior part (Brodmann's area [BA] 39; areas PGa and PGp) and the supramarginal gyrus (BA 40) that have been implicated in semantic processing in response to written and spoken words. This angular gyrus region extends posteriorly into the anterior occipital lobe.

Priming This refers to a phenomenon in which experience with a stimulus (referred to as the prime) affects the response to another stimulus (referred to as the target). Priming is typically attributed to implicit (nonconscious) memory. The relationship between the prime and target can be perceptual (i.e., both have the same or similar sensory features or properties, e.g., the words 'dog' and 'dog'), conceptual (i.e., both have the same meaning, e.g., the word 'dog' and a picture of a dog, or hearing and reading the word 'dog'), or semantic (i.e., both have associatively or categorically related meanings, e.g., the words 'nurse' and 'doctor' are associated concepts). Priming usually facilitates processing of the target, making task performance faster and more accurate but can be detrimental in some cases.

Semantic memory Semantic memory or knowledge refers to conceptual information about the meaning of words, objects, people, scenes, and facts. This meaningful information is not consciously related to specific, personally experienced events of episodes. However, concepts are formed by abstracting or generalizing across multiple individual experiences. For example, the meaning of a dog is not about a single personal event with a dog but rather the meaning of the dog category (dog-ness) is generalized across features common to many instances of dogs.

Spreading activation The process of how activation can move from one concept (or node) to another in a semantic (or associative or neural or connectionist) network. Each link between two concepts has a weight that determines how much a concept can activate the other linked concept. Concepts can be directly linked to each other and indirectly linked to each other through one or more other concepts. The combination of weights and how directly linked concepts are determines how far activation of one concept spreads to other linked concepts. Through this process, activation spreads to related concepts in the network.

Temporal lobe It is a ventrally located region of the neocortex that includes association areas for visual processing, primary and association areas for auditory processing, and multimodal association areas. The anterior temporal lobe has been proposed to be an amodal hub for semantic memory. The medial temporal lobe includes the hippocampus and the surrounding cortex of the parahippocampal region, which is composed of perirhinal cortex, parahippocampal gyrus, and entorhinal cortex, and may also represent semantic memory.

Semantic Memory Is One Type of Memory

Semantic memory is conscious long-term memory for meaning, understanding, and conceptual facts about the world. Semantic memory is one of the two main varieties of explicit, conscious, long-term memory, which is memory that can be retrieved into conscious awareness after a long delay (from several seconds to years). Endel Tulving in 1972 (building upon a distinction between two primary forms of memory by Reiff and Scheers in 1959) distinguished between semantic and episodic memory. Episodic memory refers to stored representations for personally experienced episodes from one's life within a particular spatiotemporal context (e.g., dinner in Berkeley in January this year). Semantic memory refers to stored representations for meaningful facts or world knowledge, regardless of the spatiotemporal context in which the information was acquired and without information about personal experiences surrounding learning of the information (e.g., the concept 'dinner' but not a particular dining experience), and is necessary for language. Crucially, while episodic memory involves awareness of a feeling of having personally experienced an event or item, regardless of meaning (i.e., an item could be a nonsensical figure like abstract art and so has no meaning but has been experienced before as on multiple museum visits), semantic memory involves awareness of meaning unaccompanied by a feeling of familiarity of having previously experienced the event or item or remembering the place and time of the personal learning experience(s). For example, using semantic memory, you know what a dog is and can read the word 'dog' and be aware of the meaning of this concept, but you do not remember where and when you first learned about a dog or even necessarily subsequent personal experiences with dogs that went into building your concept of what a dog is. Even without a feeling of personal experience, you know what a dog is when you see, hear, or read about a dog. Thus, you have semantic memory for meaning, regardless of a feeling of familiarity or recollection of the personal experiences that had originated from the concept.

Language, Concepts, Categories, and Semantic Networks

Hierarchical Model

Ideas about semantic memory developed from attempts to explain how human language communicates concepts. While computer scientists proposed semantic nets for translating natural language as early as 1956, the term 'semantic memory' emerged in psychology in early models of human knowledge about word concepts circa 1969. Collins and Quillian viewed semantic memory as a hierarchical network of relations among concepts. A concept refers to meaning, which is stored in semantic memory. Language enables an arbitrary symbol, such as a stream of sounds comprising a word (e.g., 'dog'), to be associated with the memory representation of the meaning of the symbol (i.e., the semantic memory of a dog). As described in concept learning research, a concept is a mental representation that places an object, event, or idea into a category. Semantic memory can thus be said to be the store of mental representations of categories. In their original formulation of the organization of semantic memory, Collins and Quillian assumed that categories are organized hierarchically, and defining features compose each category. For example, an animal has skin, moves, eats, and breathes. In 1976, Eleanor Rosch proposed different levels of categories. For example, song and field sparrows are subordinate categories of the more general category of sparrow, which is a basic-level category, along with eagle and cardinal of the superordinate-level category of birds, and, at a still more general level, birds and fish are animals. Collins and Quillian's theory predicts that the response time to classify whether a feature belongs to a category depends upon how many nodes or levels of the hierarchy must be traversed to do the task, which was confirmed experimentally.

Feature Overlap

Smith and colleagues modified this basic framework to suggest that the meaning of a concept is a set of features, as opposed to a single node. Further, defining features are essential (e.g., robins have red breasts), whereas characteristic features are merely typical of a concept (e.g., robins are wild, bipedal, have wings, perch in trees). Consistent with this feature overlap model, people rate robins and sparrows as more typical birds than ducks and geese, and robins and sparrow are rated as more similar to each other than the other birds. However, there may be no defining features; as noted by the philosopher Wittgenstein in 1953, there is no feature that all games share. Also, feature overlap models compare features to decide the concept, but evidence indicates that other kinds of knowledge are relevant. For example, while a butterfly is readily categorized as an insect, subjects instructed to generate members of the insect category infrequently mention a butterfly. Such problems motivated alternative theories that continue to be debated and tested. The main competing theories can be grouped into those that propose that categories depend upon a prototype representation, which is an average of all examples, or many representations composed of each of the exemplars (or instances) of the category (e.g., each example of a dog experienced), referred to as prototype versus exemplar theories, respectively.

Spreading Activation

Most current theories organize concepts and categories as nodes in a network. Nodes connect to one another via a semantic link, thereby associating together related concepts or categories. The length of the link in a semantic network model varies with the relatedness and associations between concepts. For example, car, truck, and bus may be connected directly via short links, and each of these connects to fire engine via a longer link. Nodes can be connected directly or indirectly via links to other nodes. For example, apple may connect directly to red and connect indirectly to fire engine through the red node. As in the earlier Collins and Quilian model, the properties of a concept/category can be connected to its node. Semantic network theories propose that activation spreads from one node to another along the links between them, allowing for even indirectly linked concepts to activate one another. Semantic networks can easily explain retrieval of meaning. For example, when thinking about apples, one might activate the concept of red, which might trigger one to think about fire engines, stoplights, or bricks.

The semantic network approach has the advantages over other theories of predictive power (perhaps too much so that it becomes unfalsifiable, according to some critics) and being readily modeled using neurocomputational methods (i.e., connectionist or parallel distributed processing models, as described by Rumelhart and McClelland). A node can be modeled as a neuronal cell, and the dendrites (input) and axons (output) that interconnect neurons to each other are modeled as links between nodes. Neural network models incorporate recurrent and feedback connections that are well-known principles of neocortical organization. A node in a semantic network has a level of activation representing the probability that the neuron will fire, thereby potentially activating a connected neuron sufficiently that it also fires. Activation in one node could thereby spread to other nodes connected to it directly or eventually indirectly. Semantic memory is acquired using learning rules (e.g., hebbian plasticity) that determine network connectivity by modifying how strongly neurons connect to each other based on experience. Contemporary neural network models have more biological realism.

Compound Cue

Compound cue models propose that semantic memory operates like other types of memory. For example, in the case of episodic recognition, memory is an interconnected feature set representing the item (i.e., its meaning), its learning context, and its relation with other such feature sets. Recognition cues are held in mind briefly to probe the feature sets, producing a familiarity signal sent to a decision process, enabling a decision that the stimulus is old or new. Likewise, in the types of priming (implicit memory) tasks used to assess semantic memory, additional cues are relevant beyond those used for recognition. For example, in the lexical decision task people decide faster whether a letter string is a real word (or not, e.g., xutkifoq) when the target word (e.g., doctor) is preceded by a word that is related (e.g., nurse) than unrelated (e.g., butter). Prime and target are both cues that together constitute a third type of association besides the associations between target and context plus target and other feature sets, which are available for recognition. Compound cue theory attributes faster performance for prime and target pairs that are related to the greater number of shared associates between them than for unrelated pairs.

Knowledge and Generic Memory Encompass Semantic and Nonsemantic Memory

The common label, semantic memory, may not be the most appropriate but rather the term generic memory (suggested by D. L. Hintzman) or knowledge (suggested here) can include nonsemantic information about perceptual form and motor action-related processing. Consider that, in general, knowledge is what you know (e.g., that dogs bark, your house number, the capital of France, the color of spinach, the shape of a cat, as well as their meanings). Linguistic stimuli (i.e., words) activate meaning, but objects, scenes, and people are also meaningful. To activate meaning, the perceptual features of the stimulus must be matched to stored memory of these sensory-based features. For example, to categorize a dog, its perceived shape or other identifying perceptual attribute(s) (e.g., a bark) must match successfully to memory for the perceptual form associated with the dog category. Likewise, to activate the meaning of a word, the word form being currently perceived must match memory for the perceptual form of that word. Thus, semantic memory depends upon nonsemantic memory for perceptual form to mediate between the perceived cue and its meaning. In addition, activation of nonsemantic memory can also activate associated nonsemantic information about the stimulus, as when observing a dog and becoming aware of its meaning and associated perceptual (e.g., its color, sound, smell), motor (e.g., its movements), emotional (e.g., fear), or mental state information.

Like semantic memory, nonsemantic knowledge is distinct from episodic memory. For example, patients with visual object agnosia are slow and make errors categorizing common objects when visually presented (e.g., seeing a dog but being unable to name or describe it meaningfully as a dog). However, these patients can tell that they saw the object before, demonstrating episodic memory. Moreover, all forms of visual object agnosia involve some impaired perceptual processing, even associative (i.e., semantic) subtypes; a knowledge system for the perceptual form of an object is required in order to know also about its meaning. In most theories, this perceptual matching stage must, to some extent, succeed in order for semantic memory to become active. Substantial parallel and interactive processing between perceptual form and meaning can occur. Thus, activating meaning always requires matching memory to the perceptual form of the referent, be it a word, object, face, or place.

Knowledge, Priming, and Awareness

Semantic memory and nonsemantic (perceptual and motor) knowledge are nonepisodic, and aspects of these memories may be conscious, while others lie outside of awareness. Conscious semantic memory is primarily the variety of explicit memory that has been distinguished from episodic memory.

After all, clearly, one can become aware of a concept in a semantic network, as when you are aware that you know what a word means. However, one is not necessarily conscious of activating the nodes or links in the network itself that lead to awareness of meaning or aware of the processes that match a perceptual form to its nonsemantic memory. Nonetheless, these nonconscious processes can lead ultimately to awareness of the shape, color, category, and meaning of the object.

By contrast, nonconscious implicit memory is thought to include nonsemantic memory as well as situations in which semantic memory activates nonconsciously. Implicit memory is typically probed by repeating information. In such priming paradigms, the item (e.g., doctor) or a version of it (a picture of a doctor) or a related item (e.g., nurse) is presented for study, as in the lexical decision task used commonly to assess semantic memory. Then, following a delay, the target item (doctor) is presented again in the memory test phase. Relative to unrepeated (i.e., new) items, repeated items exhibit faster and more accurate performance, as well as different brain response characteristics. Repetition priming (i.e., doctor–doctor), conceptual priming (i.e., a picture of, and then the word for, doctor), and semantic priming (i.e., nurse–doctor) are varieties of implicit (nonconscious) memory. It is important to note, however, that evidence is accumulating that consciousness is not the critical factor distinguishing varieties of learning and memory. Instead, the computational and decision demands of the task, and how these recruit different brain structures, are primary.

Standard Theory of the Semantic Memory System

Research has focused on how meaningful (semantic) representations are organized, leaving nonsemantic knowledge organization relatively less understood. Multiple memory systems theory distinguishes between a semantic memory system and a nonsemantic perceptual representation system that can be matched to a currently perceived stimulus, for example, to determine what an object is, such as a dog, based on its perceived shape. This distinction of memory systems theory essentially reflects its adoption of the standard theory of meaning that proposes that conceptual knowledge resides in a single amodal system with a uniform architecture and exists separate from modal sensorimotor systems.

Anterior Temporal Lobe Stores Amodal Meaning

Multiple memory systems theory (e.g., Elizabeth Warrington in 1979) adopted the distinction between semantic and episodic memory and added the proposal that different brain systems support each type. In particular, while episodic memory depends upon the medial temporal lobe (MTL), semantic memory depends upon association areas of neocortex that lie outside primary sensorimotor areas and outside the MTL. Studies of patients with semantic memory problems indicate that an amodal system may reside in the anterior temporal lobe (ATL). The ATL is considered to be the best candidate for an amodal hub for meaning based on convergent evidence from patients with semantic memory problems and its anatomical connectivity. The ATL lies next to limbic system structures, including the amygdala and the orbitofrontal cortex, which have been implicated in emotion, reward, and motivation processing, thereby enabling associations among these abilities and sensorimotor and linguistic aspects of concepts. Further, the ATL lies next to the anterior MTL system for episodic memory, which is thought to contribute to learning conceptual knowledge gradually over multiple experiences, as when many personal experiences with a variety of dogs gradually result in a concept of the dog category. Hub theories do not equate amodal with cross-modal (i.e., picture and word modalities), emphasizing that a cross-modal (or multimodal) region that integrates information from multiple sensory and/or motor regions may not perform the true amodal function required of a semantic hub. For example, the angular gyrus performs multimodal sensory integration but may not function as a semantic system for linguistic purposes.

However, it is unclear what exactly is the difference between amodal and cross-modal/multimodal, and this distinction will be critical for determining the anatomical locus of an amodal hub for meaning that abstracts across stimulus form. Consider that any region that integrates information, (a) across sensory modalities, (b) multiple sensory plus motor or linguistic information, or (c) any of these plus emotion or mental state information, would meet the definitions of multimodal, cross-modal, and amodal (i.e., a similar pattern of neural activity is activated by more than one type of physical stimulus or type of response in the case of motor output). Moreover, alternative views about the organization of semantic memory, including those that posit no amodal hub, can accommodate the anatomical definition offered for the amodal semantic hub (i.e., integrates sensorimotor and emotion/reward information).

Further, anatomical evidence suggests that the ATL may not be amodal (or fully multimodal) or a domain-general semantic hub. Some evidence suggests that the ATL stores knowledge about a unique item (e.g., an individual person, a famous landmark). This may be particularly necessary for socially relevant knowledge, as social information necessarily involves two or more unique persons. Consider also that the hippocampus receives nonspatial (or object) information computed along the ventral visual pathway from the perirhinal cortex in the MTL and spatial information from the dorsal visual pathway via the parahippocampal gyrus in the MTL, and both perirhinal and parahippocampal areas lie adjacent to and receive input from the associative cortex in the ATL. It is unclear why information in the MTL would be modal (e.g., spatial vs. object), whereas the adjacent ATL that feeds into it would be amodal, as the standard theory of semantic memory suggests. If the ATL is amodal, then why would segregated, modal nonspatial, and spatial inputs be sent into the MTL, which lies at a more advanced stage of hierarchical processing from the ATL? Modal segregation is difficult to reconcile with a definition of semantic memory organization that requires an amodal semantic hub where both spatial and nonspatial (object) information must be combined. Further, other types of sensorimotor, emotion, and reward inputs also send segregated inputs into the MTL via the ATL.

Medial Temporal Lobe, Episodic Memory, and Meaning

Perhaps the brain structure that shows the most amodal (or multimodal) properties is the MTL. The MTL shows highly sensory-invariant response properties. For example, MTL neurons respond to single individuals (e.g., Jennifer Aniston), regardless of the form of the stimulus (i.e., varieties of pictures, names), showing seemingly complete invariance, and have been suggested to represent meaning in long-term semantic memory. Further, MTL structures have been proposed to construct representations of integrated multimodal percepts that are sensitive to semantic variables.

Spared new learning of knowledge in amnesia suggests that the MTL is necessary not only for episodic memory but also for semantic memory. However, this idea is hard to reconcile with the substantial evidence dissociating episodic and semantic memory. For example, patients with developmental amnesia in which the MTL is dysfunctional from childhood have impaired episodic memory but remarkably spared semantic memory. Some evidence suggests that MTL amnesics can acquire some new explicit knowledge, but this is limited in amount and generalization and attributable to the remaining spared MTL structures, clearly so in some cases and possibly in others. Whether new explicit knowledge learning is spared in amnesia remains controversial in part due to the inherent difficulties of the lesion approach involving human patients; controlled, targeted lesions cannot be done in humans and so residual sparing of critical structures is hard to rule out. Overall, the evidence suggests that knowledge can be acquired using primarily cortical mechanisms but only through substantial repeated exposure. Episodic encoding processes of the MTL accelerate knowledge learning by integrating across multiple episodes in a way that also facilitates generalization and abstraction of knowledge. This is consistent with evidence that episodic and semantic memory are interlinked. Episodic and semantic memory systems have substantial mutual interdependence during encoding and retrieval.

Semantic Memory Includes Embodied (Grounded) Knowledge

Neuroscience largely invalidates the strong form of the standard theory. All current views about the organization of knowledge incorporate an embodied (or grounded) cognition framework that says that knowledge depends upon multiple modality-specific systems, including those for sensorimotor properties in perceptual systems based on the senses (e.g., vision) and action systems for motor planning as well as emotion and mental states. For example, different modal knowledge systems in the extrastriate occipitotemporal cortex support face, word, and object knowledge. Different parts of each system can vary in the perceptual-specificity of the representation. Some knowledge is more specific for the shape, orientation, or other physical property (e.g., visually specific object knowledge) and others less so. The latter knowledge is more abstract from perceptual form) showing, for example, more invariance across changes in physical properties between experiences (e.g., an object from different viewpoints) or cross-/multi-modal activation patterns as when stimuli with the same associated meaning (i.e., a picture, sound, and word for dog) produce similar patterns of performance or brain activity. By an embodied account, a brain area can be both nonsemantic (e.g., sensorimotor), supporting, for example, both perceptual processing and perceptual memory, and semantic, supporting human symbolic abilities. Hybrid theories suggest that one or more separate amodal system(s) act as hub(s) or convergence zone(s) that interact reciprocally with embodied knowledge systems.

A key argument against embodied cognition is that so-called abstract words, such as truth and freedom, are unrelated to sensorimotor processes. The main counterargument is that internal states, such as metacognition and emotion, are also stored as knowledge, and introspective states provide information that is central to representing abstract concepts. Unfortunately, relatively little is known about abstract concepts even though they play central roles in human cognition, as most research has focused on concrete concepts.

Brain Basis of Knowledge

Word Meaning

Mental lexicon

How words activate meaning has been a central question in language and semantic memory studies. The mental lexicon stores word information, including meanings (i.e., semantic memory for words), syntax, and perceptual word forms. Most studies focused on speech comprehension, with early accounts (e.g., by Levelt) positing a processing sequence from word sounds to syntax and finally to concepts in semantic memory. Due to the importance of sequential processing for language theory and the fact that language comprehension is rapid, with all word identification achieved even before sentences end, the timing of semantic activation with words has been of greater interest than anatomy. Consequently, most neuroscience studies of semantics from words measured electromagnetic potentials that have high temporal resolution that is lacking in anatomical methods like functional magnetic resonance imaging (fMRI), which instead has been used to locate the brain regions.

Linguistic N400 to words

Most studies of language and semantic memory focus on the linguistic N400, which is a scalp-recorded, negative electrical potential, peaking around 400 ms, that varies with semantic processing between 300 and 500 ms in response to written words and spoken words for which the onset is slightly earlier. The N400 indexes a multimodal, relatively abstract knowledge system for word meaning. This system is sensitive to ongoing context, constructive, and processes semantic information over an extended time period and across multiple brain regions. Thus, the meaning of a word is extracted within about 300 ms of processing. However, some lexical processing, including semantics, has been argued recently to occur before the N400 since ERPs to words between 200 and 300 ms seem sensitive to lexical processes.

Anatomy of word concepts

The N400 in response to words indexes activity in the ATL and the superior temporal gyrus, which are considered storage sites, and the ventrolateral prefrontal cortex (VLPFC), which supports efficient retrieval and encoding of this semantic knowledge. Electromagnetic potential and fMRI findings were combined to infer these neural generators. However, fMRI findings alone suggest that a more extensive, left-lateralized network (i.e., more activity in the left cerebral hemisphere) activates semantic memory in response to written and spoken words. The temporal lobe regions recruited extend (a) posteriorly into the modal visual association cortex implicated in category-specific semantic deficits and semantic dementia and may store object knowledge specifying perceptual and conceptual attributes and support multimodal integration, and (b) medially into the parahippocampal region of the MTL, implicating it as an interfacing region between the more lateral temporal cortex and the episodic memory system in the hippocampus of the MTL. Notably, the left superior temporal gyrus region implicated in language comprehension problems of Wernicke's aphasia is mainly the modal auditory cortex for speech perception and has not been implicated in word meaning, though the most ventral part may contribute to processing abstract concepts. Nearby, in the lateral inferior parietal lobe, an angular gyrus region is greatly expanded in humans, receives multimodal inputs, and may support the conceptual retrieval, integration, and fluent combination processes critical for understanding discourse. While these regions are on the lateral surface, other regions lie medially. Specifically, the posterior cingulate region includes the retrosplenial cortex, which connects directly and bidirectionally with the MTL system for episodic memory and may promote episodic and semantic memory interactions. This cingulate region has been implicated in visuospatial, mental imagery, and simulation functions of both memory systems. In the frontal lobe, dorsomedial parts (BA 8) may support internally guiding semantic memory retrieval, while ventromedial parts support the emotional significance of concepts.

