INTRODUCTION

Patients with category-specific semantic deficits—a greater impairment for one domain or category of concepts than another—have played a key role in the development of theories of the organisation of conceptual knowledge in semantic memory. The most widely debated dissociation has been that between knowledge of living and non-living things, and this will be the focus of the current chapter. Numerous reports in the neuropsychological literature suggest that brain damage can disrupt knowledge of living things to a significantly greater extent than non-living things in some patients, whereas in other, albeit rarer, cases the reverse pattern is found (Barbarotto, Capitani, Spinnler, & Trivelli, 1995; Basso, Capitani, & Laiaccona, 1988; Caramazza & Shelton, 1998; De Renzi & Lucchelli, 1994; Farah, Hammond, Mehta, & Ratcliff, 1989; Forde et al., 1997; Laiacona, Capitani, & Barbarotto, 1997; McCarthy & Warrington, 1988; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998; Pietrini et al., 1988; Sacchetti & Humphreys, 1992; Sartori & Job, 1988; Silveri & Gainotti, 1988; Warrington & McCarthy, 1987; Warrington & Shallice, 1984; for a review see Forde & Humphreys, 1999).

The simplest account of selective semantic impairments is that the behavioural dissociations between different categories of knowledge are a direct reflection of the underlying organisation of the conceptual system, implying that there are distinct, independent stores for each category of information (Goodglass, Klein, Carey, & Jones, 1966). An important recent
development of this account suggests that certain domains of knowledge, such as animal and plant life, have their own dedicated neural systems as a result of their importance in evolutionary terms (Caramazza & Shelton, 1998). These neural systems can be independently affected by focal brain damage, so resulting in truly selective deficits. An influential alternative has been the sensory/functional account developed by Warrington and colleagues (McCarthy & Warrington, 1988; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). This suggests that the first-order organising principle in semantic memory is not category or domain of knowledge, but type of semantic property. It is argued that semantic memory is fractionated into separate stores for sensory/perceptual information and for functional (sometimes referred to as associative) information. Living things concepts are claimed to be more dependent on perceptual properties, and therefore more severely affected by damage to the perceptual subsystem, whereas the reverse tends to be true for non-living things, with greater impairments resulting from damage to the store of functional information.

The domain-specific account and the sensory/functional account have been influential but both have their limitations. The sensory/functional account has recently been challenged by reports of patients who have living things deficits without an accompanying deficit for perceptual properties (Laiaccona et al., 1997; Lambon Ralph, Howard, Nightingale, & Ellis, 1998; Moss et al., 1998), or who have poor knowledge of perceptual properties without an accompanying deficit for living things (Lambon Ralph et al., 1998). The domain-specific account predicts that there should be a strong association between focal lesions in specific regions of the brain and the domain of knowledge that is impaired. While there is some support for this link, with bilateral medial temporal damage often associated with impairments for living things and left frontoparietal damage with deficits for artefacts (Gainotti, Silveri, Daniele, & Giustolisi, 1995) there are certainly exceptions, and there are also reports of patients with category-specific deficits in the context of diffuse rather than focal brain damage (Gonnerman, Andersen, Devlin, & Seidenberg, 1997; Silveri, Danieli, Giustolisi, & Gainotti, 1991; Moss & Tyler, 2000). Functional neuroimaging studies also provide mixed results, with some reports suggesting regional specialisation for domains or categories of knowledge (Martin, Wiggs, Ungerleider & Haxby.

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1The term “category” is used inconsistently in the literature. We will use the term “domain” to refer to the higher level distinction between living and non-living things, and reserve “category” for groups within those domains such as animals, fruit, tools, and vehicles.

2Other accounts have been put forward in the literature in which the deficit for living things is explained in terms of their lower familiarity (e.g. Funnell & Sheridan, 1992), greater visual complexity (e.g. Gaffan & Heywood, 1993) or some other “difficulty” factor. However, this kind of account cannot accommodate the reverse pattern of a greater deficit for non-living objects, and so we do not discuss them further here.
1996; Perani et al., 1995) and others more consistent with a unitary distributed semantic system (Devlin et al., 2000, 2002) or with organisation based on attribute type (e.g. motion/visual form) rather than domain per se (e.g. Chao, Haxby, & Martin, 1999; Mummery, Patterson, Hodges, & Price, 1998). Even if there are dedicated neural systems for certain domains of knowledge, the domain-specific account does not elucidate the organisation of information within domain-specific stores and so cannot explain the different patterns of breakdown of conceptual knowledge across domains that we discuss later in this chapter.

A NEW APPROACH: CONCEPTUAL STRUCTURE AND THE STRUCTURE OF CONCEPTS

We have recently begun to develop a new account of conceptual representation and category-specific deficits by bringing together theoretical insights and data from different disciplines with the aim of providing an integrated framework in which to model normal and disordered conceptual systems. At the heart of our approach is the investigation of the internal structure of concepts of different types, and hence we refer to it as the “conceptual structure account” (Durrant-Peatfield, Tyler, Moss, & Levy, 1997; Moss & Tyler, unpublished data; Tyler et al., 1996; Tyler, Moss, Durrant-Peatfield, & Levy, 2000). This account is fundamentally different from those outlined above in that we do not assume any explicit fractionation of semantic memory along either category/domain- or property-type boundaries. Rather, we suggest that there is a single, highly distributed network, in which all concepts are represented as patterns of activation over many nodes corresponding to semantic properties or “microfeatures”. Damage to this kind of unitary, distributed system can potentially affect one category of concepts more than another because similar concepts are represented close together in semantic space—they have overlapping patterns of activation (for related similarity-based models, see Caramazza, Hillis, Rapp & Romani, 1990; also Dixon, Bub, & Arguin, 1997; Forde et al., 1997; Humphreys, Riddoch & Quinlan, 1988).

On the conceptual structure account, not only do similar concepts tend to activate overlapping sets of semantic features, but there are also systematic differences in the internal structure of concepts in different categories and domains. The central tenets of the account are that: (i) each concept has a specific structure, which is determined by the set of features it activates and the relations among those features; (ii) concepts in different categories and domains have characteristically different internal structure; and (ii) random, global damage throughout the system will affect concepts in different ways, as a function of their internal structure. Following McRae, de Sa, and Seidenberg (1997) and Devlin, Gonnerman, Andersen, and Seidenberg (1998) we claim that correlation is a key relation among semantic properties. Properties
are correlated to the extent that they frequently occur together in concepts, such that the presence of one predicts that presence of the other. For example, the properties of “having eyes” and “being able to see” are very strongly correlated because they always occur together and do not occur separately. The significance of correlation is that in a distributed connectionist system, correlated properties support each other with mutual activation (Devlin et al., 1998). This means that strongly correlated properties are more resilient to damage within the semantic system than those that are more weakly correlated. Hence, different patterns of correlation among properties within a concept will lead to different patterns of loss and preservation of information, given the same degree of overall damage.

We claim that the structure of concepts in the living and non-living domains differs in systematic ways. The conceptual structure account addresses a criticism of earlier unitary, distributed models, such as OUCH (Organised Unitary Content Hypothesis; Caramazza et al., 1990), which was that such models are so flexible that they can explain any pattern of deficit, and are therefore theoretically unhelpful (Caramazza & Shelton, 1998). By developing very specific claims about conceptual structure, we are able to constrain the power of the account and make falsifiable predictions, thus overcoming this kind of objection. Our starting point was to base our theoretical assumptions about conceptual structure on well-supported claims in the psychological literature. First, living things (and most typically, animals) have many properties and many of these are shared among all members of a category (e.g. all mammals breathe, move, have eyes, can see, have live young, eat, and so on). Moreover, these shared properties co-occur frequently and so are strongly correlated (Keil, 1986, 1989; Malt & Smith, 1984). Living things also have distinctive properties that are informative in distinguishing one category member from another (e.g. “having stripes” versus “having spots”), although these tend to be correlated weakly, or not correlated at all, with other properties and so are vulnerable to damage. Artefacts have fewer properties in total, and they tend to be relatively more distinctive, with a smaller pool of information shared across all members of a category.

Another key aspect of the conceptual structure model, and the major difference from other correlation based models that have implemented some of the same fundamental assumptions (e.g. Devlin et al., 1998; McRae et al., 1997) is that we incorporate a set of claims about the relations between form (perceptual properties) and function in the living and non-living domains. These claims are again based on psychological research, drawing particularly heavily on the developmental literature, which investigates how children learn the relations among properties of concepts. We claim that an essential aspect of conceptual structure is the pattern of correlations between form and function (Tversky & Hemenway, 1984). Our argument goes as follows: if a perceptual form is consistently observed performing a function, then a
system that is sensitive to co-occurrences will learn that a specific form implies a specific function (Madole, Oakes, & Cohen, 1993; Mandler, 1992). The nature of these form–function relations distinguishes between living things and artefacts. Artefacts have distinctive forms, which are consistently associated with the functions for which they were created (De Renzi & Lucchelli, 1994; Keil, 1986, 1989; see also Caramazza et al.’s [1990] claim of privileged relations among properties for a similar view). Artefacts are generally designed to perform a single distinctive function so that their form is as distinctive as the function. In contrast, living things tend to “do” similar things and they tend to resemble each other, thus they share many features. Individual variations in form tend not to be functionally significant (e.g. “a lion’s mane”). Even so, living things (like artefacts) also have form–function correlations. But whereas the form–function correlations for artefacts involve distinctive properties, for living things it is the shared properties (e.g. “eyes”, “legs”) that are involved in form–function correlations (e.g. “eyes-see”; “legs-move”). We refer to these as biological functions (for further detail see Durrant-Peatfield et al., 1997; Tyler et al., 2000; Tyler & Moss, 1997).

In summary, the internal structure of concepts in the broad domains of living things and artefacts differ in that living things have more properties overall, more shared properties and more correlations among shared properties than do artefacts, while artefact structure is typically characterised by strong correlations between small sets of distinctive form and function properties. Because correlated properties support each other with mutual activation, distinctive properties of artefacts will be more resistant to damage than those of living things, while the reverse will tend to be the case for shared properties. Unlike the sensory/functional account, we are not claiming that functional information is more important for artefacts than for living things, but rather that there is a difference across domains in the kind of functional information that is most strongly correlated—and therefore most robust to damage. Living things have many, very important functional properties, but the most important ones concern their biological activities and are frequently shared across most or all members of a category, rather than their intended use or purpose in relation to human beings (Tyler & Moss, 1997).

The conceptual structure model comprises a set of claims about the nature of a central, distributed conceptual system and, as such, is applicable only to category-specific effects that arise as a result of damage to this system. Several researchers have suggested that the category-specific deficits of certain patients arise from damage outside of the conceptual system, in either: (i) a presemantic structural description system (Forde et al., 1997; Sartori, et al., 1993); or (ii) a postsemantic lexical system (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Hart, Berndt, & Caramazza, 1985). In the former case, this would give rise to deficits in recognising visually presented objects or pictures for items with a high degree of structural similarity, while in the
latter case problems would be manifest in tasks requiring the production of lexical labels for objects. At this stage in its development, the conceptual structure account is not tied to specific claims about the nature of the object recognition and lexical output processes that must clearly be a part of any complete cognitive theory. The scope of the current model is to characterise the structure of the conceptual system itself, and to accommodate data from those patients whose category-specific behaviour arises from an impairment located within the conceptual system rather than pre- or post-semantic processes—as revealed by pervasive deficits within one category or domain of knowledge, not restricted to any specific modality of input or output.

CONCEPTUAL STRUCTURE: A COMPUTATIONAL SIMULATION

The first phase of our research within the framework of the conceptual structure account was to implement our representational assumptions in a small-scale computational model and to simulate the effects of random damage. It is essential for our approach to demonstrate that random damage to a distributed semantic system can, in principle, have differential effects on conceptual representations that vary systematically in their internal structure in the ways outlined above, and to determine the patterns of behaviour that may result from these differential effects.

Our main representational claims were implemented in a simplified way in a small-scale connectionist model (Durrant-Peatfield et al., 1997; Tyler et al., 2000) in which concepts were represented by sets of “functional” and “perceptual” properties. The properties were either shared (active for all members of a category) or distinctive (active only for a single concept). We constructed 16 concepts (or “semantic vectors”) of which eight corresponded to living things and eight to artefacts. Within each domain we simulated two categories of four vectors each, such that the concepts with a category shared a proportion of their semantic properties. The proportion of shared to distinctive properties was higher for the living things than for the artefacts. The domains of artefacts and living things were further distinguished by the manner in which functional properties were correlated with perceptual properties. Specifically, the shared perceptual properties of living things (e.g. “has legs”) were correlated with shared biological functions (e.g. “can move”), whereas distinctive perceptual properties (e.g. “a tiger’s stripes”) were not

3 "Perceptual" and “functional” are in quotes, because in reality the features in this model were unnamed abstractions. Throughout the discussion of the model, we refer to named features such as “has legs” but these are just examples to illustrate the structure of the vectors in a more concrete way.
correlated with any other properties. In contrast, the eight artefacts had few shared, correlated properties and it was the distinctive perceptual properties (e.g. "has a serrated edge") that were strongly correlated with a specific function (e.g. "used for cutting").

After training a connectionist autoassociator on the 16 semantic vectors, the connections between layers were randomly chosen and progressively "lesioned" to simulate widespread damage to the system. For each level of lesioning, a percentage of connection weights (from 10% to 100%) were set to zero. We then evaluated the model’s ability to correctly reproduce the semantic pattern for each item in the training set on its output layer, at each level of lesioning. Our predictions about the behaviour of the lesioned model were based on the assumption that loss of distinctive properties leads to errors in reproducing the correct target pattern, and that correlations protect properties in proportion to the strength of the correlation. So, we predicted that initially the model would make errors in correctly "identifying" living things because damage would have affected the vulnerable distinctive properties. We also predicted that mapping errors for living things would tend to be members of the same category because shared properties for living things are robust to damage due to their greater density of correlations. In contrast, we predicted that distinctive properties of artefacts would be preserved because they are correlated, allowing more accurate identification of the concept until the most severe levels of damage.

This was indeed what we found (Durrant-peatfield et al., 1997; Tyler et al., 2000). For artefact concepts, the distinctive form–function correlations were preserved, enabling individual artefact concepts to be distinguished from each other. In contrast, the distinctive properties of living things were less well preserved whereas shared properties were robust to damage. Thus lesioning tended to make living things concepts hard to distinguish from each other while preserving their category membership. The model exhibited a selective deficit for living things, except at the most severe levels of lesioning. At this point, artefacts became more difficult to identify than living things, because severe damage overwhelmed both the shared properties and form–function-correlated properties of artefacts, leaving only the densely intercorrelated, shared biological functional correlations of living things. At this extreme level of damage, overall performance was very poor, but the remaining shared properties favoured living things over artefacts, giving them a small but significant advantage. The main results are presented in Figure 5.1.

In summary, the computational simulation demonstrates how the internal structure of concepts in terms of the patterns of correlation among properties produces differential effects of random damage through the system. Selective deficits for living things emerged at most levels of lesioning severity, but greater deficits for artefacts can arise on rare occasions when damage is
Figure 5.1. Percentage of correct-identity mappings for living and non-living things in the connectionist model as a function of lesion severity (percentage of connections set to zero). Adapted from Tyler et al. (2000).

particularly severe.\textsuperscript{4} The model also simulates loss and preservation of particular kinds of semantic properties for items in the different domains as well as the overall dissociation—patterns of performance that can be directly tested in behavioural tests with semantically impaired patients (this is discussed later). We acknowledge that the model is small and over-simple, in that it includes only 16 artificially constructed concepts. Nevertheless, these vectors straightforwardly instantiated our major representational assumptions, which have also been supported by evidence from empirical studies of people's conceptual knowledge, as described in the following section.

CONCEPTUAL STRUCTURE: EMPIRICAL EVIDENCE SUPPORTING THE REPRESENTATIONAL ASSUMPTIONS

In the conceptual structure account we make a number of claims concerning the structure of concepts and how this differs across the living and non-living domains. As outlined above, these claims were based on findings in the

\textsuperscript{4}This prediction contrasts with that of the Devlin et al. (1998) model, where artefact deficits were seen only at the mildest level of damage, followed by living things deficits damage, which was more severe. The difference in the two models is due to the pattern of form–function correlations in our conceptual representations, based on our specific theoretical claims, which were not instantiated in the Devlin et al. model.
psychological and developmental literature. We have also been able to examine these assumptions more directly in a large-scale normative study of the properties generated for a set of concepts by unimpaired young adults (Moss et al., unpublished data). Although property generation is a metalinguistic task and cannot provide a completely transparent window onto people’s mental representations of concepts, it can give a good indication of the properties that people can readily retrieve and at least approximates their underlying conceptual knowledge. We asked 45 people to list the properties of 93 basic level concepts, taken from the categories of animals, fruit, tools, and vehicles. Items were matched for familiarity as far as possible across the living and non-living domain according to the ratings in the MRC database (Coltheart, 1981). The mean familiarity rating was 5.1 for living things and 5.16 for non-living things, $t (68) < 1$. Familiarity was also matched over the two categories within each domain (animals and fruit, 4.98 and 5.25, respectively, $t (37) = 1.39, p > .1$; tools and vehicles, 5.38 and 4.94, respectively, $t (29) = 1.55, p > .1$). Within the constraints of matching for familiarity, we chose as many exemplars as reasonably possible in order to provide a good estimate of conceptual structure within the category.

Once the properties had been compiled, we carried out a set of analyses to determine the distributional statistics for each domain, focusing on the variables relevant to the conceptual structure account. First we calculated the distinctiveness of each feature—this measures the amount of information that a feature provides about an object’s identity. As in Devlin et al. (1998) the distinctiveness of a property is one over the number of words that property occurs in. Each property has a distinctiveness value associated with it ranging from one (highly distinctive) to zero (not distinctive). We then calculated the mean distinctiveness value for each concept as the average distinctiveness of each feature within the concept. As predicted, the mean distinctiveness of features within artefact concepts (.73) was significantly greater than for living things (.64; $t (89) = 3.6, p < .01$). The corollary of this finding is that living things had reliably more shared properties than artefacts, defining a shared property as one which was generated for more than one concept (a mean of 15 shared properties for living things and 8 for artefacts: $t (89) = 10.9, p < .001$).

The analyses also showed that living things concepts had more properties overall (mean = 17.7 versus 11.3, $t (89) = 10.67, p < .001$) and more pairs of properties that were significantly correlated with each other (where the cut-off level for significance was $\alpha = .05$; mean = 115 versus 47, $t (89) = 9.95, p < .001$). Finally, where there were significant form–function correlations (e.g. has “a blade”—“is used for cutting”), these were significantly more distinctive for non-living things than for living things (mean = 0.56 versus 0.46, $t (89) = 8.5, p < .001$), which is consistent with the hallmark claim of the conceptual structure account, that the distinctive properties of artefacts tend to be
correlated in form–function relations, while for living things it is primarily the shared biological functional and perceptual properties that are correlated with one another.

In addition to the systematic differences across the living and non-living domains, we also found that there were interesting differences between the categories within each domain, i.e. between fruit and animals and between tools and vehicles. For example, the form–function correlations for tools were significantly more distinctive than those for vehicles, as well as those for the living things, whereas they were less distinctive for fruit than for animals. Differences across individual concepts within categories and across categories within domains are entirely consistent with our account, because all the key variables are continuous, rather than all-or-none. In spite of this variation, the domain-level differences were still significant, and in the predicted directions. This is the essential result for our prediction that damage to the system can affect the living and non-living domains in different ways.

Nevertheless, certain categories might be more or less typical of their domains and so different degrees of impairment over categories could also emerge. It should therefore be possible to generate more fine-grained predictions concerning the expected patterns of behaviour for specific categories within the living and non-living domains. At present, these predictions are more speculative than those at the domain level, as we do not yet have an implemented computational model of conceptual structure for specific categories. Our predictions are based on the distributional statistics from the property norm study, which showed that although the predicted differences over domains were generally true, there was also considerable variation across categories within domains. These data suggest that our claims about the living and non-living domains are most faithfully reflected by the categories of animals and tools, respectively, because animals have many shared, correlated properties with relatively few distinctive properties, whereas tools have little shared information and strong correlations among pairs of highly distinctive form and function properties. Therefore, we predict that the domain differences outlined above will all be most apparent if we compare data for animals versus tools. In addition, we predict that the concepts in the category of fruit (and vegetables) will be among the most vulnerable at all levels of damage because they are close together in semantic space and have very few, poorly correlated distinctive properties as well as fewer shared properties than other living things, such as animals. Within the artefact domain, vehicles pattern more closely with living things in some respects than do other artefacts such as tools, in that they have more shared, correlated properties. This leads to the prediction that, at severe levels of damage, it is tools that will most clearly show the predicted disadvantage for artefacts, due to their small number of shared, correlated properties. Figure 5.2 shows a schematic representation of the predicted effects on the four categories at increasingly severe levels of
damage. This is an attempt to make the predictions concrete, although it is of course an oversimplification, because these effects will be modulated by many other variables such as concept familiarity, modality of input and output and the precise demands of the task. We present the current discussion as speculation, which might encourage further refinement of category-level predictions and lead to studies that can address these issues.

**CONCEPTUAL STRUCTURE: NEUROPSYCHOLOGICAL EVIDENCE**

A number of predictions are generated by the conceptual structure account. First, we expect that deficits for living things will frequently occur, as a result of both mild and moderate levels of damage to the semantic system, due to the vulnerability of the distinctive properties of living things concepts. Given
that distinctive properties are necessary to uniquely identify concepts and to distinguish among them, loss of this information will disrupt performance on the majority of semantic tasks, including naming, matching, and property decisions. Critically for our account, the disproportionate loss of distinctive information for living things is predicted to occur even when damage is diffuse or patchy, for example in dementia of the Alzheimer’s type (DAT) or generalised cerebral atrophy. Deficits for artefacts are predicted to be rarer, because the distinctive properties are more strongly correlated with each other. It is only at the most severe levels of damage, when the system has essentially lost all distinctive information, that living things will be at a slight advantage, due to the greater number of shared, correlated properties that can support at least some comprehension of living things concepts. In this context it is also important to note that a general prediction made by our account is that dissociations among living and non-living things will tend to be graded rather than all or none, because there will be different degrees of loss of properties across the domains rather than selective damage to independent stores of information.

Second, we predict a characteristic pattern of loss and preservation of semantic properties of different kinds. Distinctive properties of living things should be most vulnerable to loss, while shared information is highly robust. For artefacts, the difference between shared and distinctive information will be less marked, because shared properties will be relatively less robust (as they are fewer and less densely correlated) and distinctive properties will be relatively more robust (as they are more strongly correlated, especially in form–function correlations). We should be able to test this prediction directly by probing patients’ knowledge of the shared and distinctive properties of concepts in different categories and domains. The pattern of loss and preservation of distinctive/shared information will also interact with the demands of different kinds of semantic tasks. Those that require intact distinctive properties will be most impaired for living things—including picture naming and word–picture matching with close category foils—while those that can be performed using shared information—such as category level sorting—should be less impaired for living things. The predictions of the conceptual structure account concerning the expected patterns of feature loss can be contrasted with the predictions of the sensory/functional account—that living things deficits will be associated with greater loss of perceptual than functional properties. The conceptual structure account does not predict a perceptual/functional dissociation, assuming that distinctiveness is held constant over these feature types. In the following sections we examine the evidence pertinent to these two sets of predictions, both from our own patient studies and from cases reported in the literature.
Domain dissociations and severity of damage

The computational simulation of the conceptual structure account revealed an interaction between severity of damage throughout the semantic system and the direction of impairment. Living things were more impaired at most levels of damage, but when damage was very severe and overall performance very inaccurate, living things had a slight advantage over artefacts. We suggest that this is due to the large number of highly intercorrelated shared properties for living things, which is the only information that can withstand this degree of damage, allowing a small percentage of living things trials to be correct (see Moss & Tyler [2000] for further details). This interaction means that the conceptual structure account can accommodate the double dissociation between living things and artefacts, with the proviso that artefact deficits are associated with the most severe semantic impairments, while mild or moderate impairments should generally produce deficits for living things. However, as will be discussed later it is not necessarily a simple matter to compare the severity of the semantic deficit across patients.

It is certainly the case that deficits for living things are much more frequently observed in general than artefact deficits, as is clear from the number of reported cases in the literature. Examination of reported results also confirms the prediction that selective deficits are rarely all-or-none but are a matter of degree, with performance in the "preserved" domain frequently below the normal range. For example, JBR (Warrington & Shallice, 1984), Michelangelo (Sartori & Job, 1988) Giulietta (Sartori et al., 1993), NV (Basso, Capitani, & Laiacoma, 1988), and RC (Moss et al., 1998) all show performance below the control range for non-living things, as for well as living things, for several tasks. In some patients, the graded effect is more apparent on some tasks than others, with performance for the preserved category within the normal range for certain tasks such as word–picture matching, but still falling below the normal range for the more demanding tasks like picture naming (e.g. EW, Caramazza & Shelton, 1998). One or two other patients in the literature do seem to show a highly selective deficit (MF, Barbarotto et al., 1995; KR, Hart & Gordon, 1992), although for some it is not clear to what extent performance in the "preserved" category falls within or below the control range, as this is not reported (e.g. KR, Hart & Gordon, 1992). Nevertheless, performance is not truly selective for the vast majority of patients.

The most controversial issue is whether the small number of cases of selective deficit for artefacts that have been reported in the literature do indeed have very profound semantic impairments. It is possible that this was the case for the two patients reported by Warrington and McCarthy (1983, 1987). VER and YOT had severe global dysphasia and so only matching to
sample techniques was possible. However, it is difficult to assess the severity of the semantic impairment given the profound production and comprehension impairments. Moreover, materials in these studies were not matched for familiarity and other variables that we now know may be important in determining the level of accuracy. Other patients reported to have deficits for the artefact domain do not seem to have particularly profound deficits (JJ, Hillis & Caramazza, 1991; CW, Sacchett & Humphreys, 1992). At this stage we are not sure whether it is possible to account for these individual patients within our framework without weakening our assumptions. In the conceptual structure account we adopt the radical stance of attempting to account for dissociations in terms of purely random damage throughout the semantic system. However, it has also been demonstrated that even in a purely distributed system with no predefined category boundaries, similar concepts with overlapping patterns of activation will be represented close together in “lumpy” semantic space (Caramazza et al., 1990; Small, Hart, Nguyen, & Gordon, 1995; Zorzi, Perry, Ziegler, & Coltheart, 1999). Networks are self-organising, and members of a category could be captured by the same hidden units. This suggests that it would be possible for focal damage affecting specific clusters of microfeatures or hidden units to have disproportionate effects on individual categories, over and above the general patterns predicted by the structural characteristics of concepts in those categories. It is possible that occasional artefact deficits could arise at mild levels of damage in this way.

Several reports have suggested that there might be category-specific impairments in patients with DAT (e.g. Silveri et al., 1991) although data from group studies are mixed, and no clear interaction of the direction of category-specific deficits with severity of semantic disorder has emerged (Garrard, Patterson, Watson, & Hodges, 1998; Gonnerman et al., 1997). In general it is difficult to evaluate relative severity and extent of brain lesion across different patients, whether recovering from herpes simplex encephalitis (HSE) or cardiovascular accident (CVA), or those with progressive deficits, because comparable tests and data are rarely reported. It is not clear how to define the appropriate criteria of severity, particularly for patients with more wide-ranging cognitive and/or linguistic impairments.

A more promising approach is to carry out longitudinal studies of individual patients with progressive semantic disorders, which enables us to track the nature of category-specific effects over the course of the disorder. Longitudinal studies of two DAT patients are reported by Gonnerman, Andersen, and Kempler (1997). One patient showed a consistent deficit for living things, whereas the other showed a deficit for artefacts, although this was not

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5 Other intriguing reports of artefact deficits exist, but as only picture naming was tested, it is not clear to what extent these were cases of category-specific anomia rather than semantic deficits per se (e.g. Tippet, Glosser, & Farah, 1996; Silveri, et al., 1997).
significant at most of the testing sessions. It is possible that the former patient would have progressed to show the predicted artefact deficit, but it was not possible to carry out further testing, presumably due to the more widespread cognitive deficits associated with DAT. The pattern for the latter patient is unclear.

In a recent study we were able to investigate the nature of semantic impairments during the progression of the disorder for a patient with a generalised cerebral atrophy but whose cognitive functions in other domains were less compromised than those of DAT patients at comparable levels of semantic impairment.\(^6\) ES showed a marked deficit for artefacts only at a late stage of the disorder, as predicted by our model. Earlier in the disease she either showed no difference between living things and artefacts or, in some tasks, a deficit for living things (Moss & Tyler, 2000). For example, we asked ES to name the set of Snodgrass and Vanderwart (1980) pictures at five time slices during the progression of her illness. Although ES was initially better at naming artefacts, by the final time slice her naming of artefacts had declined to the point where her accuracy was lower than for living things, as shown in Figure 5.3. This gave rise to a significant domain by time interaction, even

\[\text{Figure 5.3. Naming performance over time for patient ES on the Snodgrass and Vanderwart (1980) picture set. The time axis runs from t1 (August, 1994) to t5 (December, 1996). Reprinted from Moss and Tyler, 2000, with permission from Elsevier Science.}\]

\(^6\)ES was initially diagnosed as having semantic dementia because of her impairment of naming and comprehension in the context of good everyday memory and orientation. This diagnosis was later revised to generalised cerebral atrophy. ES clearly had cognitive deficits other than a breakdown of conceptual knowledge, but these remained quite stable over the 2 years of our study, while her conceptual knowledge declined steadily. For example, ES’s scaled scores were 21 and 19 on the verbal and performance components of the WAIS test in September 1994, and were well maintained at 17 and 22 respectively over a year later.
when factors such as familiarity and age of acquisition of the items were partialled out. A similar pattern was found in other tasks, including semantic priming, property verification, and generation of definitions, demonstrating that this was a semantic effect, rather than pure anoma.

A similar pattern has also begun to emerge for a second progressive aphasic patient, AA, with a similar progressive decline in semantic knowledge (Moss & Tyler, 2000). We tested AA’s naming on a new set of colour pictures of living things (animals, insects, fruit, and vegetables) and artefacts (vehicles, toys, clothing, and tools), carefully matched for familiarity and other potentially important variables (Bunn, Tyler, & Moss, 1998). As shown in Figure 5.4, AA also showed a significant interaction of domain and time, over three time slices in a period of about 18 months, when factors such as familiarity and picture complexity were taken into account (logistic regression: Wald = 6.9, $p < .005$). By the fourth time slice, however, AA’s performance had deteriorated dramatically and the difference was no longer apparent.\(^7\) Again, a similar pattern was observed in other tasks, although the interaction did not reach significance.

Our computational simulation of domain dissociations as a function of severity of damage also highlighted that the nature of errors should change over time for the different domains. Specifically, the loss of distinctive information for living things should lead to within-category errors for living things

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure5_4.png}
\caption{Naming performance over time for patient AA on the CSL colour photograph set (Bunn et al., 1998). The time axis runs from t1 (April, 1997) to t4 (October, 1998).}
\end{figure}

\(^7\)We would have predicted an advantage for living things over artefacts to still be apparent at t4. However, it was very difficult to test AA at this point and significant attentional deficits interfered with her naming performance.
at an early point in the progression of the disorder. However, cross-category or cross-domain errors should be very rare, because of the well-preserved shared properties. Shared information for artefacts is less robust, and so errors could cross category, and even domain, boundaries when damage is severe. For example, shared properties of tools, such as “has a handle” and “is small” are not as numerous or densely intercorrelated with other properties as are the shared properties of animals (e.g. “has legs”, “breathes”, “has eyes”, “can see”). Therefore, these properties are more vulnerable to loss, so allowing the system to sometimes misidentify a tool as a vehicle, for example, because the mismatching shared properties like “has a handle” are no longer present to help the system settle into the correct general pattern for some kind of tool. Our claim is not that cross-category errors are necessarily very common for artefacts, but rather that they will be more likely than for living things, for which between-category errors should hardly ever occur, even in the most severe deficits. This was the pattern demonstrated by the simulation, as shown in Figure 5.5.

There is some evidence for this pattern in longitudinal studies of picture naming performance. Hodges, Graham, and Patterson (1995) report a detailed breakdown of the naming errors of a semantic dementia patient, JL, over a period of 18 months. For living things, JL makes progressively more category-coordinate and superordinate errors, but he never produces a name that crosses categories (e.g. animal/fruit) or domains. However, for artefacts, occasional cross-category (e.g. “paintbrush”–“piece of vehicle”) and even cross-domain (telephone–animal) errors emerge at the later time slices.

We have carried out a similar analysis of the naming errors for one of the progressive aphasic patients mentioned above. AA did not produce a single cross-category or cross-domain error for living things until the last test session, when there were two such responses out of 69 items (“rabbit”–“the boys”; “cauliflower”–“camel”). For artefacts, in contrast, occasional cross-domain errors (e.g. “skittles”–“orange”) were produced, even at the first test session when she was already significantly impaired and, by the last two sessions there were eight and six such errors, respectively, including such striking examples as “pram”–“banana”, “table–umbrella” and “book–candle”. Although the absolute numbers of cross-category and cross-domain errors are small, there appears to be a consistent tendency for such errors to be produced in greater numbers for artefacts than living things, and to increase over time, as predicted by our account. Moreover, a similar pattern can be observed in AA’s word–picture matching data. In this task, the experimenter says a word aloud and the patient has to point to the pictured target from an array of four pictures containing the target (e.g. “lion”), a

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8 We have not been able to analyze the data for ES in the same way as her naming errors were almost always circumlocutions or no responses, rather than an incorrect item name.
Figure 5.5. Percentage of within- and between-category errors in the computational model as a function of lesion severity (percentage of connections set to zero) for (A) living things and (B) artefacts. Adapted from Tyler et al. (2000).
within-category foil (e.g. “tiger”) and two foils from a category within the other domain (e.g. “car” and “bus”). Errors are coded as within-category (e.g. “lion”—“tiger”) or between-category (e.g. “lion”—“bus”). This is comparable to the task simulated in our computational model. As shown in Figure 5.6, AA’s pattern of errors closely matches that predicted by the simulation. She shows more within-category errors than between-category errors for living things from the first test session onwards. She makes fewer errors overall for artefacts, and these errors are as likely to be between-category as within-category.

Patterns of loss and preservation of properties within domains

The conceptual structure account predicts that patients with deficits for living things will have impaired knowledge of distinctive relative to shared properties, but with relatively good preservation of distinctive knowledge for artefacts. We have reported precisely this pattern of knowledge for patient RC, who developed a semantic deficit following an HSE infection in 1992 (Moss et al., 1998). Preliminary tests revealed that RC had a significantly greater impairment for living things than artefacts. For example, he was able to name 49% of the artefacts in our colour picture set but only 10% of living things. Similarly, he scored 88% correct for artefacts and 67% correct for living things in a word–picture matching task that contained within-category foils. We compared RC’s knowledge of distinctive and shared information for the two domains in a property verification task. He was asked say “yes” or “no” to spoken property questions. Half of the properties were distinctive—they were true of only one or a few members of a category (“Does a zebra have black and white stripes?”) and the other half were shared by all members of the category (“Does a zebra have eyes?”). We also varied whether the questions concerned a perceptual or functional property of the concept. Control subjects were between 85 and 100% accurate in all conditions. RC showed a highly selective deficit for the distinctive properties of living things (55% correct), with scores of around 80% correct for all other conditions, including the shared properties of living things. Consistent with the conceptual structure account, RC showed no difference in accuracy for perceptual and functional properties. This is problematic for the sensory/functional account on which we would expect a patient with a clear-cut deficit for living things to have relatively greater problems with perceptually based properties. We also reported that RC’s preserved knowledge of shared properties of living things supported his ability to do well in certain tasks where distinctive properties were not necessary. For example, when asked to sort living things by category (animals versus fruit) he was able to do this very well, and in fact, slightly better than the equivalent task for artefacts (vehicles versus tools). He was
Figure 5.6. Number of within- and between-category errors over time for patient AA in a word–picture matching task for (A) living things and (B) artefacts.
also able to score 96% correct on a word–picture matching task in which the within-category foil was removed and replaced with one from a different category within the same domain.

A similar pattern of relatively preserved knowledge of shared properties and impaired knowledge of distinctive properties of living things has recently been reported for a patient, EW, who has a category-specific deficit for animals (Caramazza & Shelton, 1998). For most other patients in the literature, the appropriate contrasts between distinctive and shared information are not tested, so we cannot determine whether there is a particular problem with the distinctive properties of living things. However, in several reports, there are hints that this is the case. For example, Sartori and Job (1988) asked their patient, Michelangelo, to fill in the missing parts of incomplete drawings; they remark “the patient knows that he has to add parts of a superordinate category . . . he adds fins to fishes, wings to birds, and horns to certain animals, but he has great problems in distinguishing, e.g. the horn of a rhinoceros from the antlers of a deer”.

We have recently devised a new test of property knowledge to further investigate knowledge of shared and distinctive information. We selected 20 living things (10 animals and 10 fruit) and 20 artefacts (10 tools and 10 vehicles) and presented them each with four different true properties; these were either functional or perceptual, shared or distinctive. The distinctiveness of each property was determined by our property generation study described earlier. For each property we calculated the percentage of concepts within the category that had been attributed with that property. A property was counted as distinctive if it had been given for less than 50% of the category members (much less than 50% in most cases) and as shared if given for more than 50% of members (again, nearer to 100% for most properties). Concepts across domains were matched for frequency, familiarity, imageability, and objective age of acquisition (see Table 5.1). An equal number of false properties were created for each condition (shared/distinctive × functional/perceptual) by pairing concepts with properties from other items (e.g. “cat”—“does it have a curly tail?” / “cat”—“does it have wheels?”).

We have carried out this test with RC and four other patients with relatively greater deficits for living than non-living things following HSE infection. We have discussed three of the patients in detail in earlier papers (JBR, Bunn et al., 1998; RC, Moss et al., 1998; SE, Moss, Tyler, & Jennings, 1997). Brief case details for each patient are given in the Appendix (p. 146). The same test was carried out with a control group of twelve normal subjects between the ages of 59 and 73 years.9

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9The control group are older than all the patients except for SE. However, we do not envisage that a younger control group would show qualitatively different responses in this task which does not involve any reaction time component.
TABLE 5.1
Characteristics of stimuli in the property knowledge test

<table>
<thead>
<tr>
<th></th>
<th>Living things</th>
<th>Artefacts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Concept frequency</td>
<td>23</td>
<td>24</td>
</tr>
<tr>
<td>Concept familiarity</td>
<td>5.3</td>
<td>5.4</td>
</tr>
<tr>
<td>Imageability</td>
<td>6.4</td>
<td>6.2</td>
</tr>
<tr>
<td>Objective age of acquisition</td>
<td>44</td>
<td>48</td>
</tr>
<tr>
<td>Distinctiveness (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distinctive properties</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Shared properties</td>
<td>88</td>
<td>74</td>
</tr>
</tbody>
</table>

* CELEX (Baayen, Pipenbrook, & Guilikers, 1995).
  
  * MRC database (Coltheart, 1981) and our own ratings.
  
  * Morrison, Chappell, and Ellis (1997).

As shown in the Appendix, the HSE patients vary in terms of the overall severity of their semantic impairment and in degree of impairment for living things relative to non-living things. Nevertheless, all patients show a significant dissociation in at least one task. JBR and RC show the most marked dissociations, with significant impairments for living things in all three tasks shown (picture naming, naming to description, and word–picture matching). JH has an intermediate level of impairment, and also shows significant deficits for living things on all tasks. MW and SE show the mildest impairment, and the difference between living and non-living things reaches significance only in the picture naming task. However, we suggest that these patients do have a central semantic deficit (albeit mild) rather than a pure category-specific anoma. First, both show greater difficulty with the distinctive properties of living things in the current task (as discussed later). Second, we have documented SE’s impairment for living things in tasks such as priming and property verification elsewhere (Moss et al., 1997).

We excluded the category of fruit from the main analysis because control subjects had difficulty with many of the distinctive properties of these items (mean accuracy only 73%) and so it is not clear that the properties chosen were familiar enough to provide a valid test for the patients. The results for the control group and the five patients are shown in Figure 5.7, which plots the percentage of correct responses for distinctive versus shared properties for animals, vehicles, and tools.

As can be seen in Figure 5.7, control subjects were able to respond accurately in all six conditions, with scores as follows: animals shared, mean = 97% (range = 87–100%); animals distinctive, mean = 93% (range = 86–100%); vehicles shared, mean = 98% (range = 95–100%); vehicles distinctive, mean = 96% (range = 86–100%); tools shared, mean = 99% (range = 92–100%); tools distinctive, mean = 97%, range = 88–100%). The patients showed varying
degrees of difficulty on this task, with overall accuracy ranging from 70% for RC to 93% for MW. Four of the five patients showed a consistent pattern, with a selective deficit for the distinctive properties of animals relative to the non-living categories (tools and vehicles combined). This was the case for JBR ($\chi^2 = 16.6, p < .01$), SE ($\chi^2 = 5.2, p < .05$), MW ($\chi^2 = 3.37, 0.05 > p < .1$) and RC ($\chi^2 = 2.77, 0.05 > p < .1$). In contrast, these patients did not show any difference between animals and vehicles on the shared properties ($p > .1$ for all four patients). These results are consistent with the prediction of the conceptual structure account that the weakly correlated distinctive properties of living things such as animals will be particularly vulnerable to damage, and the densely correlated properties will be robust. For patients with the mildest degree of semantic loss (SE and MW), it is only the distinctive properties of animals that are impaired enough to fall below the control range, with the other three conditions preserved. The more severely affected patients, JBR and RC, show an exacerbation of the same pattern, with: (i) very low scores on the distinctive properties of animals, with accuracy falling at chance (40% and 49% correct for RC and JBR respectively); (ii) some degree of impairment for the distinctive properties of non-living things as well, although this is much milder for JBR (84%, and only a little below the control range); (iii) preservation of shared information for animals, vehicles, and tools, with accuracy still well within the normal range for both JBR and just below for RC.

In contrast, none of the patients showed a difference in accuracy of responses for perceptual as compared to functional properties, either for animals or for vehicles ($p > .05$ in all $\chi^2$ tests). The sensory–functional theory suggests that deficits for living things are associated with greater loss of perceptual semantic properties because these are crucial for distinguishing among members of living things categories, such as animals. This prediction was not supported by these results.

We turn now to the one patient who did not show the selective deficit for distinctive properties of animals relative to vehicles in the current analyses. Unlike the other four, JH did not show a significant reduction in accuracy for animals relative to the combined non-living categories $\chi^2 = 1.8, p > .1$). Inspection of Figure 5.7 shows that this is because of her low score for the distinctive properties of tools (63%), which is no different to that for animals (57%, $\chi^2 < 1$). In contrast, she was accurate on the distinctive properties of vehicles (79%; vehicles versus animals, $\chi^2 = 3.06, p < .1$). We believe that this anomalous effect may be due to the specific circumstances of this patient, who was only 16 years old when she was taken ill with HSE and is now densely amnesic. It is likely that she is less familiar with some of the items in the tools category than the normal adult population (e.g. “axe”, “chisel”, “saw”, “hammer”).

Figure 5.7 also reveals a discrepancy between the two non-living categories
Figure 5.7. Percentage correct verification responses for shared and distinctive properties of animals, tools, and vehicles for control subjects and five HSE patients.
for patient, RC. In this case, the combined score for the distinctive properties of non-living things is significantly higher than that for animals, but it is clear that this effect is largely due to the category of tools (68% correct), while his scores for the distinctive properties of vehicles are really no better than for those of animals (50% versus 40%, respectively; $\chi^2<1$). This difference is consistent with the results of our property generation study, which suggested that tools are more typical of the non-living domain than are vehicles, in that they have fewer properties with more highly distinctive form–function correlations. Vehicles pattern with living things in some ways, because the correlated properties are not as distinctive. This may be the basis for RC’s scores in the property knowledge task. We know from earlier studies that he has extensive damage to the semantic system, which primarily affects weakly correlated properties. In the current task, this leads to a deficit for the distinctive properties of vehicles as well as of animals. Nevertheless, the distinctive properties of vehicles are still somewhat more strongly correlated that those of animals, and so they are less vulnerable to loss in the more mildly impaired patients (SE, MW, and JBR).

GENERAL DISCUSSION

In this chapter we have given an overview of how the conceptual structure account of semantic representation explains category-specific deficits for living and non-living things. We have presented supporting data for the account, in terms of: (i) computational simulations of the predicted interactions of random damage and conceptual structure; (ii) distributional analyses of large-scale property generation norms that support the theoretical claims concerning the structure of concepts in the different domains; (iii) neuropsychological data from previously reported studies; and (iv) data from five HSE patients with living things deficits on a new property knowledge task that contrasts distinctive and shared properties across the domains. These studies show that the patients with living things deficits have disproportionate loss of distinctive properties of animals relative to non-living things, while knowledge of shared properties remains intact. Finally, a series of neuroimaging studies recently carried out in our laboratory provides a different kind of support for our account. In recent PET and fMRI studies, in which subjects carried out lexical decision and semantic categorisation tasks for sets of living and non-living things, closely matched according to familiarity, concreteness and length, we have found that there is activation of a large conceptual network for semantic tasks relative to baseline (e.g. letter detection or classification) with activation primarily in the left hemisphere involving the inferior and middle temporal gyri and the temporal pole. In none of these studies do we find any evidence of regional specialisation as a function of the living/non-living distinction or specific categories within those
domains, including animals, fruit, tools, and vehicles, that is, there are no activations specific to either domain or category that reach significance when appropriately corrected for multiple comparisons (Devlin et al., 2000, 2002).

At this stage, the conceptual structure account is still a theory in development. We are currently working on a larger scale computational model, using the sets of properties generated for each concept in our property generation study as the basis for the conceptual representations. This will allow us to investigate the effects of damage in a more realistic model. We will also be able to compare the effects of damage on the individual categories within the broad domains of living and non-living things. The property norms suggest that categories within domains differ in important ways and this should lead to different patterns of damage in our model. Predictions will then be tested against the behavioural data of the neuropsychological patients in studies where theoretically important properties of carefully matched concepts in each category are contrasted. Future developments will also involve taking additional variables into account. Our current model includes the variables of distinctiveness and correlation, but we know from the psychological literature that there are other ways in which properties differ that may also be important determinants of conceptual structure—such as salience and of degree context-dependence (Barsalou, 1983; Medin & Shoben, 1988;). Similarly there are ways in which the concepts themselves differ, which we have not yet taken into account but that no doubt play an important part. For example, although it seems that the familiarity of concepts cannot be the full explanation of category-specific deficits, it is certainly the case that familiarity is an important additional variable, with the most familiar concepts in any category almost always the most likely to be preserved (Funnel & Sheridan, 1992; Stewart, Parkin, & Hunkin, 1992). Therefore, it is important to implement this variable in a complete model.

Finally, we acknowledge that our model in its current stage of development does not account for every patient with a deficit for living or non-living things reported in the literature. It is possible that some of these patterns will be more tractable to our model when we have developed it further along the lines described above. It is also worth noting that none of the other well-known alternative models provides a satisfactory model of the entire spectrum of neuropsychological data. For example, as we discussed above, we predict that artefact deficits will be associated with severe rather than mild deficits. There are at least two patients who seem to contradict this prediction, CW (Sacchett & Humphreys, 1992) and JJ (Hillis & Caramazza, 1991). But it is not only the conceptual structure account that runs into difficulty here. Patient JJ presents problems for the domain-specific account in which separate neural systems support each domain of knowledge; he has a deficit for artefacts, but is reported to have a left temporal lobe infarct, outside the "frontoparietal" region, which has frequently been claimed to be associated
with the representation of artefact concepts. Moreover, JJ’s deficit did not only extend to artefacts, but also to fruit and vegetables (effectively an isolated sparing of animal knowledge). This would imply a lesion to two separate semantic systems on the domain-specific account (one for plant life and the other for artefacts). Similarly, on the sensory–functional account, JJ would presumably be interpreted as having a deficit for functional information (resulting in the problem for artefacts) as well as for sensory information (resulting in the problem for fruit and vegetables), in which case it is not clear what kind of property knowledge would be intact to support his good knowledge of animals.

In summary, although there are many challenges to address, our research so far suggests that it might not be necessary to propose separate domain-based or property-based stores within semantic memory to account for selective semantic deficits, and that an approach that emphasises the structure of concepts in different domains and categories of knowledge provides a promising framework for future explorations.

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