

The Conceptual Structure Account: A cognitive model of semantic memory and its neural instantiation

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The work described in this chapter is motivated by the conviction that a cognitive theory of semantic memory is best-suited to investigate the functional and neural bases of the semantic memory system. The advantage of this approach is that detailed hypotheses about the structure and function of the semantic system can be formulated and then tested in behavioral experiments with healthy individuals and neurologically impaired patients. The challenge is then to identify the neural correlates of these experimentally validated cognitive structures and processes, i.e., their neural substrates and mechanisms. The cognitive model provides a detailed framework for this investigation which, when combined with the appropriate functional-neuroanatomical technique, provides the potential to meet this challenge.

The first part of this chapter describes the Conceptual Structure Account (CSA), a cognitive model developed at the Centre for Speech and Language. We will present the results of neuropsychological studies with patients and healthy volunteers that have tested the main claims of this model¹. The CSA has been the driving force in the generation of hypotheses on the neural organization of semantic memory. In the second part of this chapter, we will describe our attempts to investigate the neural instantiation of the CSA using functional imaging techniques. In particular, we will concentrate on our recent research efforts which have combined the hypotheses of the CSA with those of a hierarchical model of object processing in the ventral temporal lobe, developed in non-human primates, to guide the fine-grained testing of neural systems involved in semantic memory of objects (Bright et al., 2005, Moss et al., 2005, Tyler et al., 2004).

¹ A discussion of the computational modeling studies investigating the CSA lie beyond the scope of this chapter, and can be found elsewhere (Durrant-Peatfield et al., 1997, Greer et al., 2001, Moss et al., 2002, Randall et al., 2004, Tyler et al., 2000a).

The Conceptual Structure Account: A cognitive model of semantic memory

The model

Patients with selective deficits in one specific category of knowledge have stimulated the development of exciting new classes of neural models of semantic memory. The most common form of these category-specific semantic deficits is an impairment for living things (Forde and Humphreys, 1999), a pattern we will focus on in the current text. One class of models that have been proposed to account for this pattern are modular in nature: they postulate that neuroanatomically distinct regions house different categories or domains (i.e., living and nonliving things) of knowledge (e.g., the categories of living animate, living inanimate, conspecifics and perhaps tools; Caramazza and Shelton, 1998, Caramazza and Mahon, 2003, Caramazza and Mahon, 2005) or the features that typify living and nonliving things (e.g., visual semantic features central to the representation of living things, functional semantic features for nonliving things; Warrington and McCarthy, 1983, Warrington and McCarthy, 1987, Warrington and Shallice, 1984; see also Martin and Chao, 2001, Martin et al., 2000, for a more recent characterization of this view). Alternatively, Tranel and colleagues (Tranel et al., 1997) suggested that distinct neural regions do not actually store concept representations belonging to different categories (e.g. persons, animals and tools), but rather are critical for the concerted retrieval of information belonging to the concepts in different categories. Category-specific semantic deficits for living things are hypothesized to arise when the neural tissue housing e.g. animals (Caramazza and Shelton, 1998), the visual semantic features claimed to be central to the representation of living things (Warrington and McCarthy, 1987), or the region responsible for retrieving features belonging to animals (Tranel et al., 1997) is damaged.

However, two aspects of the qualitative neuropsychological performances of patients with

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category-specific semantic deficits for living things appear at odds with modular theories and provided the impetus for an alternative account of these deficits. First, patients' performances with concepts from the "spared", nonliving domain are rarely within normal limits, nor do patients lose all information about concepts in the impaired, living domain. Instead, their deficits are graded, with *relatively* more deficient performance with living compared to nonliving things (Moss et al., 2002). This pattern is inconsistent with a modular view that proposes that different domains of knowledge are represented in distinct neural regions. Secondly, the *kind* of conceptual information about living things that is lost is relatively specific: those features of a living thing that distinguish it from other concepts in the category are impaired (e.g., that a tiger *has stripes*), while the information that many living things share (i.e., non-distinctive information) is typically spared (e.g., that a *tiger has four legs, has a tail and has eyes*; Moss et al., 1998, see also Hart and Gordon, 1992).

This pattern of feature loss is strikingly evident in the drawings of a Herpes Simplex Encephalitis (HSE) patient (SE) who presented with a category-specific semantic impairment for living things (see Figure 12.1). SE's drawings of nonliving things contained both distinctive and non-distinctive features, allowing these objects to be distinguished from one another and identified (Figure 12.1a). His depictions of animals, on the other hand, contained non-distinctive information that typically co-occurs in many animals (e.g., *four legs, has a tail*), but lacked the distinctive features required to uniquely identify each animal (e.g., the hump of a camel; see Figure 12.1b; target concepts in figure footnote; Moss et al., 1997). Since modular theories do not distinguish between these two kinds of features, they are not able to explain how SE's brain damage resulted in the selective impairment of the distinctive features of animals without additional assumptions about the internal organization of separate categories of knowledge.

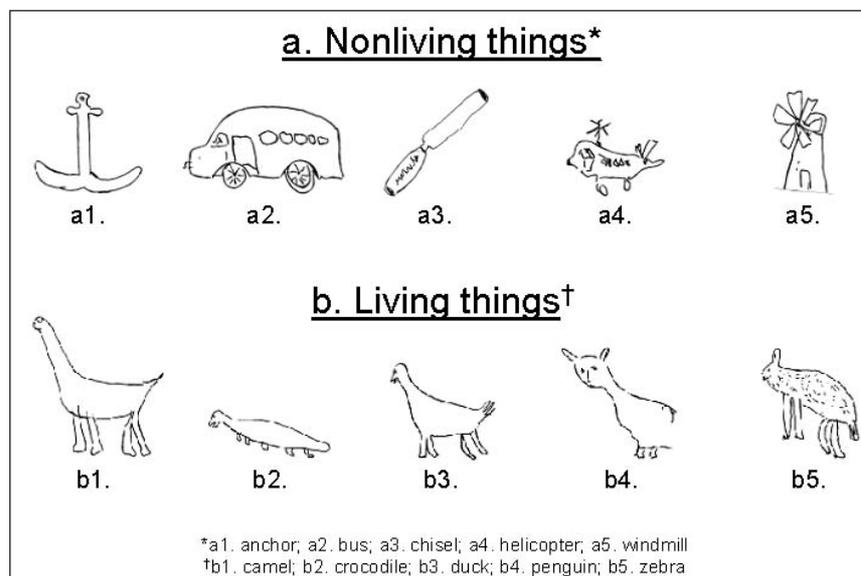


Figure 12.1. Drawing performance of patient SE.

These two observations - the graded nature of category-specific semantic deficits and the specificity with which certain kinds of features are damaged - were among those central to the development of the Conceptual Structure Account (CSA) of semantic memory (Tyler et al., 2000a, Tyler and Moss, 2001). The basic assumptions in our model are that concepts are instantiated in a distributed connectionist system composed of units representing semantic properties and where the processing of a concept corresponds to overlapping patterns of activation across units representing the concept (Greer et al., 2001, Moss et al., 2002, Tyler and Moss, 2001, Tyler et al., 2000a; see Devlin et al., 1998, Masson, 1995 and McRae et al., 1997, for similar proposals). Thus, the CSA differs fundamentally from modular theories of semantic memory in that it contends that categories of knowledge are represented in a distributed network containing the conceptual features of all knowledge categories with no explicit category or domain boundaries. Such distributed systems are ideally suited to account for the neuropsychological findings of graded deficits, i.e.

relatively poorer performance of one domain of knowledge over the other, as has been demonstrated by the graceful degradation of computational simulations of these systems (Devlin et al., 1998, Plaut and Shallice, 1993). Moreover, the CSA adopts a set of claims about the nature of features in the distributed system which can explain the selective feature deficit in category-specific semantic impairments for living things. Specifically, the CSA proposes that all features in the distributed system vary in the extent to which they are shared by different concepts (or alternatively, the degree to which they are distinctive for a particular concept) and the frequency with which they co-occur with other features. These two dimensions, distinctiveness and correlation, respectively, give rise to the internal structure of the semantic system.

SE's animal drawings (see Figure 12.1b) illustrate how some features can be more informative about a concept than others. Those features that are shared by many concepts, e.g. *has ears, has a tail*, are indicative of category membership (animals) but are not helpful in identifying what the specific object is, while other features

(e.g. *has a hump*) are distinctive to certain objects and therefore much more informative about the object. Thus, features vary in the extent to which they are shared or distinctive, with shared features typically indicating category membership and distinctive features being highly discriminatory and critical for the unique identification of a concept. Distinctive features therefore occupy a special status in object processing (identification, recognition), and appear to be those selectively lost in category-specific semantic deficits for living things.

But how could the semantic system be organized such that brain damage affects only the distinctive (but not shared) features of living (but not nonliving) things? A lower frequency of distinctive relative to shared features may provide part of the answer, as object and object feature familiarity are known to influence the vulnerability of objects to brain damage (Funnell and Sheridan, 1992, Funnell, 1995). However, patients show specific deficits with distinctive, living features compared to distinctive, nonliving features even when feature frequency is controlled for (Moss and Tyler, unpublished observations).

The critical factor may not be the frequency of occurrence and associated familiarity, but the frequency of feature co-occurrence.

Features also vary in the degree to which they are correlated with, or co-occur with, other features (Cree and McRae, 2003, Devlin et al., 1998, McRae et al., 1997, McRae et al., 1999, Rosch, 1978): we rarely see a creature with eyes but no nose, and we rarely encounter a creature with eyes that cannot see. Thus, the feature *has eyes* commonly co-occurs with other object features (*has a nose, can see*), the entire set being co-activated upon each encounter with an object. Within a hebbian-like framework, this mutual co-activation is thought to strengthen the connections between the features, making highly correlated features more resilient to the effects of brain damage (Devlin et al., 1998, Gonnerman et al., 1997). Conversely, those features which do not typically co-occur (e.g., *has a hump, has a nose*) do not benefit from a strengthened association and are more vulnerable to the effects of brain damage.

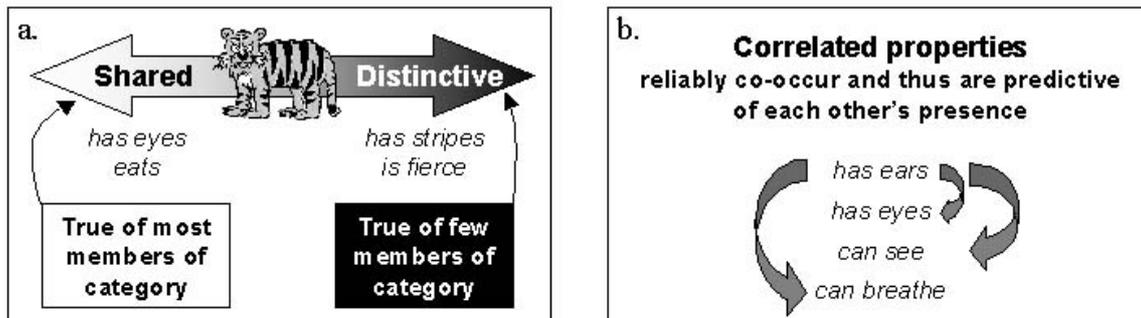


Figure 2. Dimensions manifesting the internal structure of concepts: (a) distinctiveness and (b) correlation.

Feature distinctiveness and correlation are two dimensions which are hypothesized to structure the semantic space (see Figure 12.2), with the former playing a critical role in object identification and the latter in protecting features from the effects of brain damage. The critical claim of the CSA, and that which differentiates it from similar models (Caramazza et al., 1990, Devlin et al., 1998, McRae et al., 1997), is that distinctiveness and correlation interact with domain, giving rise to qualitatively different internal structures for living and nonliving things. In other words, the CSA claims that the two domains differ with respect to the degree to which their distinctive and shared object features are correlated with the other features of the object. While living things tend to have many shared, highly correlated properties (e.g., *has eyes, has a nose*; see also Humphreys et al., 1988, Keil, 1986, Malt and Smith, 1984), their distinctive properties are weakly correlated with the object's other features (e.g., *has a hump, has a nose*). Nonliving things (e.g. tools), on the other hand, tend to have highly distinctive features that are richly correlated with the other features of the nonliving object, partly as a result of strong form-function mappings (e.g. *has a blade and used for cutting*), whereas their shared features are relatively fewer in number and less densely correlated (e.g. *has a blade, has a handle*). Since correlated properties are more

resilient to damage in this kind of network, the CSA predicts that the distinctive, but not shared, properties of living things will be particularly vulnerable to damage, while the distinctive features of nonliving things will be relatively spared by damage² (see Figure 12.3). The experimental neuropsychological studies that test these central predictions of the CSA are presented below.

Behavioral evidence

Property generation studies

One way to acquire a model of a feature-based semantic system with which to test the CSA's claims is to ask healthy individuals to provide one. Accordingly, property generation studies instruct healthy participants to list all the features they can think of for specific concepts. The distinctiveness of properties can be estimated as the

² Clearly, distinctiveness and correlation are inversely related - highly distinctive properties occurring for only a few concepts tend to be less correlated since they are infrequent. However, the CSA stresses the *relative*, and not absolute, differences in the degree of correlation between distinctive living and nonliving features.

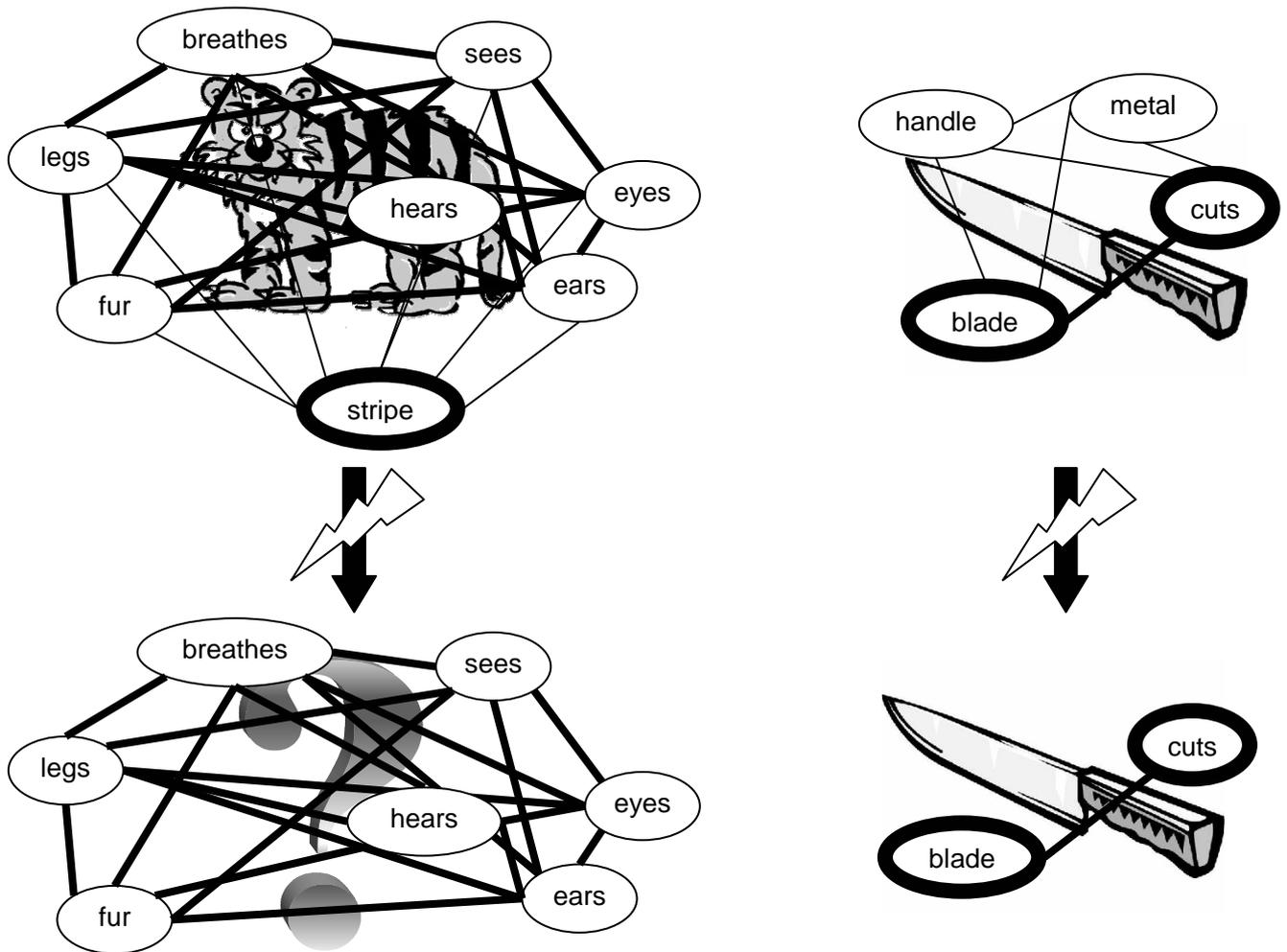


Figure 12.3. The Conceptual Structure Account. Thin circles represent non-distinctive (shared) and thick circles distinctive features. Thin straight lines represent weak and thick lines strong correlations between features. The CSA proposes that category-specific semantic deficits for living things arise because the internal structures of concepts in the living and nonliving domains differ in critical ways: the distinctive features of living things (left panel) are weakly correlated with other features, making them susceptible to damage, while the distinctive features of nonliving things are strongly correlated, protecting them from damage. Since distinctive features are relatively more important for the identification of objects, brain damage will more likely result in a category-specific semantic impairment for living things.

inverse of the number of concepts for which a property occurs (Devlin et al., 1998). For example, a unique feature such as *has an udder* which is listed for only one concept would have a maximal distinctiveness value of 1 (1/1), whereas a shared feature such as *has fur* would have a low distinctiveness value (1/[a high number of concepts]). Features can also be categorized as distinctive or shared by setting an arbitrary cut-off point, e.g. distinctive features are those that occur in two or fewer concepts. The degree to which features co-occur with the other features of a concept can be estimated with Pearson product-moment correlations among feature pairs, as well as the number of feature pairs whose Pearson product-moment correlation exceeds an arbitrarily defined cut-off point (correlated property pairs; e.g., $p < .05$). The featural structures of concepts in the two domains can then be statistically compared (Greer et al., 2001, McRae and Cree, 2002, McRae et al., in press, Randall et al., 2004).

We conducted a property generation study in which 45 healthy participants listed the features of concepts belonging to the living (31 animals, 16 fruits) and nonliving (22 tools, 24 vehicles) domains (as well as 47 filler items; Randall et al., 2004; see also Greer et al., 2001). As illustrated in Table 12.1, living things had larger clusters of correlated features (CPPs; see also Devlin et al., 1998, McRae et al., 1993), but the mean distinctiveness of features was greater in the nonliving than living domain. The shared features of living things were more correlated with other features of living thing than the shared features of nonliving things. Critically, however, the distinctive features of nonliving things were significantly more correlated with the other features of nonliving things than the distinctive features of living things. Thus, these differences in the distinctiveness and correlation of features in the living and nonliving domains support the CSA's claims, providing a framework with which to

explain category-specific semantic deficits for living things: since a high correlation is thought to protect features from the effects of brain damage, the relatively weakly correlated distinctive features of living things will be more vulnerable than the relatively more strongly

correlated distinctive features of nonliving things. Since distinctive features are more important for the differentiation and identification of specific objects, this loss will pattern as a category-specific semantic deficit for living things.

Table 12.1. Results of a property generation study (n = 45) of 93 living (animals, fruits; n = 47) and non-living (tools, vehicles; n = 46) concepts (Randall et al., 2004).

	Living Things	Nonliving Things	p
Number of correlated property pairs (CPPs)*	60	25	< .001
Mean distinctiveness [†] of properties	0.33	0.45	< .001
Correlational strength [‡] of shared properties	.35	.32	< .001
Percentage of distinctive CPPs**	16%	30%	< .001

* defined as any property pair with a significant ($p < .05$) Pearson product-moment correlation.

[†] defined as the inverse of the number of concepts for which a feature was listed.

[‡] defined as the mean correlation between a given feature and all other features of a concept.

** defined as CPPs occurring in two or fewer concepts.

Naturally, the internal structures of concepts in different categories in the living and nonliving domains are not identical, but vary slightly from the typical pattern described above. For example, vehicles tend to have more properties which are also more highly correlated and on average less distinctive than the properties of tools (but not as highly correlated or shared as the properties of animals). Therefore, the CSA predicts that patients with category-specific semantic impairments for living things will perform worse with vehicles than with tools (but not as poorly as with animals). This pattern has indeed been demonstrated in case studies of patients with category-specific semantic impairments (see Tyler and Moss, 2001). The internal structure of the fruits and vegetable category also deviates from the prototypical structure of living things: they have fewer distinctive properties, and these are even more weakly correlated than those of animals³. Thus, the CSA predicts that the fruits and vegetable category will be most impaired at any level of damage (Moss et al., 2002). Indeed, an isolated category-specific semantic impairment for fruits and vegetables has been documented (Hart et al., 1985, Sheridan and Humphreys, 1993), and some patients with category-specific semantic deficits for living things perform worse with fruits and vegetables than with animals (Bunn et al., 1998, Laiacona et al., 1997; but see De Renzi and Lucchelli, 1994). These patterns highlight a key premise of the CSA, namely that it is not domain *per se*, but the nature of the internal structure of the properties of concepts in these domains (and categories) which determine which domain (and category) will be spared and impaired following brain damage.

Neuropsychological patient studies

³ Of course, the fruits and vegetable and the vehicle categories differ from other categories in their respective domains in many other ways. These differences are examined in detail by Cree and McRae (2003).

The CSA generates a number of predictions about the kinds of information and types of processes that will be impaired and spared in patients with category-specific semantic impairments. The most obvious prediction is that category-specific semantic impairments for living things should be more frequent than specific impairments with nonliving things, as indeed appears to be the case (see Forde and Humphreys, 1999, and Gainotti, 2000 for overviews). As described above, the CSA proposes that the weak correlation of living things' distinctive features makes them vulnerable to the effects of brain damage, since correlation is thought to strengthen the association between features, a protective effect. A further consequence of this relationship is that as the severity of brain damage increases, more and more strongly correlated features will be lost. At the same time, we know that familiarity protects features from the effects of brain damage (Funnell and Sheridan, 1992, Funnell, 1995), such that, at comparable levels of correlation, more familiar, shared features will have an advantage over less familiar, distinctive features since the former are more frequent. Thus, the CSA predicts that the distinctive properties of nonliving things will be affected at more severe levels of brain damage, resulting in an additional semantic impairment for nonliving things (i.e., a global semantic impairment). At the most severe level of brain damage, only the most strongly correlated and familiar features will survive. These features are most likely to be the shared features of living things, as they are greater in number and more highly correlated than the shared features of nonliving things (see Table 12.1). The availability of these shared features of living things will presumably support some conceptual processing of living things, such that the overall pattern of performance will cross over to reflect a category-specific semantic impairment for nonliving

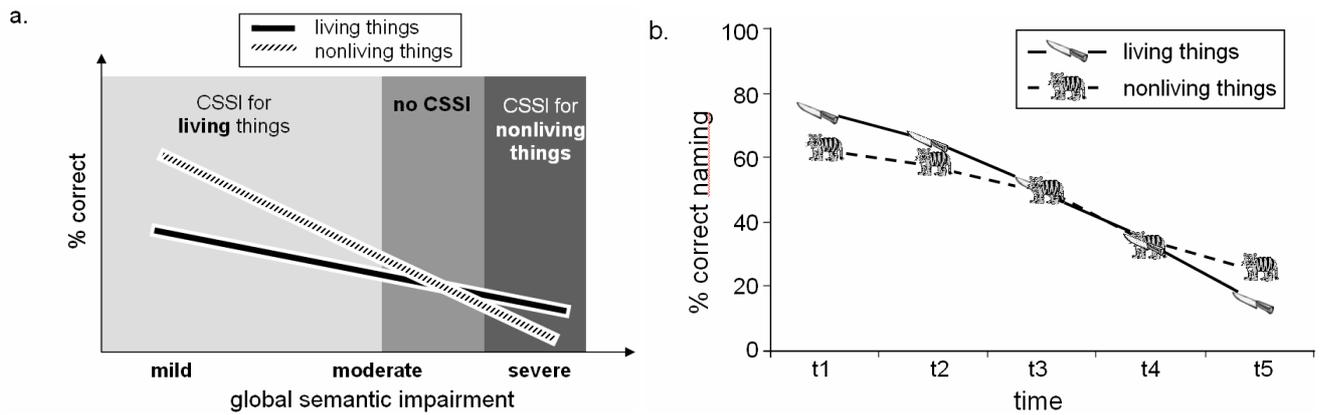


Figure 12.4. (a) The CSA predicts that category specific semantic impairments (CSSI) for living things will be apparent at the mildest level of global semantic impairment, and that this CSSI will cross-over to one for nonliving things at the most severe level of global semantic impairment (see text for details). (b) The longitudinal naming performance of a patient with progressive cerebral atrophy supports the prediction outlined in (a) (Moss and Tyler, 2000, Moss and Tyler, 1997).

things⁴ albeit in the context of very poor overall performance (see Figure 12.4a; Moss and Tyler, 2000, Moss et al., 2002; see also Moss et al., 1998).