Semantic (default mode) network for words

Intriguingly, the lateral temporal lobe regions, the angular gyrus, posterior cingulate, and medial prefrontal regions of this proposed semantic memory network for words (i.e., all word meaning regions except VLPFC) are all key components of the default mode network (Figure 1(a) and 1(b)). This network activates in an anticorrelated manner with an active task network, which essentially includes the rest of the neocortex (Figure 1(c). The active task network activates more than the default mode network during tasks demanding greater selective attention, working memory, and executive functions. By contrast, the default mode network activates more than the active task network in many language studies, episodic memory tasks (for which the MTL also activates), and rest (i.e., when minimally engaged with a task). The default mode network is affected earlier and more than other brain systems in Alzheimer's disease patients who develop progressively severe problems encoding new long-term episodic memory and retrieving knowledge. The default mode network may thus have a greater role in semantic memory, consistent with proposals that this network supports mental imagery or simulation processes that creatively synthesize, integrate, and associate multimodal information, especially episodic memory from the MTL, across past experiences. These functions would be crucial for constructing sequential, higher-order concepts from multiple life episodes, such as generalizing across numerous restaurant visit to construct a framework to comprehend the next such visit. Such a knowledge representation is known as a schema. Multiple schemas can combine to predict and anticipate how the next such visit will unfold over time. Such a sequential knowledge representation is known as a script. However, it is unclear whether default mode network regions are sufficient to support all aspects of meaning, as such studies focused on words. After all, other regions in the active task network as well as the VLFPC are implicated in semantic memory and contribute important processes to knowledge encoding and retrieval and to mental imagery. For example, script knowledge evoked by linguistic and nonlinguistic (e.g., picture) sequences involves active task network regions that interact with basal ganglia structures implicated in sequential processing and implicit learning more than the default mode network.

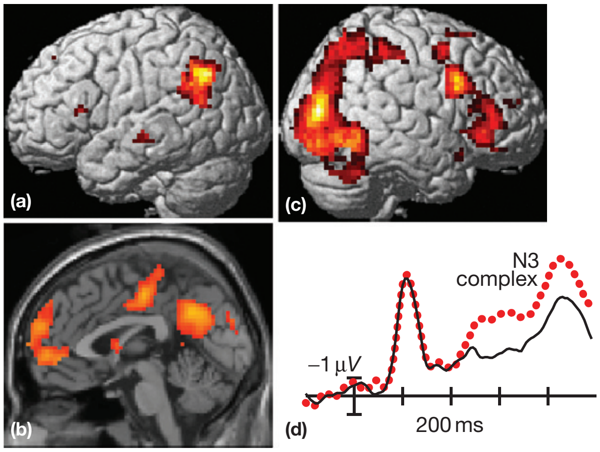

Figure 1 Brain systems for knowledge. (a) Rendering of the left lateral neocortex (Montreal Neurological Institute individual canonical brain, SPM99) showing the lateral inferior posterior parietal regions, including the angular gyrus, and superior temporal gyrus parts of the default state network implicated in semantic memory for words. (b) Sagittal slice through the medial cortex showing the medial areas that form most of the default state network implicated in semantic memory for words. (c) Rendering as in a, except showing the right lateral neocortex and parts of the active task network implicated in knowledge about visually presented objects during a categorization task. (d) The negative event-related potential called the N3 complex in response to visually presented known objects (from an experiment like that in c). *Note*, a and c were computed based on data from an experiment described in Schendan and Stern (2008), results in a are from the contrast of old > new objects (uncorrected $p < 0.001$) on an episodic recognition task; results in c are from the contrast of unusual > canonical views of known visual objects (e.g., dog) on a categorization task (uncorrected $p < 0.05$). Results in b were computed from the contrast of control > mental rotation (uncorrected $p < 0.05$) based on data from Schendan and Stern (2007). Results in d are based on an ERP version of that used for fMRI in c; the N3 is more negative for unusual than canonical views of known visual objects for which knowledge is more challenging to activate.

Multiple Knowledge Systems

Nonlinguistic knowledge

The focus on semantic memory to words has left meaning in response to nonlinguistic stimuli relatively less well understood. Most work with nonlinguistic stimuli used pictures, revealing visual object knowledge. This knowledge is the most important to study in order to explain human cognition. After all, vision is our dominant sensory modality, and objects are the focus of visual processing and attention. Research on visual object knowledge is also necessary to define the neural underpinnings of semantic memory from neural circuits to systems. Such research enables direct links between human and nonhuman animals not afforded by word studies. After all, nonhuman animals have at best only very limited linguistic capacity, precluding studies with words. Further, nonhuman animal work must be incorporated into semantic memory theory because most neuroscience questions cannot be addressed in humans for ethical reasons.

Object N3 complex

In response to a visually presented object, an N400-like scalp electrical potential, the N3 complex (aka N300, N350, N390), indexes neurophysiological processes between 200 and 500 ms involved in acquiring categorical knowledge, retrieving knowledge and implicit memory about objects, and making cognitive decisions based on object knowledge (Figure 1(d)). The N3 complex peaks around 350 ms, differs in scalp distribution from the N400 (i.e., the N3 has a frontal maximum and can become positive over occipitotemporal locations, whereas the N400 is centroparietal), and cognitive manipulations affect it earlier, around 200 ms, than the N400. The earlier time course of the N3 relative to the N400 suggests that the arbitrary relationship between a word and its meaning takes longer to activate than the (nonarbitrary) association between a perceived object and its meaning; note, the shape and other physical properties are part of its meaning by an embodied cognition account. The N3 complex indexes a modal knowledge system from more visually specific to more abstract or invariant representations stored in extrastriate occipital and ventral temporal cortex. Crucial evidence that the processes underlying the N3 complex are part of a semantic memory system is that the N3 is sensitive to similar contextual, memory, and conceptual manipulations as the linguistic N400. For example, semantic priming, that is, preceding an item by a semantically related item (e.g., doctor preceded by nurse), reduces both brain potentials and response time. The different scalp distributions of the N3 and N400 indicate multiple, modality-specific knowledge systems. This is due to recruitment of the occipitotemporal cortex involved in storing object knowledge (N3) versus anterior and superior temporal regions involved in storing word knowledge (N400). The VLPFC has a general role in semantic memory, however, controlling posterior cortical processes for both object and word knowledge to accomplish task-relevant goals and for decision-making (e.g., categorization). Notably, faces also evoke a functionally similar frontal N400-like potential. In sum, functionally similar but somewhat anatomically distinct semantic memory systems support knowledge about words, faces, and other objects.

Anatomy of object knowledge

Multiple knowledge systems are consistent with the functionally localized, hierarchical organization of the neocortex. From posterior to anterior areas along the ventral stream, stimulus selectivity becomes increasingly complex from more elementary, local features and greater visual-specificity to higher-order global shapes and combinations of features and increasing visual object constancy (i.e., similar responses despite changes in orientation, size, or other visual properties). Human occipitotemporal cortex is necessary for normal behavior on wide-ranging object cognition tasks. Patients with occipitotemporal damage have visual object agnosia: impaired perceiving, categorizing, and recognizing of visual objects with the pattern of deficits varying with the locus of damage. Occipitotemporal areas are retinotopic (adjacent) and object-sensitive (i.e., responding more strongly to intact images of objects than scrambled versions with no coherent object structure). However, recent evidence suggests that object-sensitivity, object perception, and invariant object knowledge continue into the MTL, including the hippocampus. Extended object processing and memory from the occipital into the MTL accords with embodied cognition but not the standard theory of an amodal system.

Domains of knowledge

Multiple knowledge systems are consistent with embodied cognition and an alternative, but not incompatible, idea that object domain primarily constrains conceptual knowledge organization. Distributed domain-specific theories propose that evolutionary history influences development, which thereby determines object domain. Convergent findings suggest that the domains are living animate (e.g., mammals), living inanimate (e.g., trees), conspecifics (e.g., humans), and tools. For example, a brain-damaged patient can display category-specific semantic problems with multimodal input, implicating abstract representations of conceptual knowledge. Both picture-naming and verbal questions about objects can be impaired for living animate objects (e.g., animals) but spared for nonanimals. Even so, the patients can also have problems with nonsemantic, visual structural processing and knowledge. These and other findings motivated other multiple semantic system accounts to distinguish instead between nonliving things, animals, and fruits/vegetables. They propose that visual motion and functional information are more important for knowing about nonliving things, and other kinds of sensory information are more important for knowing about living things, of which fruits/vegetables depend more on color and taste information (than animals do). Notably, a domain account need not imply that semantic memory is modular. Instead, current ideas emphasize that domain-specific neural networks are distributed across multiple cortical regions. Each domain of knowledge can be further subdivided according to the sensorimotor, affect, and mental state processes posited in embodied cognition theories, enabling a rapprochement between theories. A central idea in hybrid accounts is that sensory processing within a specific domain (e.g., how a conspecific human looks based on visual processing) will be connected (e.g., via links in the semantic network) to other processes (e.g., how a conspecific human also sounds, emotes, or acts based on auditory, affective, or motor processing, respectively). Overall, findings converge on the idea that knowledge is organized across multiple cortical systems, contrary to the standard theory of meaning incorporated in multiple memory systems theory, but debates continue over the organizational principles governing the divisions (embodiment, domains, sensory-functional).

Frontal Lobe Controls Knowledge Encoding and Retrieval

The VLPFC controls encoding of mappings between knowledge stored in posterior areas and decision processes in frontal areas and subsequent retrieval. The human lateral prefrontal cortex (PFC) is organized functionally along a gradient from abstract decision and action planning processes in more rostral parts (e.g., VLPFC) to increasingly more concrete response-related processes in more caudal parts (e.g., premotor cortex (PM)). This prefrontal system maintains patterns of activity for various types of information (e.g., linguistic, visuospatial, object, rules) in functionally distinct neural populations. Each influences (controls) other areas to accomplish a mental or overt action. For example, to decide the category of a visual object, dorsolateral PFC (DLPFC) and PM accumulate and compare visual evidence obtained from the occipitotemporal cortex to compute a decision according to a rule that determines the choice, which involves more rostral frontopolar (BA 10) areas. In the parietal lobe, the intraparietal sulcus (IPS) also accumulates evidence, consistent with its strong bidirectional connections with some decision-making regions. The VLPFC has an important role in disambiguating knowledge, as when multiple interpretations of the input result from initial processing (e.g., ambiguous figures, impoverished percepts, multiple alternative meanings or knowledge types are competing), and it interacts reciprocally with DLPFC and PM to recruit working memory resources to resolve uncertainty.

Simulation, Mental Imagery, and Semantic Memory

Embodied cognition theories propose mental imagery, particularly automatic simulation varieties, as a core mechanism for deep conceptual processing, rather than language with which semantic memory has been commonly allied. For example, hearing the word dog automatically simulates the sensorimotor, affect, and/or mental state associated with experiences of dogs (e.g., what they look like, how they move, feel, etc.). The idea is that embodied processes encoded into the knowledge system during the initial experience are later recapitulated via cortical network simulation mechanisms in response to the original stimulus (e.g., seeing a dog) or associated stimuli (e.g., the word, dog). The human capacity for symbolic cognition arises from interactions between simulation in the cortical knowledge network and linguistic processing. By this view, nonhumans lack symbolic cognition insofar as they lack linguistic processes, even though nonhuman animals have simulation abilities like those in humans by virtue of common cortical architectures for sensorimotor, emotion, and mental state processes.

However, mental imagery research has primarily investigated not automatic imagery but rather strategic mental imagery. Such studies, moreover, mainly use recently trained stimuli for which episodic memory (not semantic memory) likely dominates processing. For example, people are trained to memorize a few pictures until they can visualize them mentally with clear vivid detail. Later, while trying to visualize these pictures (i.e., strategically), they answer questions about them that require accurate mental images, such as whether a specific object part falls within a location of a grid on a computer screen. Consequently, little is known about mental imagery that is evoked automatically when semantic memory is activated. What is known comes mostly from studies of embodied cognition and two neuroimaging studies comparing episodic and semantic memory sources. The latter evidence implicates similar structures for imagery from episodic and semantic memory, including visual association areas, the amygdala, which supports emotional processing, the MTL, and parts of the active task and default mode networks. Notably, the right VLPFC is activated more during mental imagery based on episodic than semantic memory. This is consistent with the possibility that most prior mental imagery studies reveal how strategic mental imagery from episodic memory works, which depends more on the frontal lobe, but not necessarily automatic mental simulation (imagery) from semantic memory.

Summary

Semantic and nonsemantic perceptual and motor memory systems store knowledge based on experience with the world independent from episodic memory about the originating personal experiences. Initial studies aimed to solve how language communicates concepts, inspiring cognitive models describing hierarchies of concepts composed of sets of overlapping features, semantic networks that operate by activation spreading along links between concepts, or memory decisions based on cues to conceptual associations. Meaning may be embodied in sensorimotor, emotion, and mental state information processing but also may be organized by domain in multiple semantic systems and may include an amodal hub in the anterior temporal lobe. While words activate meaning between 300 and 500 ms, knowledge evoked by nonlinguistic objects (for which the perceptual form may convey aspects of meaning, according to embodied cognition theory) starts earlier by 200 ms. Anticorrelated active task and default mode networks may support different aspects of meaning, while the lateral prefrontal cortex controls semantic memory retrieval and encoding. Conceptual processing depends critically upon automatic mental imagery simulating information processing in these brain networks, which, in humans, interacts with language to accomplish symbolic reasoning functions.

See also: Alzheimer's Disease; Amnesia and the Brain; Associative Learning; Electroencephalography; Empirical Challenges to Conventional Mind–Brain Theory; Episodic Memory; Event-Related Potentials (ERPs); Memory; Memory, Neural Substrates; Mental Imagery; The Mirror Mechanism; Our Cognitive Map; Psychology of Reading; Visual Motion Perception; Visual Perception; Word Retrieval.

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