A central question in psychology concerns how knowledge is represented and organized in the brain. Researchers examine the contents and representation of information "in" semantic memory and distinguish this type of knowledge from other types of knowledge, such as autobiographical memory (e.g., Tulving, 1985). Semantic memory consists of knowledge about the world, such as what we know about animals, negotiating, tools, clothing, cooking, furniture, etc. Several avenues of research bear directly on the issues of representation and organization of semantic knowledge, including results with nonbrain-damaged individuals, children, and brain-damaged populations. Our intent in this chapter is to provide an overview of the issues currently being addressed and to relate relevant results to our understanding of the neural organization of knowledge.

Perhaps the most intriguing results come from the neuropsychological literature. As the result of brain damage, some patients show specific problems with certain types of semantic categories, such as selective impairment to knowledge about animals, or plant life, or artefacts (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). Patients JJ and PS, reported by Hillis and Caramazza (1991), illustrate this type of deficit. JJ suffered a stroke when he was in his late sixties, resulting in damage to the left temporal lobe and basal ganglia. PS sustained a severe blow to the head when he was in his middle forties, resulting in damage to a large area of the left temporal lobe, and smaller areas of the right temporal and frontal lobes. Both patients showed disproportionate difficulties naming and understanding certain categories of items relative to other categories of items. For example, JJ named line-drawings of animals very well (42 out of 46 = 91% correct) but performed quite poorly on all other categories (20 out of 98 = 21% correct). In contrast, PS had significant problems naming line-drawings of animals (18 out of 46 = 39% correct) and vegetables (3 out of 12 = 25% correct) but performed quite well on all other categories (32 out of 86 = 38% correct). A comparison of their ability to provide definitions for items within the animal and the nonanimal categories further demonstrates their selective difficulties in naming and understanding living (PS) or nonliving (JJ) concepts:

\[\text{We refer to all living things (i.e., animals and plants, including fruits and vegetables) as living items and the animal subset as animate items.}\]
JJ: lion: a large animal, about 4 feet tall, maybe taller at the shoulders, it has a long body and very large paws and stands on all four legs. It has a monstrous head with which it grows; and it has a mane—a large body of hair. It lives in Africa.

melon: I'm not sure. It's a fruit, a soft material. I don't remember if it is yellow or green or orange. I've forgotten too many things.

PS: heron: a fish

apricot: like a peach, only smaller. You can buy them canned or dried or fresh.

As these cases illustrate, brain injured patients may show selective problems with certain categories of items but not others, and this observation has now been established in a large number of patients (see Forde & Humphreys, 1999; Gainotti, Silveri, Daniele, & Guistoli, 1995; Shelton & Caramazza, 1999; for reviews). The fact that damage to certain areas of the brain can result in problems restricted to some domains of knowledge but not others could lead to the remarkable conclusion that different domains of knowledge are organized in different areas of the brain. While it has long been known that different areas of the brain are responsible for different functions (e.g., motor, vision, audition, etc.), the idea that brain areas might be dedicated to specific knowledge domains remains controversial.

We begin this chapter by discussing whether true category-specific knowledge effects exist in brain-damaged populations or whether the effects emerge merely because of processing difficulty as measured by variables such as familiarity and visual complexity. The "processing difficulty" hypothesis was proposed to explain the disproportionate number of cases reported who have deficits with living things, since living things tend to be less familiar and more visually complex (e.g., Funnell & Sheridan, 1992; Gaffan & Heywood, 1993). We will show that although it is likely that at least some of the reported cases may not be true category-specific deficits, but rather reflect greater processing difficulty with living things, not all reported cases of category-specific deficits can be explained by processing difficulty. We will argue that a category-specific deficit is a true effect for many of the reported cases.

We then present three types of theories of semantic memory: modality-specific theories, feature-intercorrelation theories, and domain-specific theories. The first two theories do not allow for semantic organization according to categorical knowledge and explain category-specific effects as emerging from the properties by which semantic knowledge is organized. By contrast, the domain-specific theory suggests that knowledge is broadly organized into specific knowledge domains, i.e., that certain brain areas are dedicated to the processing of specific domains of knowledge.

Modality-specific theories suggest that semantic knowledge is organized into perceptual and nonperceptual information that is differentially important for certain categories of knowledge such that damage to a specific type of knowledge (e.g., perceptual knowledge) will necessarily result in deficits to those categories of items for which that knowledge is critical (e.g., some have hypothesized that perceptual knowledge is crucial for the understanding of living things). For example, damage to the brain areas in which perceptual knowledge is represented will result in disproportionate difficulty with living things (and any other category for which perceptual information is important). Although various results in patient studies, computer modeling, and normal studies, were initially interpreted to provide support for the sensory/functional theory, recent work reveals weaknesses in the data cited in support of the theory as well as limitations of the theory in explaining a number of empirical facts.

Feature intercorrelation theories provide an alternative framework for the organization of semantic memory. Although specific theories differ in detail, the general idea is that certain properties of items are shared (are intercorrelated) among members of a given category and that members of the living things category tend to share more common properties than members of artefact categories. Properties that are highly correlated are hypothesized to be clustered together in the brain, and therefore, damage to a certain brain area can result in damage to categories for which these properties are important. Because living things tend to
share more common properties, items from the living things category are more likely to be damaged together. Different variations of this general idea will be discussed, along with computational models that have been developed to account for the patient data from lesion studies and also from studies of category-specific effects in dementia. Although these types of theories can account for a range of reported results, they too fail to capture certain aspects of the data.

A final class of theory proposes that specific areas of the brain are dedicated to the processing of evolutionarily important domains of knowledge (e.g., animals and plant life). According to this hypothesis, category-specific effects arise from damage to those brain areas which are important for the processing of certain domains of knowledge. This theory offers a broad organizational scheme that can accommodate the relevant data reported thus far. However, the theory is silent as to the way in which knowledge is organized within domains.

We hasten to point out that although these three classes of theories are distinct in the ways in which knowledge is thought to be organized, they need not be mutually exclusive. There are likely to be many levels of organization of semantic knowledge in the brain such that a broad distinction such as biological versus nonbiological domains does not preclude a more fine-grained organization at a specific level of knowledge. For example, we can ask whether or not there is further structure within the category of biological concepts (and we will later show that we must distinguish between animate and inanimate biological objects). We can then ask whether there is further structure within the category of animate items and if so, what might be its organizational principles (e.g., perhaps intercorrelations between properties play an important role in organizing knowledge at a more detailed level). Therefore, the hypothesis of domain-specific knowledge organization provides a general scheme of organization but does not imply necessarily a categorical structure at more detailed levels of organization.

In the final section of the chapter we will discuss findings from lesion and neuroimaging studies in an attempt to outline what brain areas might be important in processing semantic memory, in general, and certain types or categories of information, more specifically. Results from these studies can provide additional information regarding the organization of semantic categories in the brain.

ARE THERE TRUE CATEGORY-SPECIFIC DEFICITS?

In the early 1990s, researchers questioned whether deficits to specific categories of knowledge were true category effects or whether they emerged merely from the influence of familiarity, frequency, visual complexity, or a combination of these factors (e.g., Funnell & Sheridan, 1992; Gaffan & Heywood, 1993; Stewart, Parkin, & Hunkin, 1992). Most patients reported to show category-specific effects have had deficits to knowledge of animals and living things (e.g., see Forde & Humphreys, 1999, for review). Funnell and Sheridan (1992) demonstrated that item familiarity (as determined by familiarity ratings provided by normal subjects from the Snodgrass & Vanderwart, 1980, picture set) had a strong influence on naming performance in their patient, SL. In fact, when items in living and nonliving categories were matched on familiarity, the previously demonstrated "category-specific" effect found with SL was no longer statistically reliable (see Table 17.1).

Stewart et al. (1992) reported similar results: Their patient, HO, demonstrated a strong effect of category in picture naming, with living things being named at a much lower rate than nonliving things (see Table 17.1). However, when items were matched on familiarity, word frequency, and the visual complexity of the picture, the category effect was no longer obtained (see Table 17.1).

In general, living things tend to be more difficult to process for non-brain-damaged subjects. Capitani, Laiacoma, Barbarotto, and Trivelli (1994) demonstrated that both normal elderly subjects and normal young subjects had greater difficulty answering questions about living things than nonliving things, even when the items on which knowledge was assessed were
Table 17.1
Effects of Processing Difficulty on Performance (Proportion Correct)

Funnell & Sheridan, 1992: Patient SL

<table>
<thead>
<tr>
<th>Experiment 1: Naming of Low-Frequency Items</th>
<th>Living</th>
<th>Nonliving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2/16 (.13)</td>
<td>14/26 (.54)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experiment 2: Naming of Items Matched on Frequency and Familiarity</th>
<th>Living</th>
<th>Nonliving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>16/34 (.47)</td>
<td>12/34 (.36)</td>
</tr>
</tbody>
</table>

Stewart, Parkin & Hunkin, 1992: Patient HO

<table>
<thead>
<tr>
<th>Experiment 1: Naming of Items Matched on Frequency</th>
<th>Living</th>
<th>Nonliving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>18/43 (.43)</td>
<td>40/50 (.80)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experiment 2: Naming of Items Matched on Frequency, Familiarity, and Complexity</th>
<th>Living</th>
<th>Nonliving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15/38 (.42)</td>
<td>13/36 (.36)</td>
</tr>
</tbody>
</table>

matched for prototypicality, familiarity, and frequency. Gaffan and Heywood (1993) also demonstrated a difference between processing of living and nonliving things, with living things being harder to visually discriminate than nonliving things. These results all suggest that the so-called category-specific impairment for animals or living things may actually be the result of a greater overall difficulty with these items, due to their greater visual complexity and lower familiarity.

Not all cases of category-specific effects can be explained in this manner, however. For example, there are patients who demonstrate greater difficulty with nonliving things, the “easier,” “more familiar” category. As discussed in the introduction, two cases, PS and JJ, showed similar overall levels of performance but contrasting effects of category (Hillis & Caramazza, 1991; also see Table 17.6 for further comparison of performance). PS had the greatest difficulty naming and defining living things, whereas JJ had the greatest difficulty naming and defining nonliving things. If the effect were just one of difficulty due to factors such as familiarity and visual complexity, we would not expect patients to show a greater difficulty with nonliving things (see also, Cappa, Frugoni, Pasquali, Perani, & Zorat, 1998; Sacchetti & Humphreys, 1992; Warrington & McCarthy, 1983, 1987).

Moreover, recent results demonstrate that some patients show category-specific effects even after items have been matched in terms of processing difficulty. For example, our patient EW demonstrated a significant naming and comprehension problem for animals but normal naming and comprehension of nonanimals (Caramazza & Shelton, 1998), even after items were matched for frequency and familiarity (see Table 2): naming animals: 33%–55%, naming nonanimals: 67%–94%. For comprehension, we matched knowledge of items (and the items

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1In this study, items were matched for familiarity but the probe knowledge was not.

2For picture naming, items were taken from the set used by Funnell & Sheridan (1992) which were not matched on visual complexity. However, visual complexity is not important when testing comprehension using sentence verification, since pictures are not used as stimuli. In these tasks, EW (and several other patients) demonstrate category-specific effects for items matched on familiarity and frequency.
themselves) on familiarity by having elderly control subjects rate how familiar they were with each question asked about an item. For example, questions such as “does a giraffe live on land?” and “does a robin have 4 legs” were given to the elderly subjects and they had to answer the question and then rate how familiar this information was to them. After gathering this information, we matched items in the animal and nonanimal categories and examined EW’s performance (see Table 17.2). She still performed poorly with animals and normally with nonanimals. Many other reports have recently demonstrated that after controlling for processing difficulty, patients still show category-specific deficits (e.g., Farah, Meyer, & McMullen, 1996; Gainotti & Silveri, 1996; Hart & Gordon, 1992; Kurbat, 1997; Laiacoana, Barbarotto & Capitani, 1993; Laiacoana, Capitani, & Barbarotto, 1997; Moss, Tyler, Durrant-Pestfield, & Bunn, 1998; Sheridan & Humphreys, 1993).

However, a recent finding reported by Capitani, Laiacoana, and Barbarotto (1999) raises questions concerning the appropriateness of using only familiarity ratings as a means for equating different semantic categories. They found that gender influenced semantic fluency, with males outperforming females on tools and females outperforming males on fruits. No other significant gender differences between categories emerged. Also, Capitani, Albanese, Barbarotto, and Laiacoana (1999) found that females rate living categories as more familiar than males, and there was no difference between nonliving categories (see also Laiacoana, Barbarotto, & Capitani, 1998). However, when reanalyzing two previously-reported cases of category-specific effects, one female who performed best with living things and one male who performed best with nonliving things, Capitani et al. (1999) found that category-specific effects were still present after controlling for gender-specific familiarity ratings. Thus, gender differences do not necessarily invalidate category-specific effects.

Although Capitani et al. (in press) demonstrated that gender can have an influence on performance with specific categories, there is still an abundance of evidence to suggest that once processing difficulty is matched between categories, patients may still demonstrate category-specific effects. And, there is the contrasting effect of worse performance for inanimate items as compared to animate items, which cannot be explained by processing difficulty.

We conclude then that at least some patients do show true category-specific effects, although we will argue below that this is especially difficult to establish in some of the early published cases in which processing difficulty was not controlled. We will also argue that processing difficulty (i.e., familiarity) very likely influenced certain results regarding performance on different types of information (sensory vs. nonsensory information) within categories.

<table>
<thead>
<tr>
<th>Table 17.2</th>
<th>Categorical Effects for items Matched on Processing Difficulty (Proportion Correct)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Caramazza &amp; Shelton, 1998: Patient EW</td>
</tr>
<tr>
<td>Naming</td>
<td>Animate</td>
</tr>
<tr>
<td>High-familiarity</td>
<td>6/11 (.54)</td>
</tr>
<tr>
<td>Low Familiarity</td>
<td>10/36 (.29)</td>
</tr>
<tr>
<td>Comprehension (items and attributes matched on familiarity)</td>
<td>Animate</td>
</tr>
<tr>
<td></td>
<td>425/601 (.71)</td>
</tr>
</tbody>
</table>
IS SEMANTIC INFORMATION REPRESENTED AND ORGANIZED ACCORDING TO SENSORY MODALITIES OF KNOWLEDGE?

In this section we discuss results from three areas of work that are taken as support for the modality-specific knowledge theories: patient studies, computational modeling, and studies of priming effects in normal subjects. We then present criticisms and challenges to the data and raise questions regarding theoretical issues, concluding there is little support from these data for modality-specific knowledge organization.

A prevalent idea concerning the representation of knowledge is that information is distinguished according to modality of information—that is, the brain segregates information according to the type of information (e.g., perceptual or nonperceptual) represented. This type of scheme has been proposed by a number of authors (e.g., Allport, 1985; Farah & McGlone, 1991; Warrington & McCarthy, 1983, 1987; Warrington & Shallice, 1984). In fact, Allport (1985) outlined a model of semantic memory in which each type of sensory information was represented in separately organized but connected “nodes.” In his model, information belongs to a certain node depending on the content of that information: action-oriented elements, kinesthetic elements, visual elements, tactile elements, auditory elements. Thus, information about an object is represented in a distributed fashion throughout the brain depending on the modality of information.

Warrington and Shallice (1984) provided the first well documented evidence of category-specific processing deficits in four patients suffering from brain-damage. The two patients studied most in depth, JBR and SBY, showed dramatic differences in naming, defining, and comprehending concepts associated with different natural categories. Examples of their definitions include:

JBR: tent: temporary outhouse, living home
   briefcase: small case used by students to carry papers
   daffodil: plant
   snail: insect animal

SBY: towel: material used to dry people
   submarine: ship that goes underneath sea
   wasp: bird that flies
   holly: what you drink

The difference in performance for living and nonliving items was quite striking: SBY identified or defined 75% (36 out of 48) of nonliving things but no living things and JBR identified or defined 94% (45 out of 48) of nonliving things but only 4% (2 out of 48) of living things. However, these category-specific effects did not honor strict category boundaries (i.e., a living/nonliving dichotomy). JBR was impaired not only on living things but also on items in categories such as musical instruments, gemstones, metals, fabrics, and foods (see Table 17.3). Other patients have also been reported to have problems with categories falling outside the natural boundaries of the living/nonliving distinction and include associations between deficits to animals and foods (e.g., De Renzi & Lucchelli, 1994; Sheridan & Humphreys, 1993; Silveri & Gainotti, 1988) and living things and musical instruments (e.g., Silveri & Gainotti, 1988).

The co-occurrence of damage to multiple categories that do not respect category boundaries was taken to support the view that semantic knowledge is organized according to modality (or type) of information. Warrington and colleagues (Warrington & McCarthy, 1983; 1987; Warrington & Shallice, 1984) argued that category-specific effects result from damage to a particular type of knowledge—either perceptual or nonperceptual knowledge. They argued that

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4 We refer to the distinction as perceptual and nonperceptual, which was the initial hypothesis. However, the terms “visual” versus “functional” came to be shorthand terms for this distinction, and Warrington and colleagues tend to support the notion that the distinction between visual and functional information is the most important.
perceptual attributes are especially important for identification and understanding of living things whereas nonperceptual attributes are especially important for identification and understanding of nonliving things. There is an association of deficits to categories outside the living/nonliving distinction, then, because those categories also have a strong emphasis on perceptual information. So, for example, perceptual properties are hypothesized to be important chiefly for understanding living things, foods, and musical instruments, and when damage occurs to those brain areas that important for processing perceptual information, category-specific effects can emerge.

This interpretation of category-specific effects makes the prediction that damage to perceptual properties should result in damage to any category that is strongly defined by these properties. A second prediction is that patients should have disproportionate difficulty with questions regarding the damaged information; that is, a co-occurrence of category-specific and modality-specific deficits. A third prediction is based on an additional, common assumption of the modality specific semantics hypothesis. The assumption is that perceptual and nonperceptual semantic subsystems are interdependent (see Farah & McClelland, 1991). This interdependence is such that for concepts composed largely of perceptual features, nonperceptual information is negatively affected by damage to the perceptual semantic system. Additionally, in a complementary manner, for concepts composed largely of nonperceptual features, the nonperceptual features provide support to the damaged perceptual features. On this basis, we should expect that (a) although there should be some detriment in performance with perceptual information across all categories, those categories that are defined primarily by nonperceptual information should show less difficulties with perceptual information and (b) there should be an additional detriment in performance with nonperceptual information for those categories that depend strongly on perceptual information. Thus the third prediction of the modality specific semantics hypothesis is that we should observe a modality by category interaction when all appropriate conditions are tested.

As mentioned earlier, cases were reported to show deficits to associated categories for which perceptual information is hypothesized to be most important (and conversely, for associated categories for which nonperceptual information is most important, e.g., Warrington & McCarthy, 1983, 1987). Moreover, patients were reported to show the expected impairment in performance with the critical information associated with the damaged categories, (i.e., a co-occurrence...
rence of category and modality-specific deficits; e.g., Basso, Capitani, & Laiacoma, 1988; Farah, Hammond, Mehta, & Ratcliff, 1989; Hart & Gordon, 1992; Sartori & Job, 1988; Silveri & Gainotti, 1988). For example, Silveri and Gainotti demonstrated that their patient, LA, was impaired in regard to living things as compared to nonliving things (e.g., 20% vs. 79%, respectively) and was more impaired with visual than nonvisual information associated with living things (9% vs. 58%, respectively), the predicted co-occurrence of category and modality-specific deficits. Thus, initially there appeared to be independent support for the idea that category-specific effects emerged from damage to a type of information that is disproportionately important for some categories than others.

Category-Specific Knowledge deficits Fail to Support the Modality-Specific Theory

A careful examination of patient performance and careful balancing between processing difficulty of information probed within categories reveals little support for the modality-specific interpretation of category-specific knowledge deficits. The first prediction of the theory—that damage to perceptual or nonperceptual properties should result in damage to those categories most reliant on these properties—has been disconfirmed. Patients have been reported who show deficits to a subset of the living items category—animals only—and the effects are not due to influences of familiarity and frequency (e.g., Caramazza & Shelton, 1998; Hart & Gordon, 1992; Hillis & Caramazza, 1991). Moreover, these patients do not show problems with the expected associated categories such as musical instruments or foods. For example, our patient described above, KW, had a selective deficit affecting animals only and performed normally on items in the fruits and vegetables category, other food stuff, and musical instruments. Other patients have been reported to have difficulties with only fruits and vegetables (e.g., Farah & Wallace, 1992; Hart, Berndt, & Caramazza, 1985) or only body parts (e.g., Goodglass, Klein, Carey, & Jones, 1968; Semenza & Goodglass, 1988, see also Shelton, Pouch, & Caramazza, 1998; for selective sparing of body parts).

Also, several patients have been reported to have difficulty processing visual information without having any category-specific processing deficits (e.g., Coltheart et al., 1988; Lambon-Ralph, