

How, and where, do you know it?

– On Different Accounts of Semantic Memory

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[T]he air was hot and heavy. He didn't move. [...] He was simply alone someplace, out of doors, lying down, and the warmth came from far above. It was [...] pleasurable and comforting. Suddenly he perceived the word for it: sunshine. He perceived that it came from the sky.

(The Giver, pp. 84–85)

1 Introduction

In 1972, Tulving described our knowledge about words, about their referents and meanings, and about the relations among them as *semantic memory*. This part of explicit long-term memory (LTM) – as opposed to its complement, episodic memory (the store of personal events and their tempo-spatial relation) – is the locus of our concepts, our knowledge of the world and its structure. It allows us to distinguish birds from bees, classify poodles as dogs, know that Australia is on the southern hemisphere, and recognize the warmth from the sky as sunshine.

How does this capacity come about? How is it implemented, how does it develop and maintain itself? How is this store of world knowledge structured, and how can its content be accessed and modified? – These are only some of the questions to be addressed if one aims to understand semantic memory. For the purpose of this essay, I will set aside developmental questions and focus

on investigations into the structure of semantic memory and the neural systems believed to implement it in the (human) brain.

Assuming that semantic memory is a single, relatively stable and well dissociable psychological capacity¹ – a system, or *module* – it may be studied by observing its specific *breakdown patterns* (Fodor, 1983). Inferences from lesion studies are, however, generally limited: deficient systems may employ compensatory mechanisms and thus work very differently from normally functioning ones. On a related note, the same observed behavioural impairment may result from different clinical conditions. An effective complement to neuropsychological case studies is computational modelling. In 1988, Rumelhart and McClelland famously implemented an artificial neural network (ANN) that “memorised” Westside Story characters. In such supposedly brain-like parallel distributed processing (PDP) models, various interventions can be carried out with their effects being directly observable.

The *conceptual distinctness* of semantic memory does not imply the distinctness of its neurological realisers;² that is to say, semantic memory, although dissociable as a psychological phenomenon, may well be superimposed upon the same set of neurons as, say, episodic memory. Indeed, given the amount of cortical cells and their interconnections, it is unlikely to suppose any part of the brain will function in complete isolation.

¹This claim is not as uncontroversial as it may seem. Anderson and Ross (1980), for instance, argue against an episodic-semantic distinction; Nyberg and Cabeza (2001) suggest that semantic memory could be merely an *abstraction* of episodic memory rather than a separate system itself.

²Talking about “realisers” of mental/psychological phenomena, I refer to their implementing neural mechanisms. Identifying these, I take it, is the means to approach from a conceptual psychological explanation of a given phenomenon to a mechanistic explanation at the neural level (for an account of mechanistic explanations in the neurosciences see Craver (2008)).

These framing considerations in place, I will now focus on a commonly observed neuropsychological condition, viz. *category-specific impairments*, which various models of semantic memory have attempted to account for. I will sketch only a few of them. In due course, I will outline their interrelations and compare them with respect to their proposed architecture, what they can and cannot explain, support from computational modeling, and what the neural basis for their suggested components might be. Despite the overall lack of concordance, I will find a modality-based and a connectionist-inspired view to be conflatable.

2 The Suspicious Animate-Inanimate Distinction

Likely induced by a type of motor-neuron degeneration (Rhys Davies *et al.*, 2005), *semantic dementia* (SD) affects primarily tissue in medial temporal areas. Independent of input and output modalities, it yields *anomia* (the inability to name and identify objects) and expressive vocabulary reduction. Impaired object knowledge in SD cannot be attributed to general intellectual, sensory, or language deficits (Warrington, 1975). Patients may still perform normally on rather coarse object classifications as their impairments are greater for subordinate than superordinate levels³ (Warrington, 1975) This is not likely an effect of task difficulty, however: healthy participants classify objects faster and more accurately at basic as opposed to superordinate levels (Rogers & Patterson, 2007). When asked to copy animal pictures, SD patients tend to copy those features typical of a category (four legs and a tail for animals) but not those typical of the required