Thus, the CSA predicts that category-specific semantic impairments for nonliving things will be associated with severe damage to the semantic system. It follows that the detection of these patients may be hampered by their severe conceptual deficits. Published accounts of category-specific semantic impairments for nonliving things provide mixed support for this prediction: while two such patients suffered from severe global dysphasia (Warrington and McCarthy, 1983, Warrington and McCarthy, 1987), others were mildly impaired (Hillis and Caramazza, 1991, Sacchett and Humphreys, 1992). A more informative approach might be the longitudinal assessment of patients with degenerative diseases affecting the semantic system. One such patient, ES, initially presented with semantic impairments which were either nonspecific or worse for living things, depending on the task. ES was tested biannually for 2.5 years with picture naming, spoken property verification, semantic priming, definition and naming to description tasks. As predicted by the CSA, ES's performance on all but the naming to description tasks showed an increasing, selective impairment with nonliving compared to living things over time (Moss and Tyler, 2000, Moss and Tyler, 1997; see also Moss et al., 2002). The course of ES's picture naming performance was most striking: an initial disproportionate impairment for living things crossed over to a specific impairment for nonliving things with time (see Figure 12.4b). We documented a similar progressive, nonliving things deficit in a second progressive aphasic patient (AA; Moss et al., 2002). These patterns are consistent with the CSA: at milder levels of damage, the most vulnerable, weakly correlated distinctive properties of living things are affected, resulting in a category-specific semantic deficit for living things. As damage to the semantic system progresses, the more highly correlated, less familiar

distinctive features of nonliving things are affected, resulting in an additional impairment with nonliving things, i.e. no category-specific semantic deficit. At the most severe levels of damage, only the most highly correlated and familiar (shared) features are available. Since living things have many more correlated, shared features than nonliving things, performance, while poor on concepts from both domains, will be relatively better with living things; a category-specific semantic impairment for nonliving things emerges. A further implication of this set of claims is that not all patients with progressive neurodegenerative diseases affecting the semantic system will suffer from a category-specific semantic impairment for living things; instead, whether and which specific domain is impaired depends on the level of damage to the semantic system, i.e. what stage of the disease the patient is in (see Figure 12.4a).

Other authors have failed to find the predicted crossover from a category-specific semantic impairment for living to nonliving things in cross-sectional studies of patients with Alzheimer's disease (Garrard et al., 1998, Zannino et al., 2002). Moreover, category-specific semantic impairments for nonliving things have been reported in patients with relatively mild impairments (Hillis and Caramazza, 1991, Sacchett and Humphreys, 1992). Thus, this prediction of the CSA remains controversial. Additional longitudinal studies of patients with category-specific deficits for living things would help to resolve these conflicting findings.

The CSA also predicts that damage to a distributed featural system will result in graded, as opposed to all-or-none, deficits, with relatively greater impairments in the affected compared to the "spared" domain. This prediction was recently tested in a study with seven HSE patients who had varying degrees of category-specific semantic deficits for living things. The patients and a group of demographically matched control participants were tested on three semantic tasks: picture naming (Bunn et al., 1998), word-picture matching and naming to verbal description. Figure 5 shows each patient's performance on all tasks and for each domain separately, as well as the ranges of the control participants' scores on each task

⁴ See Durrant-Peatfield et al., 1997, and Tyler et al., 2000a, for computational modeling support for these claims.

(collapsed over domain; control participants performed at ceiling on the word-picture matching task). All patients performed poorer with living compared to nonliving things. However, their performances with nonliving things were also moderately impaired, falling in most cases well below the range of the control participants' performances (Moss and Tyler, unpublished observations). These performance patterns illustrate the graded nature of deficits

typically encountered in patients with "category-specific" semantic impairments, patterns we believe can most parsimoniously be explained by postulating a distributed featural system with no explicit category or domain boundaries (see also, e.g., Basso et al., 1988, Moss et al., 1998, Sartori and Job, 1988, Sartori et al., 1993, Warrington and Shallice, 1984).

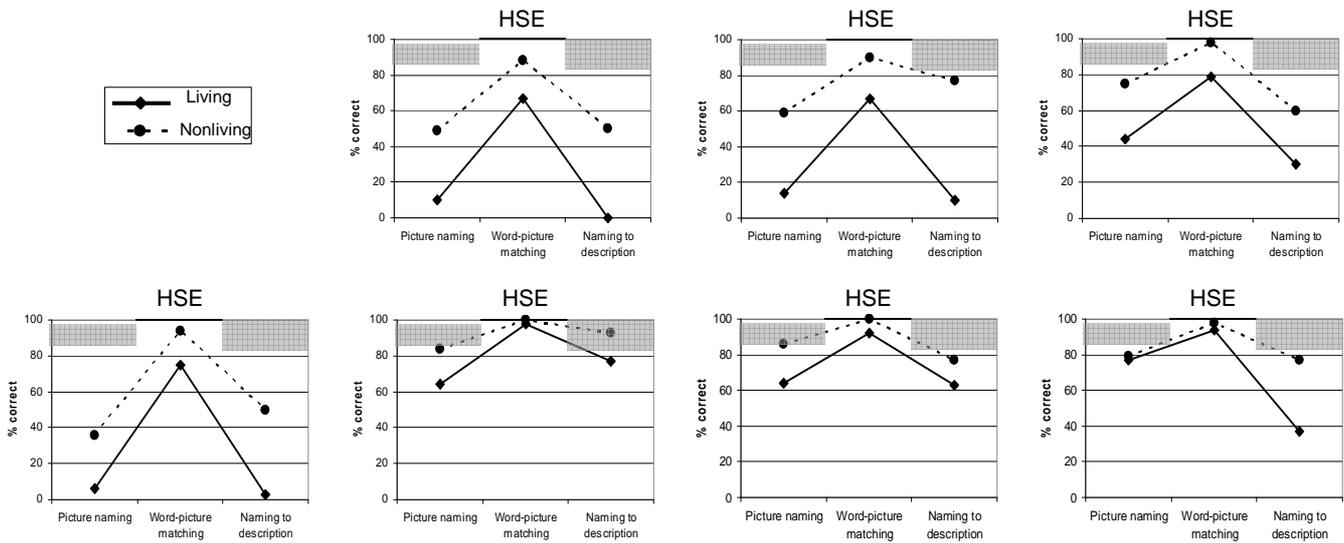


Figure 12.5. The graded nature of category-specific semantic impairments is illustrated by the performances of seven patients with Herpes Simplex Encephalitis presenting with category-specific semantic impairments for living things. While significantly more impaired with living compared to nonliving concepts, patients' performances with nonliving things were well below the range of control participants' performances on most tasks (represented by shaded areas; control participants performed at ceiling on the word-picture matching task).

At the featural level, the CSA generates hypotheses about the types of features that will be impaired in patients with category-specific semantic deficits for living things. Specifically, the CSA claims that the distinctive, weakly correlated properties of living things will be disadvantaged relative to their shared, strongly correlated properties, and relative to the relatively strongly correlated shared and distinctive properties of nonliving things. This set of hypotheses can be directly tested with property verification tasks in which patients judge whether specific (living and nonliving) concepts have specific (shared and distinctive) features. For example, patients are asked: "a butterfly – does it have legs?", "ambulance – does it have wheels?" (shared features), or "zebra – does it have black and white stripes", "drum – is it round and hollow?" (distinctive features; filler and false trials are also included). We administered this task to an HSE patient (RC) with an established category-specific semantic deficit for living things. As predicted by the CSA, RC performed significantly worse with the distinctive features of living things compared to all other feature types (Moss et al., 1998; see also Moss et al., 2002). A specific deficit with the distinctive features of living things can also be demonstrated with other tasks (e.g. sorting concepts with respect to specific semantic properties (Moss et al., 1998), and presumably underlies patients' impairments in e.g. naming and word-picture matching of living things: lacking an appreciation of the distinctive visual features, living things become visually confusable and difficult to

discriminate from one another and thus uniquely identifiable.

Patients with category-specific semantic deficits for living things still retain knowledge of the shared features of concepts in this domain. While not providing information about what the object is, features that are shared by many concepts are indicative of category membership (e.g., many animals *have four legs, have a tail, have eyes*, etc.). Therefore, the CSA predicts that patients with category-specific semantic impairments for living things will indeed be able to perform some analyses of living things if the task requires access to category-level, as opposed to concept-level, information. This appears to be the case. For example, RC, although unable to identify individual exemplars of living things, could successfully sort these same exemplars into their appropriate superordinate category (Moss et al., 1998). This interaction of task demands with conceptual structure (and indeed the precedence of task demands over domain *per se*) is a topic we will discuss in greater detail in the second part of this chapter.

We believe that the studies described above support the CSA's main claims. However, it is critical that the CSA be confirmed in studies with healthy individuals to ensure that the patients' behavioral performances reflected the workings of a merely incomplete but not a pathologically reorganized semantic system. Also, control participants typically provide more reliable measures of on-line semantic processing (RTs), and thus with the appropriate paradigms, control performances can offer

further insights into the workings of the semantic memory system.

Studies with healthy participants

The effects of distinctiveness and correlation on on-line language comprehension have only recently become the focus of investigation in healthy participants. We will address studies attempting to tap automatic semantic processing, as untimed tasks or paradigms which elicit controlled processing may emphasize cognitive processes taking place outside the semantic system.

McRae and colleagues (1997) were the first to investigate how feature correlation affects on-line word comprehension with two different priming tasks. In a first priming study with prime and target concept words, similarity in terms of correlated features predicted RTs to living, but not nonliving concepts (i.e., the higher the correlation, the faster the RTs). McRae et al. suggested that the effects of correlation were not apparent with nonliving things because they contain fewer correlated features than living things (see above), and thus a decreased likelihood of observing the effect of correlation. In a second, feature verification priming task, participants were shown prime concepts (e.g. *deer*) followed by target features (e.g. *is hunted*) which were either weakly or strongly correlated with the concept's other features, and verified whether the features were true of the concept or not. Here, correlation strength predicted feature verification reaction times to both living and nonliving things. Based on the behavior of an attractor network model designed to simulate these effects, McRae and colleagues suggested that the mutual activation among correlated features results in a faster "rise time" in activation, such that strongly correlated features reach a stable state of activation faster than weakly correlated features. This study has been replicated and extended in a second series of experiments by the same researchers (McRae et al., 1999; see also McRae, in press).

We recently performed a similar feature verification priming experiment with living and nonliving concepts to test a critical claim of the CSA. Based on the results of McRae et al.'s experiments (1997, 1999), we proposed that distinctive properties of living things would be disadvantaged compared to the distinctive properties of nonliving things as only the latter are highly correlated. We therefore hypothesized that the distinctive properties of living things would be activated more slowly than their shared properties, whereas no such effect would be evident for non-living things. This was indeed what we found in a speeded feature verification task where the emphasis was on early activation of meaningful representations (Randall et al., 2004; see Figure 12.6a). Moreover, no such interaction was evident in an untimed version of the task, suggesting that correlation affects the initial rise time of activation rather than the final level of activation when the network reaches a stable state. Significantly, these findings mirror RC's feature verification performance (described above and shown in Figure 12.6b), strongly suggesting that his deficits indeed reflected an incomplete, but not pathologically reorganized, semantic system, and providing converging evidence for one of the CSA's central claims.

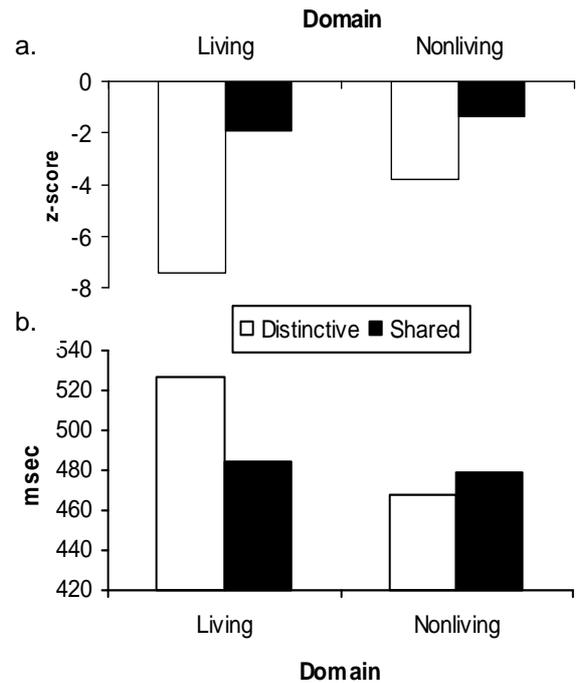


Figure 12.6. The disadvantage of weakly correlated distinctive features of living things as demonstrated by (a) the results of a speeded feature verification priming study and (b) the property verification performance of a patient with Herpes Simplex Encephalitis presenting with a category-specific semantic impairment for living things (RC).

We recently examined the effects of both correlation and distinctiveness of properties on normal, on-line language processing (Taylor et al., 2004). This study employed a semantic priming paradigm, using a lexical decision task with the prime word denoting a concept (e.g. *elephant*) followed by a target word denoting one of its properties (e.g. *trunk*). We manipulated both the distinctiveness and correlation of the properties using published property norms (McRae et al., in press), which resulted in conditions representing all four combinations (High/Low Distinctiveness x High/Low Correlation). We predicted that highly correlated properties would show greater on-line priming than weakly correlated properties (McRae et al., 1997, Randall et al., 2004). We also aimed to determine whether highly distinctive properties were likewise facilitated, and whether the effects of correlation and distinctiveness were additive. The multivariate analyses revealed that both increasing distinctiveness and correlation led to greater priming when the opposing variable was low, and that the two variables significantly interacted, such that when both distinctiveness and correlation were high, priming was reduced. This "interference" between the two variables was a surprising result. Exploration of the concept-property pairs in each condition revealed that the High Distinctiveness / High Correlation items had a significantly greater number of features per concept than did items in the other conditions. In a distributed semantic model with bi-directional lexical-semantic connections, word recognition of concepts with many features benefits from greater feedback of activation to the lexical level (Pexman et al., 2003; see also Tyler et al., 2000b). We therefore suggested that the greater

feedback activation of the prime word led to an increased inter-lexical competition affecting the activation of the subsequent property target word, negating the advantages associated with the high correlation and distinctiveness of that property. We are currently investigating this and similar hypotheses in a new series of priming studies.

These studies illustrate how complex interactions between distinctiveness and correlation can determine the automatic activation of concept features during on-line processing. There are now several findings indicating that the number of features associated with a concept may also critically influence how concepts are activated: in the above study (Taylor et al., 2004), the number of features associated with concepts appeared to negate the facilitatory effects of both distinctiveness and correlation on priming of lexical decisions; McRae et al. (1997) suggested that their lack of priming of *semantic* decisions⁵ for nonliving things was due to their lower number of features, and, as reviewed above, we postulate that patients with severe levels of brain damage will show a category-specific semantic impairment for nonliving things since they have fewer correlated features with which to support the processing of these concepts. Thus, this tripartite dimensional structure⁶ may provide the basis for emergent category differences in both intact and damaged semantic systems.

The neural instantiation of the CSA

Category-specific vs. distributed neural systems

The fundamental assumption of the CSA is that semantic knowledge is represented in a distributed, featural system with no explicit category or domain boundaries. The most obvious inference of this assumption is that different categories or domains of knowledge are not represented in neuroanatomically distinct stores, and therefore processing of concepts in these categories or domains will not activate topographically distinct regions in functional imaging experiments. Yet several such

⁵ Based on the semantic feedback activation hypothesis (Pexman et al., 2002, Pexman et al., 2003), we predict that opposite effects of number of features will be observed in priming tasks of lexical and semantic decisions (i.e., the level at which the target word is processed). The presentation of a prime concept with many features purportedly results in a large activation at the semantic level. This semantic activation feeds back to the orthographic level, i.e. to the orthographic representation of the prime and orthographic representation of semantically associated words. Lexical decisions to the target will be slowed, since semantic feedback activation will have created competition between the prime and target orthographic representations. However, semantic decisions to the target will be facilitated, since activation at the semantic level has co-activated semantically related representations.

⁶ Many more factors are known to influence semantic processing within the normal language system, and clearly the two domains differ with respect to a number of important factors (see, e.g., Cree and McRae, 2003). The objective of the CSA, however, is to determine the minimum number of factors that are both necessary and sufficient to explain category-specific semantic impairments.

studies have reported category- or domain-specific functional activation patterns, and have interpreted these findings as support for a modular organization of semantic knowledge (Cappa et al., 1998, Martin et al., 1996, Moore and Price, 1999, Mummery et al., 1996, Perani et al., 1995). For example, domain-specific activations for living compared to nonliving things have been reported in isolated regions in the right hemisphere (inferior parietal lobe (Mummery et al., 1996), posterior middle temporal cortex and anterior (Moore and Price, 1999) and anteromedial temporal lobes (Mummery et al., 1996)), extensive left hemisphere regions (medial occipital gyrus (Damasio et al., 1996), calcarine sulcus (Martin et al., 1996), lingual gyrus (Perani et al., 1995), inferior temporal gyrus (Damasio et al., 1996) including the fusiform (Moore and Price, 1999) gyrus and anterior (Moore and Price, 1999) and anteromedial temporal lobes (Mummery et al., 1996, Phillips et al., 2002) as well as other visual areas presumably mediating the processing of more complex visual living stimuli (e.g. Martin et al., 1996, Moore and Price, 1999, Perani et al., 1995)). A similarly complex set of activations have been associated with the processing of nonliving compared to living things: the right supramarginal gyrus (Martin et al., 1996), and in the left hemisphere, the medial extrastriate (Moore and Price, 1999), the occipitotemporal junction (Moore and Price, 1999; Mummery et al., 1996), inferior temporal gyrus (Damasio et al., 1996) and middle temporal gyrus (MTG; Martin et al., 1996), in particular its posterior portion (Mummery et al., 1996, Damasio et al., 1996), anterior cingulate (Martin et al., 1996) and inferior (Perani et al., 1995) and lateral inferior frontal gyrus (Martin et al., 1996).

Thus, different neuroanatomical regions have been associated with the processing of concepts from the two domains across studies. Part of this inconsistency may be due to the different kinds of stimuli used, in particular the modality the stimuli were presented in and their psycholinguistic characteristics (Tyler and Moss, 2001). For example, across a range of tasks, semantic processing of pictures is consistently associated more occipitotemporal activations, whereas word stimuli activate more anterior temporal regions (Bright et al., 2004). Perhaps more significantly, psycholinguistic stimulus variables such as familiarity, frequency and imageability have not always been matched across domain. Indeed, our recent event-related fMRI (efMRI) study, which controlled for these variables, found that living and nonliving items activated a common left-lateralized network including the left fusiform and superior and middle temporal gyri, with no category- or domain specific activations (see Figure 12.7; Tyler et al., 2003b). This study was a replication of our previous efMRI (Pilgrim et al., 2002), fMRI and PET (Devlin et al., 2000, Devlin et al., 2002b, Tyler et al., 2003a) studies which likewise found no domain-specific activations across a range of tasks (e.g. lexical decisions, semantic decisions) and with different stimulus materials (pictures and words; see also Ewbank et al., 2005), supporting the CSA's claim that the conceptual system is distributed, with no neuroanatomic boundaries for different domains of concepts (Tyler and Moss, 2001, Tyler et al., 2003a).

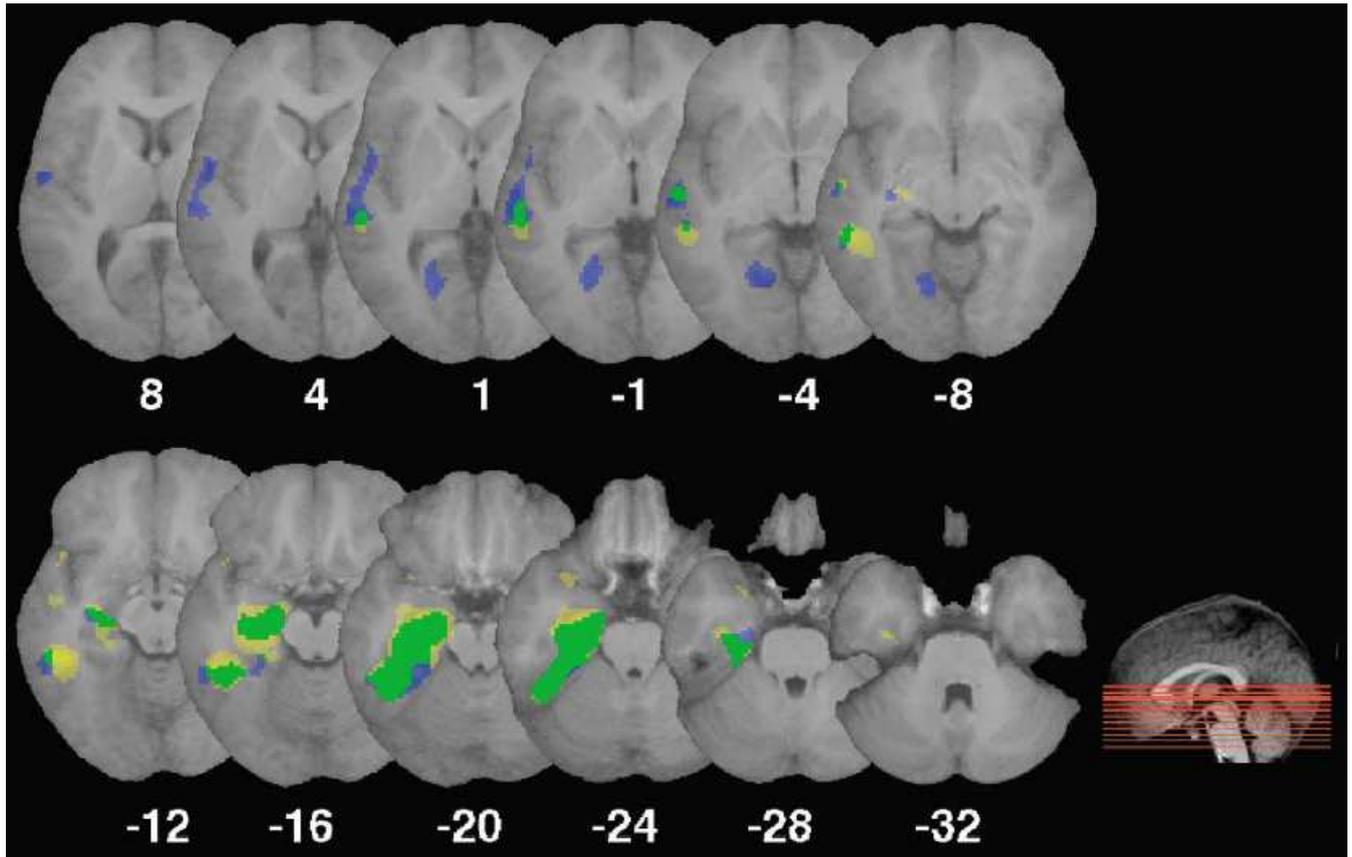


Figure 12.7. Clusters of activity associated with the processing of animal (yellow) and tool (blue) object name, and sites where these activations overlapped (green), superimposed on the averaged T1-weighted images of twelve healthy participants. The direct comparison of animal with tool processing did not result in any regions of significant activation, supporting the CSA's claim that concepts from both the living and nonliving domain are represented in the same, distributed system (numbers represent Talairach z-coordinates; red lines represent the level of the sagittal sections; Tyler et al., 2003b). Reprinted from *NeuroImage*, volume 18, Tyler, Stamatakis, Dick, Bright, Fletcher & Moss, "Objects and their actions: evidence for a neurally distributed semantic system", page 550, copyright 2003, with permission from Elsevier.

Other investigators have argued that it is not the category or domain membership *per se*, but the type of semantic property which is the organizing principle of the semantic system (Chao et al., 1999, Martin and Chao, 2001, Martin et al., 2000, Mummery et al., 1996). In an extension of Warrington, McCarthy and Shallice's account (Warrington and McCarthy, 1983, Warrington and Shallice, 1984), Martin and colleagues' sensory-motor model (Martin, 2001, Martin and Chao, 2001, Martin et al., 2000) proposed that an object's sensory and motor attributes are stored in the sensory and motor regions activated when the object was first learned, i.e. near sites responsible for perceiving the object or carrying out the motor actions associated with it. Their claims are supported by the findings of a block-design fMRI study in which participants viewed, matched and named picture stimuli, and made semantic decisions to written word stimuli from different categories (i.e., animals, tools, houses and faces; Chao et al., 1999). Regions were identified that were consistently activated by animals and tools across tasks, thus presumably coding for amodal semantic features. Compared with tools, animals commonly activated the lateral fusiform gyrus and the posterior superior temporal sulcus (STS), while tools

relative to animals activated the medial fusiform gyrus and posterior MTG. The authors suggested that different regions of the ventral temporal lobe represent object form features related to animals (i.e., lateral fusiform gyrus) and tools (medial fusiform gyrus). They further hypothesized that the posterior STS, which had previously been implicated in the perception of biological motion (Bonda et al., 1996), and the posterior MTG, previously associated with the perception of non-biological object motion (Zeki et al., 1991), stored information about the motion of biological and non-biological concepts, respectively. Thus, according to the sensory-motor model, the processing of animal and tool concepts will automatically activate neural regions storing their amodal object form representations (lateral and medial fusiform, respectively) and amodal object motion information (posterior STS and posterior MTG, respectively; see Martin, 2001, Martin and Chao, 2001, Martin et al., 2000, for overviews). It remains unclear why the majority of functional imaging studies of animal and tool processing failed to find the associated constellation of activity in the object form and motion regions specified in the sensory-motor model (e.g. Damasio et al., 2004, Devlin et al., 2000, Devlin et al., 2002b, Martin et al., 1996, Moore and Price, 1999, Perani

et al., 1995, Tyler et al., 2003a). The most robust relationship appears to be between tool processing and activity in the posterior MTG (Devlin et al., 2002a). However, most of the studies reporting this association used verb generation tasks where participants generate the appropriate action upon presentation of a noun concept (Fiez et al., 1996, Martin et al., 1995, Wise et al., 1991), tasks which induce semantic processing of the action word in addition to motion-related information. Thus, it is unclear to what extent the reported posterior MTG activity reflected the processing of action words (action verbs) and the motion attributes associated with the noun concept. We attempted to disentangle these two processes in an fMRI study in which participants were presented with nouns representing animals and tools (e.g., *tiger*, *hammer*) and

Consistent with the sensory-motor model, both object nouns and action verbs activated neural regions in the superior and middle temporal gyri⁷, indicating that object nouns indeed activate the actions associated with them (and/or action verbs automatically activate the object concept with which they are associated). Posterior STS and MTG activity, however, was not specifically associated with animal and tool nouns, respectively: instead, nouns from both object domains activated both regions. Moreover, animal and tool words did not preferentially activate the lateral and medial fusiform gyrus, respectively. Thus, both animal and tool nouns, and the action words associated with them, appear to engage the same distributed network encompassing the left fusiform gyrus and middle/superior temporal lobes purportedly mediating object form and action information, respectively (see Figure 12.8), providing further evidence for a neuroanatomically distributed semantic system (Tyler et al., 2003b).

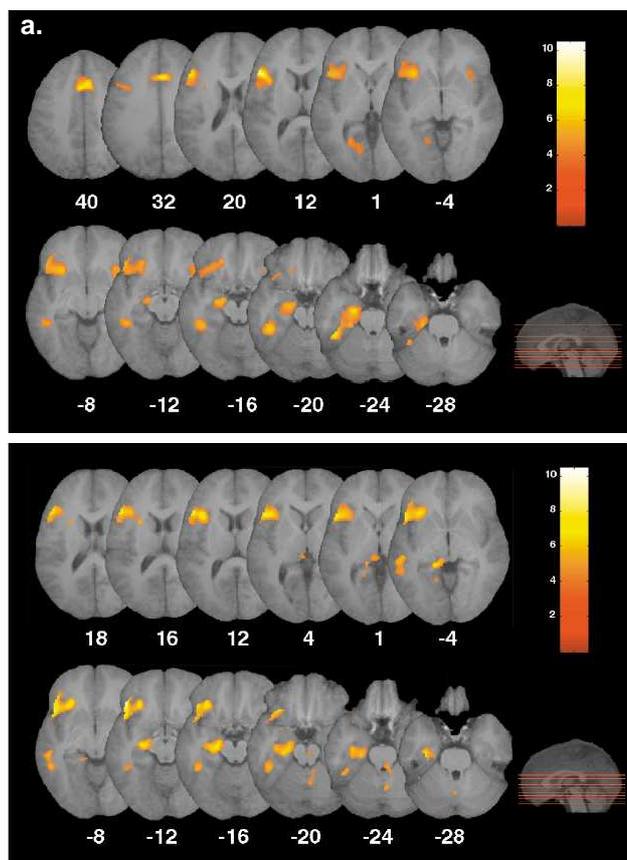


Figure 12.8. Activity associated with the semantic processing of (a) tool actions and (b) biological actions were found in the same distributed system of fusiform, middle and superior temporal gyri (numbers represent Talairach z-coordinates; red lines represent the level of the sagittal sections; Tyler et al., 2003b). Reprinted from *NeuroImage*, volume 18, Tyler, Stamatakis, Dick, Bright, Fletcher & Moss, “Objects and their actions: evidence for a neurally distributed semantic system”, pages 550-1, copyright 2003, with permission from Elsevier.

action verbs representing the actions associated with these objects (e.g., *galloping*, *drilling*). Words were matched on familiarity, frequency, and letter length, while imageability ratings, which could not be matched across domain, were entered into the analyses as covariates. Participants saw two cue words presented sequentially, followed by a target word to which they made a semantic relatedness decision.

A distributed, hierarchical object processing system

The goal of our recent research has been to determine how such a distributed semantic system, and the dimensions purportedly structuring this space (Tyler and Moss, 2001), are instantiated in neural space. Towards this end, we have concentrated on a model system from the animal literature. Research with non-human primates suggests that there is a hierarchical, visual object processing system in the ventral occipitotemporal cortex (Ungerleider and Mishkin, 1982, Mishkin et al., 1983). In this feature-based system, more posterior sites process elementary visual features (e.g., line orientation), while more anterior sites operate on the output of these early processes to create increasingly more complex conjunctions of visual features. Visual similarity also appears to be coded in this system, with inferotemporal neurons which respond to similar, moderately complex visual features clustering together in columns perpendicular to the cortical surface (Tanaka, 1993, Tanaka, 1996). Thus, visual objects may be represented by the concerted activity of different inferotemporal regions corresponding to columns coding for different stimulus features. Indeed, the presentation of whole objects activated a distributed set of discrete areas (“spots”) in the inferotemporal lobes of awake monkeys, while the presentation of simplified versions of these visual objects (i.e., whole objects minus certain visual features) activated only a subset of these areas⁸ (Tsunoda et al., 2001; see Haxby et al., 2001, for the human correlate of these findings).

⁷ While action words (both for animals and tools) activated the left inferior frontal gyrus more than object words, these effects were attributed to the additional cognitive processes necessary to decode the morphological structures of these regularly inflected verbs (Marslen-Wilson and Tyler, 1997, Tyler et al., 2005).

⁸ Other discrete regions were also activated during the presentation of degraded objects, regions purportedly inhibited during the processing of whole objects (Tsunoda et al., 2001).

Mounting evidence suggests that the perirhinal cortex of the anteromedial temporal lobe represents the endpoint of this hierarchical object processing pathway, integrating the most complex combinations of visual object features (Bussey et al., 2005, Murray and Bussey, 1999, Murray and Richmond, 2001). For example, Buckley, Gaffan and colleagues found that rhesus monkeys with bilateral perirhinal lesions were impaired on complex object discrimination tasks which required the integration of several stimulus features (e.g., objects degraded with visual masks), but retained the ability to discriminate objects based on simple perceptual features such as color, shape and size (Buckley et al., 2001; see also Buckley and Gaffan, 1998, Bussey et al., 2003, Eacott et al., 2001). Bussey, Saksida and colleagues have conceptualized this function of the perirhinal cortex as one of ambiguity resolution. An ambiguous feature is one that is rewarded when it appears together with some, but not other, visual features in a stimulus display. Thus, in order to know which visual stimulus display is meaningful, an animal must integrate the ambiguous visual feature with the other visual features in the display. The demands of visual feature integration increase with the proportion of ambiguous features in a display. As predicted, animals with ablated perirhinal cortices performed increasingly worse as the proportion of ambiguous visual features, i.e. as the complexity of visual feature integration, increased (Bussey et al., 2002; see also Bussey and Saksida, 2002, Bussey et al., 2003).

Theories on how such similarly organized hierarchical object processing pathways could be implemented in the human system have since been forwarded. The Conceptual Topography Theory (CTT; Simmons and Barsalou, 2003), which borrows heavily from Damasio's convergence zone theory (Damasio, 1989a), postulates that each sensory and motor system contains "feature maps" processing the respective elementary sensory object features. These sensory and motor features are bound together into increasing more complex feature conjunctions from early to later regions in a hierarchical system of conceptual "convergence zones" (association areas) in each sensory and motor stream⁹. The perirhinal cortex also plays a key role in the CTT by purportedly performing the most complex conjunction of visual object features.

Thus, hierarchical models of object processing in humans (and non-human primates) exhibit two key characteristics. Firstly, objects are represented in a distributed fashion, with several distinct regions in each sensory or motor system coding for the respective sensory and motor features associated with the object. This claim is a neuroanatomical reflection of distributed cognitive theories of semantic memory, such as the CSA, and is supported by our functional imaging studies showing no category- or domain-specific activations (see above). Secondly, such models hypothesize that increasingly more

complex combinations of sensory and motor features are coded from early to later regions of each sensory and motor system. This hierarchical organization implies that different regions of the e.g. ventral occipitotemporal stream will be engaged depending on the complexity of visual analysis required by the task: posterior sites will support simple visual analyses of objects, while more anterior and anteromedial temporal lobe regions will be necessary for complex visual analyses.

Evidence that the human occipitotemporal processing stream may be hierarchically organized has recently emerged from functional imaging studies in humans. Lerner et al. (2001) presented healthy participants with intact images of cars and images of the same objects scrambled to different degrees. They postulated that scrambled images would induce activity in regions coding for simple stimulus features, while whole images would engage regions coding more complex feature conjunctions. Consistent with a hierarchical object processing system, these investigators demonstrated that scrambled images predicted activity in more posterior sites (V1, V2, V3, V4/V8) while intact images predicted activity in more anterior regions (lateral occipital sulcus and posterior fusiform gyrus; lateral occipital complex). The hypothesized role of anteromedial structures in complex visual discriminations was confirmed in another series of fMRI studies (Moss et al., 2005, Tyler et al., 2004). In these studies, healthy control participants were presented with two naming tasks. During domain-level naming, participants silently named the domain to which the object belonged, a task which required only a broad visual appraisal of the object, i.e. an appreciation of general visual featural differences, such as curvature. The second task was to actually name the specific object (basic-level naming; e.g. *tiger*). This task required a much more detailed visual analysis of the object to distinguish it from other, visually similar objects (e.g., tiger, lion). Critically, the same picture stimuli were employed in both naming tasks. If the ventral temporal stream is organized by stimulus category, then the presentation of objects from one category should result in a circumscribed pattern of activation, irrespective of the task. However, if the system is organized in a hierarchical fashion, then the activation associated with the same stimulus will differ depending on the task demands (i.e., depending on whether a simple or complex visual analysis is required). Consistent with this latter hypothesis, domain-level naming resulted in posterior occipital and ventral temporal activations, while basic-level naming additionally activated the anteromedial temporal lobe including the perirhinal cortex (Tyler et al., 2004; see also Moss et al., 2005; see Figure 12.9). Similar, task-dependent BOLD effects have since been reported in the fusiform gyrus (Raposo et al., 2004, Rogers et al., 2005), and the critical role of the anteromedial temporal lobe, including perirhinal cortex, in complex visual discriminations has been confirmed in several studies with brain lesioned patients (Barense et al., 2005, Lee et al., 2005, Moss et al., 2005, Tyler et al., 2004). Taken together, these findings provide preliminary support for a distributed, hierarchical visual object processing system in the human ventral occipitotemporal lobe, similar to the non-human primate system, which codes for increasingly

⁹ The CTT differs critically from Damasio's convergence zone hypothesis in that it postulates that groups of bound features can function as stand-alone representations, independent of their sensory and motor feature maps, to support object processing during automatic tasks (e.g. categorization).

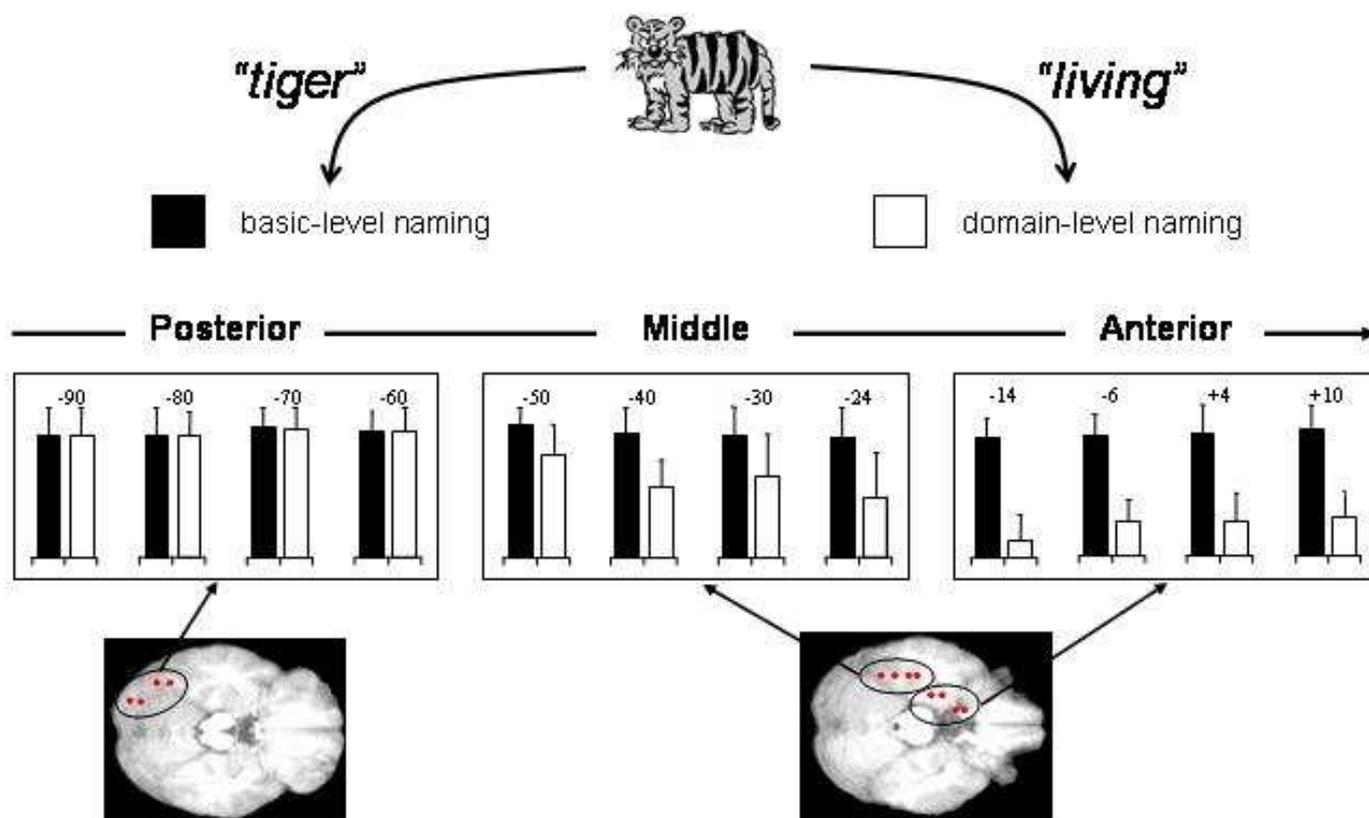


Figure 12.9. A recent fMRI study presented participants with the same object stimuli for two naming tasks: domain-level naming (e.g. *living*) required only a coarser visual analysis of the object, while basic-level naming (e.g., *tiger*) required a complex visual appraisal of the object to distinguish it from other, visually similar objects (upper panel). Consistent with the predictions of hierarchical object processing models, signal change plots revealed that activity associated with domain-level naming was restricted to more posterior occipitotemporal sites, while basic-level naming of the same object stimuli was associated with both posterior occipitotemporal and anteromedial temporal lobe activation; Tyler et al., 2004). (The approximate loci of the signal change plots are indicated on sagittal (top) and axial (bottom) slices of a normalized T1-weighted scan; MNI coordinates are reported).

more complex conjunctions of visual features from posterior to anterior and anteromedial regions¹⁰.

We have recently focused on investigating how the internal structure of concepts – their feature correlation and distinctiveness – relates to the hierarchical object processing system of the ventral temporal lobe. As described in the first part of this chapter, living things tend to have many shared, highly correlated properties, and fewer weakly correlated distinctive properties. Comparatively, nonliving things have more distinctive features which are also more highly correlated with the concept's other features. The greater proportion of shared to distinctive (visual and non-visual) features for living things renders these concepts more similar to one another. In terms of visual features, they are more visually confusable. We therefore predicted that the basic-level naming of living compared to nonliving things would rely on anteromedial temporal structures supporting complex visual discriminations, i.e. the perirhinal cortex, to a greater extent than the basic-level naming of nonliving things. This prediction was supported by the results of an

efMRI study with matched sets of living and nonliving pictures (animals and vehicles, and fruits/vegetables and tools). As shown in Figure 10, basic-level naming of animals compared to vehicles, and of fruits and vegetables compared to tools, resulted in anteromedial temporal lobe activity including the entorhinal and perirhinal cortices at a reduced threshold (Moss et al., 2005).

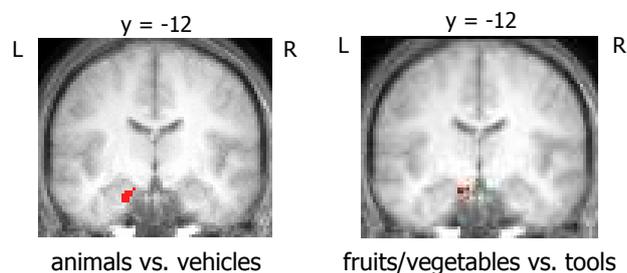


Figure 12.10. Anteromedial temporal lobe activity associated with the basic-level naming of matched sets of living compared to nonliving things (numbers refer to Talairach y-coordinates of the associated coronal slices; Moss et al., 2005).

Activity associated with the basic-level naming of living compared to nonliving things reported by Moss and colleagues was centered in the entorhinal cortex (BA8, 34), medial to the perirhinal cortex (see Figure 12.10), raising the question of whether the perirhinal or entorhinal

¹⁰ The dependency of activation patterns on task may provide an additional explanation of why domain-specific activation patterns have been so variable across studies (see above).

cortex is the critical structure for the complex visual discriminations for objects. Several lines of evidence from the animal literature indicate that these structures indeed play different roles in object processing, with perirhinal cortex primarily responsible for the integration of object-related feature information. Firstly, the macaque perirhinal cortex receives the majority of inputs from unimodal sensory regions representing unisensory object features, i.e. the anterior ventral temporal lobe (visual information), the STG (auditory information), and the insular cortex (somatosensory information), and a smaller number of inputs from polymodal association regions (orbitofrontal cortex, dorsal STS, cingulate cortex and the parahippocampal cortex). The entorhinal cortex, on the other hand, receives the majority of its inputs from polymodal association areas (orbitofrontal, parainsular, cingulate, retrosplenial, perirhinal and parahippocampal cortices and the dorsal STS), with only unimodal olfactory information being sent directly here (olfactory bulb, piriform cortex). Moreover, its inputs are not segregated, such that e.g. polymodal visual information reaches potentially every region of the entorhinal cortex. Secondly, both regions are characterized by a network of intrinsic associative connections, indicating that the information each receives is integrated in the respective structure. Thirdly, intraregional connections are feed-forward (ascending projections), typical of hierarchical processing systems. Lavanex and Amaral (2000) employed these characteristics to conceptualize this system as a “hierarchy of connectivity”. Taken together, these data indicate that information reaching the perirhinal cortex, i.e. primarily unimodal object feature information, is both necessary and *sufficient* for the representation of objects, i.e., semantic memories of objects; Murray et al., 2000, Simmons and Barsalou, 2003). Information received by the entorhinal cortex is more highly integrated, suggesting that it binds other, associative or contextual information with the object representation, providing both necessary and sufficient conditions for the formation of episodic memories, consistent with the human lesion literature (Squire et al., 2004). Unfortunately it not possible for human functional imaging to stop the perirhinal cortex from feeding the information it processes forward to the entorhinal cortex so that the independent contribution of the perirhinal cortex to object processing can be assessed, and we do not know whether participants based their basic-level naming on semantic object representations (e.g., *it has four legs and stripes, growls, and is furry to the touch – it’s a tiger*) or episodic memories (e.g., *I saw something like that on TV last night – it’s a tiger*). However, the afferent, intrinsic and intraregional connectivity within the anteromedial temporal lobe strongly suggests that the perirhinal cortex is primarily responsible for processing object-related featural information necessary to represent these meaningful objects in memory.

The convergence of sensory inputs in the perirhinal cortex (Suzuki and Amaral, 1994) indicates that it integrates not only complex visual, but also information across modalities to form multimodal object representations (Murray et al., 1998, Simmons and Barsalou, 2003). Although animal ablation studies have confirmed the role of the perirhinal region in cross-modal flavor-visual

(Parker and Gaffan, 1998) and tactile-visual (Murray et al., 1998) association learning, homologous evidence for the human perirhinal cortex is lacking. We recently conducted an efMRI to determine whether human perirhinal cortex is likewise involved in the crossmodal integration of object features (Taylor et al., 2005). Participants were presented with pictures of objects paired with environmental sounds or auditory words (crossmodal conditions) and with two parts of a sound and two parts of a picture (unimodal auditory and visual conditions, respectively). Half of the stimulus pairs in each condition were congruent (i.e., meaningfully related, e.g., a picture of a cat and the sounds *meow*) and half incongruent (i.e., not meaningfully related, e.g. a picture of an elephant and the sound *woof*), and within each congruency condition, half of the stimuli represented living and half nonliving things. We reasoned that since living things have many more shared features than nonliving things, crossmodal integration of living things would place greater demands on the complex feature integration processes supported by the perirhinal cortex. The contrast of cross-modal compared to unimodal integration resulted in two clusters of activation, one centered in the posterior STS/MTG consistent with previous reports (Beauchamp et al., 2004b, Beauchamp et al., 2004a). Significantly, crossmodal compared to unimodal integration also activated the perirhinal cortex in the group analysis, a finding which was confirmed in individual subjects (see Figure 12.11).

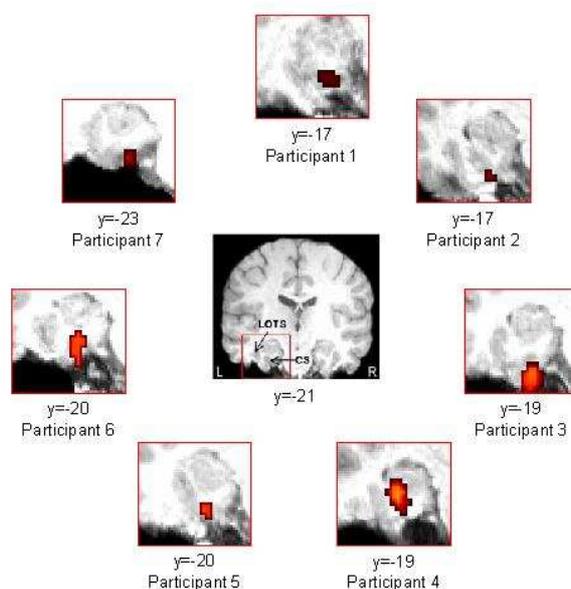


Figure 12.11. The center coronal slice shows a single subject’s T1-weighted scan and the positions of the lateral occipitotemporal sulcus (LOTS) and collateral sulcus (CS). The red box signifies the area shown in the surrounding slices, which show perirhinal cortex activity in single subjects during the crossmodal compared to unimodal integration of audiovisual object features (Taylor et al., 2005).

Moreover, only perirhinal cortex, but not posterior STS/MTG, activity was modulated by the semantic factors: responses here were greater for living compared to nonliving things, as predicted, and for incongruent compared to congruent stimuli. The behavioral performance patterns of two HSE patients with lesions

including the perirhinal cortex, but not two patients whose brain damage primarily involved the left inferior frontal gyrus and whose perirhinal cortices were spared, mirrored these efMRI findings. These results extend findings from non-human primates into the human domain by providing converging evidence that human perirhinal cortex is critically involved in binding crossmodal object features into meaningful, multimodal object representations.

Unimodal and multimodal feature binding in the perirhinal cortex may be accomplished by via feedback connections to posterior unimodal sites. The results of a single-unit recording study by Higuchi and Miyashita (1996) provided evidence for this hypothesis. Monkeys underwent anterior commissurotomy to interrupt interhemispheric communication between the anterior inferotemporal lobes, and were then taught to associate different pairs of visual fractal pattern stimuli with one another (e.g., S-S'). After this learning phase, some inferotemporal neurons evidenced 'pair-coding' properties (Sakai and Miyashita, 1991), that is, they responded as strongly to S as to S' when these stimuli were presented in isolation. Higuchi and Miyashita then unilaterally ablated the rhinal sulci of these animals, after which the animals relearned the old stimulus set and were taught a new stimulus set. Inferotemporal lobe neurons in the lesioned hemisphere were again recorded. Remarkably, these neurons no longer exhibited pair-coding properties, neither for the pre-operatively nor the post-operatively learned stimulus pairs, although they responded normally to individual visual stimuli. These findings strongly support the hypothesis that the rhinal sulcus is responsible for the pair-coding properties of posterior inferotemporal lobe neurons, presumably via feedback connections, thus binding these features together. The involvement of the perirhinal cortex in multimodal feature integration (Murray et al., 1998, Taylor et al., 2005) suggests that its role extends beyond one of maintaining purely intramodal visual associations (Higuchi and Miyashita, 1996) to that of a 'master binder', integrating not only visual, but the polymodal inputs it receives (Suzuki and Amaral, 1994) into multimodal stimulus associations underlying object representation.

Future directions

The investigation of the neuroanatomical bases of semantic memory is in its infancy. We have endeavored to contribute to this exciting venture by first developing a cognitive model of semantic memory, the CSA, and then by attempting to identify the neural correlates of the cognitive structures and processes it describes. The results of our work to date suggest that a distributed semantic system, and the combined effects of feature correlation and distinctiveness, can be instantiated in a neural theory of hierarchical object processing in which increasingly more complex conjunctions of sensory features are processed from early to late sites, with perirhinal cortex of the anteromedial temporal lobe supporting complex, polymodal feature conjunctions. The emphasis of our current work is on understanding how the effects of feature correlation, distinctiveness and number of features each

influence processing in the hierarchical object processing system. For example, Simmons and Barsalou (2003) suggested that the proximity of clumps of conjunctive neurons coding for category features increases as the similarity of the represented category exemplars increases (the "variable dispersion principle"), i.e. with increasing proportion of shared features. Are these effects demonstrable with high-resolution efMRI imaging? Moreover, Sigala and Logothetis (2002) demonstrated that with training, neurons in the monkey inferotemporal lobe became tuned to the distinguishing features of visual objects. Do human inferotemporal neurons evidence similar tunings for distinguishing features, a subset of distinctive features?

A great number of other intriguing questions await scientific enquiry. Can the seemingly contradictory functional imaging findings in support of modular and distributed semantic systems be reconciled by postulating task-induced processing demands, or is it necessary to postulate that the distributed, hierarchical object processing system contains columns of neurons coding visually similar feature combinations, as in the macaque inferotemporal lobe (Tanaka, 1993, Tanaka, 1996) (does it?)? Is re-activation of feature maps ("re-enactment") necessary for conceptual processing, as Damasio (1989b) hypothesizes and preliminary findings from a functional imaging study of semantic dementia patients seem to suggest (Mummery et al., 1999)? Or (/and?) does reactivation of feature maps depend on the automaticity of the processes involved in the task, as Simmons and Barsalou postulate (Simmons and Barsalou, 2003)? How does imagery influence ventral occipitotemporal activation? How can verbs, abstract noun and encyclopedic concepts be integrated in these models? We look forward to the results of the studies that will investigate these and other similarly exciting questions about the neuroanatomical bases of our conceptual system.

References

1. Barense, M. D., Bussey, T. J., Lee, A. C. H., Rogers, T. T., Hodges, J. R., Saksida, L. M., Murray, E. A. and Graham, K. S. (2005). Feature ambiguity influences performance on novel object discriminations in patients with damage to perirhinal cortex. *Cognitive Neuroscience Society - 2005 Annual Meeting Program*, 129.
2. Basso, A., Capitani, E. and Laiacona, M. (1988). Progressive language impairment without dementia: A case with isolated category specific semantic impairment. *Journal of Neurology, Neurosurgery & Psychiatry*, **51**, 1201-7.
3. Beauchamp, M. S., Argall, B. D., Bodurka, J., Duyn, J. H. and Martin, A. (2004a). Unraveling multisensory integration: patchy organization within human STS multisensory cortex. *Nature Neuroscience*, **7**, 1190-2.
4. Beauchamp, M. S., Lee, K. E., Argall, B. D. and Martin, A. (2004b). Integration of auditory and visual information about objects in superior temporal sulcus. *Neuron*, **41**, 809-23.

5. Bonda, E., Petrides, M., Ostry, D. and Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, **16**, 3737-44.
6. Bright, P., Moss, H. and Tyler, L. K. (2004). Unitary versus multiple semantics: PET studies of word and picture processing. *Brain and Language*, **89**, 417-32.
7. Bright, P., Moss, H. E., Stamatakis, E. A. and Tyler, L. K. (2005). The anatomy of object processing: The role of anteromedial temporal cortex. *Quarterly Journal of Experimental Psychology*, **58B**.
8. Buckley, M. J., Booth, M. C. A., Rolls, E. T. and Gaffan, D. (2001). Selective perceptual impairments after perirhinal cortex ablation. *Journal of Neuroscience*, **21**, 9824-36.
9. Buckley, M. J. and Gaffan, D. (1998). Perirhinal cortex ablation impairs visual object identification. *Journal of Neuroscience*, **18**, 2268-75.
10. Bunn, E. M., Tyler, L. K. and Moss, H. E. (1998). Category-specific semantic deficits: the role of familiarity and property type reexamined. *Neuropsychology*, **12**, 367-79.
11. Bussey, T. J. and Saksida, L. M. (2002). The organization of visual object representations: a connectionist model of effects of lesions in perirhinal cortex. *European Journal of Neuroscience*, **15**, 355-64.
12. Bussey, T. J., Saksida, L. M. and Murray, E. A. (2002). Perirhinal cortex resolves feature ambiguity in complex visual discriminations. *European Journal of Neuroscience*, **15**, 365-74.
13. Bussey, T. J., Saksida, L. M. and Murray, E. A. (2003). Impairments in visual discrimination after perirhinal cortex lesions: testing 'declarative' vs. 'perceptual-mnemonic' views of perirhinal cortex function. *European Journal of Neuroscience*, **17**, 649-60.
14. Bussey, T. J., Saksida, L. M. and Murray, E. A. (2005). The perceptual-mnemonic/feature conjunction model of perirhinal cortex function. *The Quarterly Journal of Experimental Psychology*, **58B**, 269-82.
15. Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M. and Fazio, F. (1998). The effects of semantic category and knowledge on lexical-semantic access: a PET study. *Neuroimage*, **8**, 350-359.
16. Caramazza, A., Hillis, A. E., Rapp, B. C. and Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology*, **7**, 161-89.
17. Caramazza, A. and Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends on Cognitive Sciences*, **7**, 325-74.
18. Caramazza, A. and Mahon, B. Z. (2005). The organisation of conceptual knowledge in the brain: The future's past and some future directions. *Cognitive Neuropsychology*, **22**, 1-25.
19. Caramazza, A. and Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *Journal of Cognitive Neuroscience*, **10**, 1-34.
20. Chao, L. L., Haxby, J. V. and Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, **2**, 913-9.
21. Cree, G. S. and McRae, K. (2003). Analyzing the factors underlying the structure and computation of the meaning of Chipmunk, Cherry, Chisel, Cheese, and Cello (and many other such concrete nouns). *Journal of Experimental Psychology: General*, **132**.
22. Damasio, A. R. (1989a). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation*, **1**, 123-32.
23. Damasio, A. R. (1989b). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, **33**, 25-62.
24. Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. and Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, **380**, 499-505.
25. Damasio, H., Tranel, D., Grabowski, T., Adolphs, R. and Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, **92**, 179-229.
26. De Renzi, E. and Lucchelli, F. (1994). Are semantic systems separately represented in the brain? The case of living category impairment. *Cortex*, **30**, 3-25.
27. Devlin, J. T., Gonnerman, L. M., Andersen, E. S. and Seidenberg, M. S. (1998). Category-specific semantic deficits in focal and widespread brain damage: a computational account. *Journal of Cognitive Neuroscience*, **10**, 77-94.
28. Devlin, J. T., Moore, C. J., Mummery, C. J., Gorno-Tempini, M. L., Phillips, J. A., Noppeney, U., Frackowiak, R. S. J., Friston, K. J. and Price, C. J. (2002a). Anatomic constraints on cognitive theories of category specificity. *NeuroImage*, **15**, 675-85.
29. Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Moss, H. E., Fadili, M. J. and Tyler, L. K. (2002b). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia*, **40**, 54-75.
30. Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Wilson, J., Moss, H. E., Matthews, P. M. and Tyler, L. K. (2000). Susceptibility-induced loss of signal: Comparing PET and fMRI on semantic task. *NeuroImage*, **11**, 589-600.
31. Durrant-Peatfield, M., Tyler, L. K., Moss, H. E. and Levy, J. (1997). The distinctiveness of form and function in category structure: A connectionist model. In *Proceedings of the Nineteenth Annual Conference of the Cognitive Science Society*, eds. M. G. Shafto and P. Langley. Mahwah, NJ: Erlbaum, pp. 193-8.
32. Eacott, M. J., Machin, P. E. and Gaffan, E. A. (2001). Elemental and configural visual discrimination learning following lesions to perirhinal cortex in the rat. *Behavioural Brain Research*, **124**, 55-70.
33. Ewbank, M. P., Schluppeck, D. and Andrews, T. J. (2005). fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. *NeuroImage*, **28**, 268-79.

34. Fiez, J. A., Raichle, M. E., Balota, D., Tallal, P. and Peterson, S. E. (1996). PET activation of posterior temporal regions during passive auditory word presentation and verb generation. *Cerebral Cortex*, **6**, 1-10.
35. Forde, E. M. E. and Humphreys, G. W. (1999). Category-specific recognition impairments: a review of important case studies and influential theories. *Aphasiology*, **13**, 169-93.
36. Funnell, E. (1995). Objects and properties: a study of the breakdown of semantic memory. *Memory*, **3**, 497-581.
37. Funnell, E. and Sheridan, J. (1992). Categories of knowledge: unfamiliar aspects of living and non-living things. *Cognitive Neuropsychology*, **9**, 135-53.
38. Gainotti, G. (2000). What the locus of brain lesion tells us about the nature of the cognitive defect underlying category-specific disorders: a review. *Cortex*, **36**, 539-59.
39. Garrard, P., Patterson, K., Watson, P. C. and Hodges, J. R. (1998). Category specific semantic loss in dementia of Alzheimer's type: functional-anatomical correlations from cross-sectional analyses. *Brain*, **121**, 633-46.
40. Gonnerman, L. M., Andersen, E. S., Devlin, J. T., Kempler, D. and Seidenberg, M. S. (1997). Double dissociation of semantic categories in Alzheimer's disease. *Brain and Language*, **57**, 254-79.
41. Greer, M., van Casteren, M., McClellan, S., Moss, H. E., Rodd, J., Rogers, T. and Tyler, L. K. (2001). The emergence of semantic categories from distributed featural representations. In *Proceedings of the 23rd Annual Conference of the Cognitive Science Society*, eds. J. D. Moore and K. Stenning. London: Lawrence Erlbaum Associates, pp. 358-63.
42. Hart, J. and Gordon, B. (1992). Neural subsystems for object knowledge. *Nature*, **359**, 60-4.
43. Hart, J. J., Berndt, R. S. and Caramazza, A. (1985). Category-specific naming deficit following cerebral infarction. *Nature*, **316**, 439-40.
44. Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schuten, J. L. and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, **293**, 2425-30.
45. Higuchi, S. and Miyashita, Y. (1996). Formation of mnemonic neuronal responses to visual paired associates in inferotemporal cortex is impaired by perirhinal and entorhinal lesions. *Proceedings of the National Academy of Sciences USA*, **93**, 739-43.
46. Hillis, A. E. and Caramazza, A. (1991). Category-specific naming and comprehension impairment: A double dissociation. *Brain*, **114**, 2081-94.
47. Humphreys, G. W., Riddoch, M. J. and Quinlan, P. (1988). Cascade processes in picture identification. *Cognitive Neuropsychology*, **5**, 67-103.
48. Keil, F. (1986). The acquisition of living thing and artifact terms. In *Language Learning and Concept Acquisition: Foundational Issues*, eds. W. Demopoulos and A. Marras. Norwood, NJ: Ablex.
49. Laiacona, M., Capitani, E. and Barbarotto, R. (1997). Semantic category dissociations: a longitudinal study of two cases. *Cortex*, **33**, 441-61.
50. Lavenex, P. and Amaral, D. G. (2000). Hippocampal-neocortical interaction: a hierarchy of associativity. *Hippocampus*, **10**, 420-30.
51. Lee, A. C., Bussey, T. J., Murray, E. A., Saksida, L. M., Epstein, R. A., Kapur, N., Hodges, J. R. and Graham, K. S. (2005). Perceptual deficits in amnesia: challenging the medial temporal lobe 'mnemonic' view. *Neuropsychologia*, **43**, 1-11.
52. Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M. and Malach, R. (2001). A hierarchical axis of object processing stages in the human visual cortex. *Cerebral Cortex*, **11**, 287-97.
53. Malt, B. C. and Smith, E. (1984). Correlated properties in natural categories. *Journal of Verbal Learning and Verbal Behaviour*, **23**, 250-69.
54. Marslen-Wilson, W. D. and Tyler, L. K. (1997). Dissociating types of mental computation. *Nature*, **387**, 592-4.
55. Martin, A. (2001). Functional neuroimaging of semantic memory. In *Handbook of Functional Neuroimaging of Cognition*, eds. R. Cabeza and A. Kingstone. Cambridge: MIT Press, pp. 153-86.
56. Martin, A. and Chao, L. L. (2001). Semantic memory and the brain: structure and processes. *Current Opinion in Neurobiology*, **11**, 194-201.
57. Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L. and Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, **379**, 649-52.
58. Martin, A., Ungerleider, L. G. and Haxby, J. V. (2000). Category-specificity and the brain: the sensory-motor model of semantic representations of objects. In *The Cognitive Neurosciences*, ed. M. S. Gazzaniga. Cambridge: MIT Press, pp. 1023-36.
59. Martin, Q., Wiggs, C. L., Ungerleider, L. G. and Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, **379**, 649-52.
60. Masson, M. (1995). A distributed memory model of semantic priming. *Journal of Experimental Psychology Learning, Memory, and Cognition*, **21**, 3-23.
61. McRae (in press). Semantic memory: Some insights from feature-based connectionist attractor networks. In *Psychology of Learning and Motivation*, vol. 45, ed. B. H. Ross. Amsterdam: Elsevier, .
62. McRae, K. and Cree, G. S. (2002). Factors underlying category-specific semantic deficits. In *Category-specificity in Mind and Brain*, eds. E. M. E. Forde and G. Humphreys. East Sussex: Psychology Press, pp. 211-50.
63. McRae, K., Cree, G. S., Seidenberg, M. S. and McNorgan, C. (in press). Semantic feature production norms for a large set of living and nonliving things. *Behavior Research Methods, Instruments, & Computers*, .
64. McRae, K., Cree, G. S., Westmacott, R. and de Sa, V. R. (1999). Further evidence for feature correlations in semantic memory. *Canadian Journal of Experimental Psychology*, **53**, 360-73.
65. McRae, K., de Sa, V. and Seidenberg, M. S. (1993). Semantic priming and the structure of semantic

- memory. *Journal of Clinical and Experimental Neuropsychology*, **15**, 385-86.
66. McRae, K., de Sa, V. R. and Seidenberg, M. S. (1997). On the nature and scope of featural representations of word meaning. *Journal of Experimental Psychology: General*, **126**, 99-130.
67. Mishkin, M., Ungerleider, L. G. and Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, **6**, 414-7.
68. Moore, C. J. and Price, C. J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, **122**, 943-62.
69. Moss, H. E., Rodd, J. M., Stamatakis, E. A., Bright, P. and Tyler, L. K. (2005). Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cerebral Cortex*, **15**, 616-27.
70. Moss, H. E. and Tyler, L. K. (1997). A category-specific impairment for non-living things in a case of progressive aphasia. *Brain and Language*, **60**, 55-8.
71. Moss, H. E. and Tyler, L. K. (2000). A progressive category-specific semantic deficit for non-living things. *Neuropsychologia*, **38**, 60-82.
72. Moss, H. E., Tyler, L. K. and Devlin, J. (2002). The emergence of category specific deficits in a distributed semantic system. In *Category-Specificity in Brain and Mind*, eds. E. Forde and G. W. Humphreys. Sussex: Psychology Press, pp. 115-48.
73. Moss, H. E., Tyler, L. K., Durrant-Peatfield, M. and Bunn, E. M. (1998). 'Two eyes of a see-through': Impaired and intact semantic knowledge in a case of selective deficit for living things. *Neurocase*, **4**, 291-310.
74. Moss, H. E., Tyler, L. K. and Jennings, F. (1997). When leopards lose their spots: Knowledge of visual properties in category-specific deficits for living things. *Cognitive Neuropsychology*, **14**, 901-50.
75. Mummery, C. J., Patterson, K., Hodges, J. R. and Wise, R. J. (1996). Generating 'tiger' as an animal name or a word beginning with T: differences in brain activation. *Proc. R. Soc. Lond. B Biol. Sci.*, **263**, 989-995.
76. Mummery, C. J., Patterson, K., Wise, R. J. S., Vandenberg, R., Price, C. J. and Hodges, J. R. (1999). Disrupted temporal lobe connections in semantic dementia. *Brain*, **122**, 61-73.
77. Murray, E. A. and Bussey, T. J. (1999). Perceptual-mnemonic functions of the perirhinal cortex. *Trends in Cognitive Sciences*, **3**, 142-51.
78. Murray, E. A., Bussey, T. J., Hampton, R. R. and Saksida, L. M. (2000). The parahippocampal region and object identification. *Annals of the New York Academy of Sciences*, **911**, 166-74.
79. Murray, E. A., Malkova, L. and Goulet, S. (1998). Crossmodal associations, intramodal associations, and object identification in macaque monkeys. In *Comparative Neuropsychology*, ed. A. D. Milner. Oxford: Oxford University Press, pp. 51-69.
80. Murray, E. A. and Richmond, B. J. (2001). Role of perirhinal cortex in object perception, memory, and associations. *Current Opinion in Neurobiology*, **11**, 188-93.
81. Parker, A. and Gaffan, D. (1998). Lesions of the primate rhinal cortex cause deficits in flavour-visual associative memory. *Behavioral Brain Research*, **93**, 99-105.
82. Perani, D., Cappa, S., Bettinardi, V., Bressi, S., Gorno-Tempini, M.-L., Matarrese, M. and Fazio, F. (1995). Different neural systems for the recognition of animals and man-made tools. *NeuroReport*, **6**, 1637-41.
83. Pexman, P. M., Holyk, G. G. and Monfils, M. H. (2003). Number-of-features effects and semantic processing. *Memory and Cognition*, **31**, 842-55.
84. Pexman, P. M., Lupker, S. J. and Hino, Y. (2002). The impact of feedback semantics in visual word recognition: number-of-features effects in lexical decision and naming tasks. *Psychonomic Bulletin & Review*, **9**, 542-9.
85. Phillips, J. A., Noppeney, U., Humphreys, G. W. and Price, C. J. (2002). Can segregation within the semantic system account for category-specific deficits? *Brain*, **125**, 2067-80.
86. Pilgrim, L. K., Fadili, J., Fletcher, P. and Tyler, L. K. (2002). Overcoming confounds of stimulus blocking: an event-related fMRI design of semantic processing. *NeuroImage*, **16**, 713-23.
87. Plaut, D. C. and Shallice, T. (1993). Perseverative and semantic influences on visual object naming errors in optic aphasia: A connectionist account. *Journal of Cognitive Neuroscience*, **5**, 89-117.
88. Randall, B., Moss, H. E., Rodd, J. M., Greer, M. and Tyler, L. K. (2004). Distinctiveness and correlation in conceptual structure: Behavioral and computational studies. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **30**, 393-406.
89. Raposo, A., Stamatakis, E.A., Moss, H.E. and Tyler, L.K. (2004). Interactions between processing demands and conceptual structure in object recognition: an event-related fMRI study. *Journal of Cognitive Neuroscience*, **16**, Suppl. B82.
90. Rogers, T. T., Hocking, J., Mechelli, A., Patterson, K. and Price, C. (2005). Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience*, **17**.
91. Rosch, E. (1978). Principles of categorization. In *Cognition and Categorization*, eds. E. Rosch and B. B. Lloyd. Hillsdale, NJ: Erlbaum, pp. 27-48.
92. Sacchett, C. and Humphreys, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwam: a category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, **9**, 73-86.
93. Sakai, K. and Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature*, **354**, 152-5.
94. Sartori, G. and Job, R. (1988). The oyster with four legs: a neuropsychological study on the interaction of visual and semantic information. *Cognitive Neuropsychology*, **5**, 105-32.
95. Sartori, G., Job, R., Miozzo, M., Zago, S. and Marchiori, G. (1993). Category-specific form knowledge in a patient with herpes simplex virus encephalitis. *Journal of Clinical and Experimental Neuropsychology*, **15**, 280-99.

96. Sheridan, J. and Humphreys, J. W. (1993). A verbal semantic category-specific recognition deficit. *Cognitive Neuropsychology*, **10**, 143-84.
97. Sigala, N. and Logothetis, N. K. (2002). Visual categorization shapes feature selectivity in the primate temporal cortex. *Nature*, **415**, 318-20.
98. Simmons, W. K. and Barsalou, L. W. (2003). The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cognitive Neuropsychology*, **20**, 451-86.
99. Squire, L. R., Stark, C. E. L. and Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, **27**, 279-306.
100. Suzuki, W. A. and Amaral, D. G. (1994). Perirhinal and parahippocampal cortices of the macaque monkey: cortical afferents. *The Journal of Comparative Neurology*, **350**, 497-533.
101. Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science*, **262**, 685-8.
102. Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, **19**, 109-39.
103. Taylor, K. I., Moss, H., Randall, B. and Tyler, L. K. (2004). The interplay between distinctiveness and intercorrelation in the automatic activation of word meaning (abstract). *Abstracts of the Psychonomic Society*, **9**, 109.
104. Taylor, K. I., Moss, H. E., Stamatakis, E. and Tyler, L. K. (2005). Cross-modal integration and the perirhinal cortex. *Cognitive Neuroscience Society - 2005 Annual Meeting Program*, , 217.
105. Tranel, D., Damasio, H. and Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, **35**, 1319-27.
106. Tsunoda, K., Yamane, Y., Nishizaki, M. and Tanifuji, M. (2001). Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nature Neuroscience*, **4**, 832-8.
107. Tyler, L. K., Bright, P., Dick, E., Tavares, P., Pilgrim, L., Fletcher, P., Greer, M. and Moss, H. (2003a). Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cognitive Neuropsychology*, **20**, 54-61.
108. Tyler, L. K., Marslen-Wilson, W. D. and Stamatakis, E. A. (2005). Differentiating lexical form, meaning and structure in the neural language system. *Proceedings of the National Academy of Sciences*, **102**, 8375-80.
109. Tyler, L. K. and Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, **5**, 244-52.
110. Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R. and Levy, J. P. (2000a). Conceptual structure and the structure of concepts: a distributed account of category-specific deficits. *Brain and Language*, **75**, 195-231.
111. Tyler, L. K., Stamatakis, E. A., Bright, P., Acres, K., Abdallah, S., Rodd, J. M. and Moss, H. E. (2004). Processing objects at different levels of specificity. *Journal of Cognitive Neuroscience*, **16**, 351-62.
112. Tyler, L. K., Stamatakis, E. A., Dick, E., Bright, P., Fletcher, P. and Moss, H. (2003b). Objects and their actions: evidence for a neurally distributed semantic system. *Neuroimage*, **18**, 542-57.
113. Tyler, L. K., Voice, J. K. and Moss, H. E. (2000b). The interaction of meaning and sound in spoken word recognition. *Psychological Bulletin & Review*, **7**, 320-6.
114. Ungerleider, L. G. and Mishkin, M. (1982). Two cortical visual systems. In *Analysis of Visual Behavior*, eds. D. J. Ingle, M. A. Goodale and R. J. W. Mansfield. Cambridge, MA: MIT Press, pp. 549-86.
115. Warrington, E. K. and McCarthy, R. (1983). Category specific access dysphasia. *Brain*, **106**, 859-78.
116. Warrington, E. K. and McCarthy, R. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain*, **110**, 1273-96.
117. Warrington, E. K. and Shallice, T. (1984). Category-specific semantic impairment. *Brain*, **107**, 829-53.
118. Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E. and Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain*, **114**, 1803-1817.
119. Zannino, G. D., Perri, R., Carlesimo, G. A., Pasqualetti, P. and Caltagirone, C. (2002). Category-specific impairment in patients with Alzheimer's disease as a function of disease severity: A cross-sectional investigation. *Neuropsychologia*, **40**, 2268-79.
120. Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C. and Frackowiak, R. S. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, **11**, 641-9.