³Categories at the subordinate level are fairly specific ones, such as *finch* or *poodle* while basic level categories are more general, like *bird* or *dog*; superordinate categories are even more general, e.g. *animal*.

member (stripes for a zebra, a hump for a camel) (Taylor, Moss & Tyler, 2007). Likewise, reduced category fluency⁴ has been reported in and Alzheimer's disease (AD) patients (Gonnermann, Anderson & Devlin *et al.*, 1997; Moss *et al.*, 2002). Category fluency is thought to depend on knowledge of overall *conceptual similarity* (Patterson, Nestor & Rogers, 2007) which requires generalisation across category members so as to judge what items instantiate this category. Semantic memory deficits also occur – usually less gradual than in AD/SD – after herpes simplex virus encephalitis (HSVE) which affects primarily temporal structures.

Patients are not only reported to be selectively impaired on subordinate level tasks but also to perform relatively worse on objects belonging to specific categories. Notably, *either* animate items (animals, food) (Warrington & McCarthy, 1987; Crosson *et al.*, 1997) *or* inanimate items (e.g. tools; Warrington & Shallice, 1984; Gainotti, 2000) are relatively spared. The phenomenon is graded in nature (Taylor *et al.*, 2007) and seems to be systematic rather than coincidence.

Lambon Ralph, Lowe, and Rogers (2007) successfully mimicked HSVE and SD in a trained ANN by randomly changing the weights on certain connections and removing the weights altogether, respectively. Subsequently, the SD network displayed difficulties with subordinate classifications while, strikingly, a category-specific impairment emerged in the HSVE network.

Over time, affected categories may change: Moss and Tyler (2000) present an AD patient displaying category-specific deficits for animate items in an early stage while category-specific impairments for non-living things emerge as the disease progresses.

⁴To assess category fluency, the experimenter may ask a person to name as many instances of a category as possible. While normally scoring individuals enumerate them easily, SD patients struggle performing this task (Nestor, Fryer & Hodges, 2005).

This suspicious discrepancy between animate and inanimate items places a serious challenge for models of semantic memory. For what is, memory-wise, the difference between a horse and its carriage?

A first explanation was attempted in terms of different attributes characteristic of each category. Starting from there, I will consider successors and alternative models below (see Hart (2007) for a broader overview).

3 Models of Semantic Memory: Modality-Specific Modules & Distributed Features

To account for category-specific impairments, Warrington and Shallice (1984) formulated their *sensory/functional theory of semantic memory* (SFT). According to SFT, objects' sensory (sound, colour, smell) and functional (value, use, where to find) attributes are processed in separate *channels*. As these attribute channels play differential roles in processing objects of different categories, semantic memory is categorically organised: animate objects are crucially defined by their sensory, inanimate objects by their functional attributes. Thus, damage to parts of the semantic system relevant for functional or sensory attributes will yield inanimate or animate category-specific impairments, respectively. This principle has successfully been demonstrated using computational modeling (Farah & McClelland, 1991). How attribute channels are realised in our biological brains, however, remains unspecified.

Taking the idea of distinct processing channels to the extreme, Camarazza

and colleagues (Caramazza & Shelton, 1998; Mahon & Caramazza, 2003) suggest a highly modular semantic system which stores and processes different categories in separate representational subsystems. According to their *domain-specific knowledge hypothesis* (DSK), domain-specific circuits evolved for processing animals (predator, food), plants (food, medicine), and likely tools. The overall organization of semantic memory is thus determined by our history: evolutionarily significant categories are encoded holistically in anatomically and functionally dissociable regions; which these are, however, remains unclear.

This “memory version” of *massive modularity* (Cosmides & Tooby, 1994) may explain category-specific deficits with ease. But if each category is processed in anatomically distinct modules, general subordinate level or conceptual similarity deficits require simultaneous damage to all these modules despite their anatomical and functional differentiation. I will introduce a more elaborate model using modality-unspecific representations (viz. the distributed-plus-hub view) below.

Gainotti’s (2000) *sensory-motor model of semantic knowledge* (SMT) presents a more direct, multi-modal, extension of SFT. He suggests semantic memory to be organized by sensory and motor channels through which concepts are acquired. Category-specific disorders arise from lesions to areas encoding the sensory-motor information especially relevant for processing items of the affected category.

There are two novelties in SMT as opposed to SFT and DSK: first, Gainotti extends the framework to include other lexical categories (verbs);⁵ second,

⁵Despite the progressively greater specificity of models of semantic memory, they tend to focus on concrete rather than abstract items like “God”, “love”, or “science”. Taking these into account can provide substantial information about our semantic system. If for instance, activations in regions associated with abstract words overlap with the sensory-motor centres activated by concrete words (Grossman *et al.*, 2002; Perani *et al.*, 1999), SMT may face difficulties; for abstract items cannot usually be perceived through sensory-motor channels. But a detailed discussion of different kinds of concepts and their role in semantic memory

SMT takes neuroanatomical information into account. He identifies a number of correlations between patients' patterns of impairment and the locus of their lesions: verbs and action primarily recruit areas near motor-control regions instantiating these words by bodily movement (left frontal and pre-frontal regions); nouns recruit areas more temporally – with antero-mesial and inferior temporal areas being particularly relevant for living things (not further subdivided), and left fronto-parietal regions for man-made artefacts (tools).

Many neuroimaging studies in healthy subjects support SMT reporting selective activation of cortical areas for animals and tools, respectively (Martin, Wiggs, Ungerleider & Haxby, 1996). The suggested dissociations remains controversial, however. For they may be merely artifacts of task and stimulus type (Tyler *et al.*, 2003).

Martin (2007) reviews experimental evidence for object properties being stored in modality-specific circuits throughout the brain. On their basis, he suggests – resembling SMT – object-associated sensory and motor information is stored in the brain's sensory and motor systems, respectively. While the postulation of different subsystems may be reminiscent of DSK, Martin's circuits are not shaped by evolution but by how (through which modality) we encounter the items being represented. Accordingly, animate items are supposedly processed in dedicated parts of posterior temporal cortex (with posterior superior temporal gyrus being relevant for motion, lateral fusiform gyrus for visual features), man-made artefacts (tools) in a left-lateralized network – including medial fusiform gyrus, posterior medial temporal gyrus, intraparietal sulcus, and the ventral portion of premotor cortex –, and food in insula (encoding taste), posterior orbitofrontal

would make for another essay.

cortex (a reward area), and amygdala (mediating affective responses).

Whereas the exact location of certain specialised circuits is still a matter of debate, this *distributed view* (DV) has taken hold. Although the model is “distributed” in the sense that individual aspects of the same item are encoded in different cortical areas, it inherits its modality-specificity from modular models of semantic memory.

Even more than SMT, DV is consistent with widespread activation patterns found in neuroimaging studies (Moss & Tyler, 2001). It explains category-specific impairments in terms of damage to areas storing features particularly abundant in members of the affected category. General subordinate impairments and reduced category fluency remain largely unexplained, however.

Another question for DV (indeed already for SMT) but not DSK is how local feature representations are *bound together* to form coherent object representations. Hart and Kraut (2007) offer a potential solution: a *hybrid model* in which synchronous gamma-band (30Hz) oscillations mediated by the pulvinar nucleus of the thalamus serve to integrate object knowledge stored in separate (e.g. motor, limbic, and sensory) cortical systems.

Adding to DV, Patterson *et al.* (2007) suggest a *semantic hub* – a store of unified conceptual representations independent of task and modality-specific attributes. A major motivation for their *distributed-plus-hub view* (DHub) is reduced category fluency in SD. Members of a given category may differ multimodally (in shape, texture, colour, . . .). Yet, healthy individuals enumerate them easily by assessing their overall conceptual similarity (see section 1). The amodal semantic hub, Patterson *et al.* argue, plays a pivotal role in this process.

Patterson *et al.* find that most SD/HSVE patients suffer from relatively focal

brain lesions in anterior temporal areas. Accordingly, the semantic hub must be located in the anterior temporal lobe (ATL) bilaterally. Damage to ATL thus explains modality-independent category-specific and subordinate impairments in SD/HSVE. A recent transcranial magnetic stimulation (TMS) study (Pobric, Jefferies & Lambon Ralph, 2010) provides evidence for a semantic hub in healthy participants.

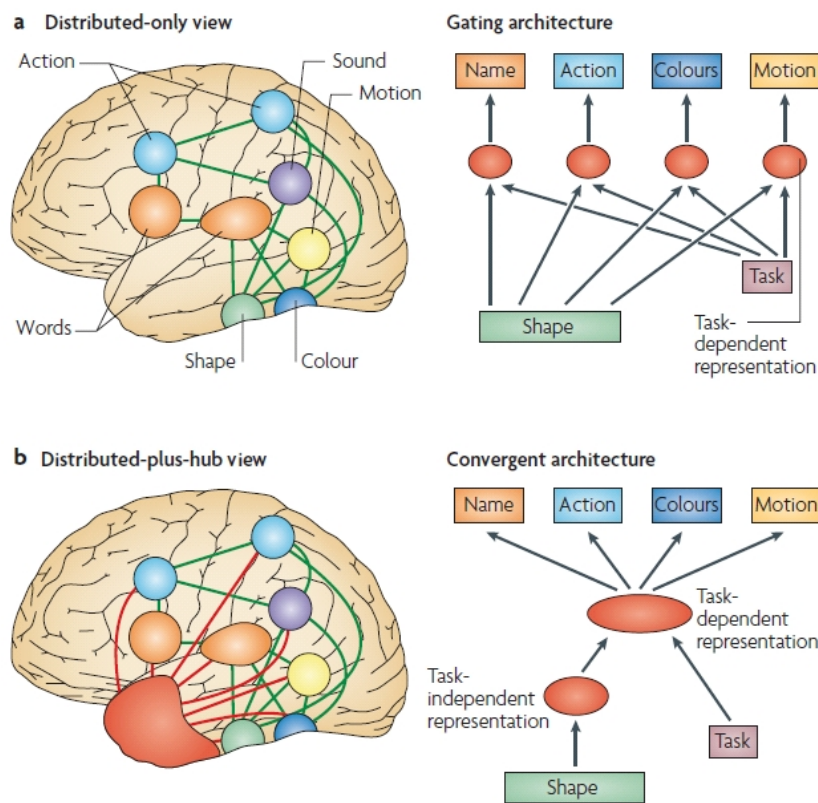


Figure 1: Adopted from Patterson *et al.* (2007).

The transition from DV to DHub converts the semantic memory model from a *gating architecture* into a *convergent architecture* (Figure 1). In the gating architecture, distinct neuroanatomical pathways are used to encode associations between different kinds of attributes; in the convergent architecture, feature

associations are stored centrally – which also solves DV'S binding problem – in a single structure allowing DHub to account for general knowledge of conceptual similarity relations and the effects of its absence in SD/HSVE. Revealing that convergent architectures are more successful in generalisation and learning overall similarity than gating architectures (Plaut, 2002; Rogers, 2004) computational models support DHub.

We have encountered many relatively smooth transitions from SFT to DHub. A radically different – though, as section 4 will show possibly compatible – view is the connectionist-inspired *conceptual structure account* (CSA) (Taylor *et al.*, 2007; Gonnermann *et al.*, 1997). According to CSA, concepts are stored in a *single* but widely *distributed* network. Conceptual processing consists of overlapping patterns of spreading activation across units. Units represent object features and the connections between them are strengthened as they are concurrently activated.⁶ Thus, the stronger the correlation between the occurrence of two features, the stronger the connection between their representing units.

Objects features can be *shared* among the members of a given category, or *distinctive* of (unique to) a particular member. While shared features (SFs) are typically encountered in concert (*correlate* with one another), distinctive features (DFs) are crucial for object recognition. Semantic memory is thus organized along two dimensions: correlation – protecting features from effects of damage to the semantic system – and distinctiveness – subserving identification.

Taylor *et al.* argue that living things have many highly correlated SFs (like *has legs, has eyes, eats*) and few DFs weakly correlated with them (*has legs, has stripes*). For non-living things, DFs are correlated with one another (*has a*

⁶This process is known as *Hebbian learning* (Hebb, 1949).

blade, cuts) whereas they correlate only weakly with SFs (*has a handle, cuts*). Since weakly correlated features are only weakly connected, DFs of living things are more likely lost in the event of damage than are DFs of non-living items (see Figure 2). Therefore, CSA suggests that rather than domain itself – as in the models discussed above – it is the differential structure of category knowledge giving rise to category-specific impairments.

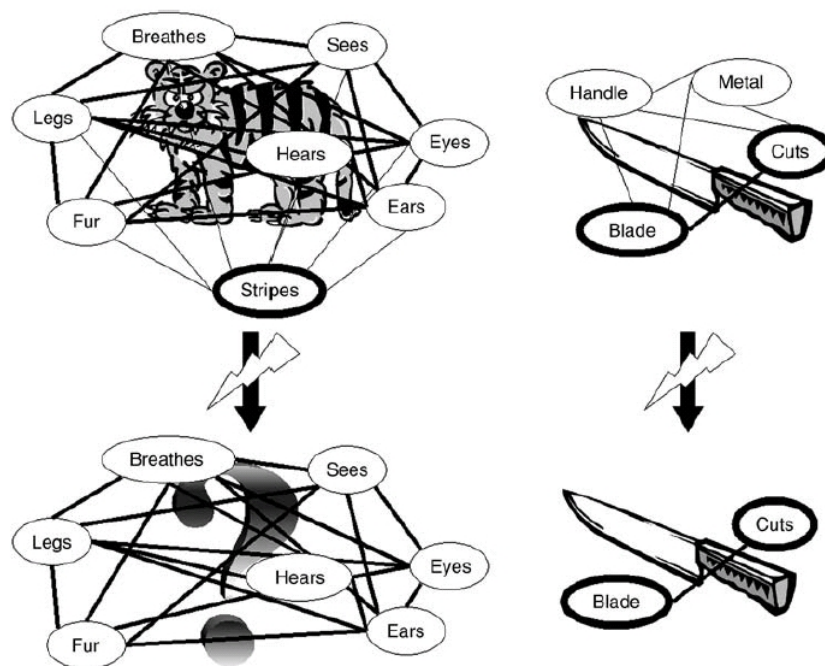


Figure 2: The conceptual structure account. SFs are indicated by thin circles, DFs by thick ones. Thick lines indicate strong, thin lines weak correlation. Left panel: weakly correlated DFs in living things are vulnerable to damage. Right panel: strongly correlated DFs of non-living things are relatively spared. Adopted from Taylor *et al.* (2007).

CSA has successfully been implemented in ANNs (Durrant-Peatfield, Tyler, Moss & Levy, 1997; Tyler *et al.*, 2000) and can – as the only model considered here – account for all the characteristics of semantic memory impairment sketched in section 1: DF loss offers a direct explanation for subordinate impair-

ments in SD/HSVE with graded impairments corresponding to graded feature loss. Similarly, DF loss predicts reduced category fluency: overall similarity in CSA is described as the proportion of SFs versus DFs; with progressive DF loss, formerly distinct concepts become indistinguishable – patients will be unable to distinguish a camel from a zebra and draw them both the same way (with neither hump nor stripes). Since DFs for living things are only weakly correlated and less frequently encountered than correlated DFs of non-living things, they are only weakly integrated into the semantic system and thus lost easiest. Thus, Taylor *et al.* argue, CSA accounts for category-specific impairments being more frequent for animate than inanimate items.

Finally, CSA predicts the cross-over pattern (see section 1) of category-specific impairments found in AD (Moss *et al.*, 2002): mild damage primarily affects DFs of living things resulting in category-specific deficits for animate objects. Moderate damage additionally affects some highly correlated features occurring less often, i.e. those likely to belong to inanimate objects; thus, both living and non-living categories will be impaired. Severe damage spares only highly frequent *and* highly correlated features (DFs of animate items); patients will thus struggle with either category but display relatively better performance recognizing living things. Indeed, the predicted cross-over could be modeled in ANNs (Sartori *et al.*, 2007; Tyler, Moss, Durrant-Peatfield & Levy, 2000). Other neuropsychological studies (Garrard, Patterson, Watson & Hodges, 1998) did not find this pattern, however. If typical SD/AD progression is indeed accompanied by the described cross-over pattern, then CSA – as the only one to account for it – may be the most powerful model of semantic memory discussed here.

4 Common Ground, After All?

The perhaps most salient aspect distinguishing CSA from other models is that it does not predict modality and/or category-specific stores. This is not to say, though, CSA is incompatible with them. The current section will elaborate on this.

DHub attributes a special role in semantic memory to temporal areas. Similarly, lesion studies in monkeys indicate a critical role for perirhinal cortex⁷ in complex object discrimination (Buckley *et al.*, 2001) which supposedly requires feature integration. In humans, Moss *et al.* (2005) found that basic-level naming, which requires fine-grained object discriminations, is accompanied by activation in the anteromedial temporal lobe, a structure encompassing perirhinal cortex. Inspired by hierarchical theories of object processing (Chao, Haxby, and Martin, 1999; Humphreys & Forde, 2001; Kyle & Barsalou, 2003; Ungerleider & Mishkin, 2001) and the apparent role of perirhinal cortex in object processing, proponents of CSA suggest that this region may serve as the necessary and sufficient basis for multimodal object representations (Taylor *et al.*, 2007).

Strikingly, although starting from completely separate conceptions, DHub and CSA (conjoined with a hierarchical theory of object processing), assign *cores* to the semantic system that are neuroanatomically extremely close; indeed, given the rather limited spatial accuracy of fMRI and ablation, they may focus on the same brain region.

⁷Perirhinal cortex is part of the medial temporal lobe. It receives multimodal inputs (Suzuki, 1996) and is believed to play a substantive role in representing feature conjunctions where the most anterior part is involved in the most complex conjunctions (Tanaka, 1996). As such, perirhinal cortex may play a crucial role in holistic object representations. In humans, it rostrally borders on the temporal pole (Buckley & Gaffan, 2006) – the part responsible for the most complex feature integrations thus is the portion closest to the temporal pole.

As CSA is suggested to be compatible with a distributed network of areas storing specific types of information (Taylor *et al.*, 2007), it may square well with DHub's modality-specific stores. Looked at this way, the only major discord between DHub and a hierarchically inspired CSA is *when* during object processing the semantic core will be recruited: Is it the initial (amodal) stage further gating the flow of information, or the final (multi-modal) feature integration stage?

In vision science, *reverse hierarchy theory* (RHT) (Hochstein & Ahissar, 2002) has begun to challenge the established conception of hierarchical processing. If RHT is true for vision and we first process the complete scene to the highest visual areas to recognize its gist before filling in the details at lower levels, analogous claims may hold for other modalities. If proponents of CSA then took their inspiration for the neuroanatomical basis of their semantic memory model from RHT rather than the classical hierarchy, they may see the temporal polar region as the multi-modal (and thus modality-independent) gist processing site that determines which specialised areas to recruit for lower-level feature processing. The predicted information flow would then correspond to the gating architecture DHub suggests.

5 Summary

Various models of semantic memory have been introduced, most of which derived iteratively from SFT. Recent models are explanatorily more powerful, more complex, and neuroanatomically better informed than their predecessors. The most recent modularity-derived account, DHub, postulates a central, amodal core for the semantic memory system.

A different model draws heavily on Hebbian learning and connectionism: according to CSA, the semantic memory system is organised not by modality but by distinctness and correlation of object features.

Both models can account for category-specific impairments, but only CSA seems to predict the complete spectrum of deficits observed in SD, HSVE, and AD patients. It is possible that both models join forces to create a superior, neuroanatomically informed model of semantic memory. A possible route drawing on RHT has been outlined.

Despite these optimistic outlooks, two things should be noted: first, these models have been constructed to account for a very restricted, highly specific group of impairments and may thus lack adequacy when applied to semantic memory as a whole (e.g. when including verbs and abstract nouns); second, we should remind ourselves that they are merely *models* – and even if they fit our experience, they may not accord with reality.

Whether Jonas knows what sunshine is because he accesses its sensory and visual properties, or because he encounters warmth in correlation with the bright circle in the sky awaits further investigation.

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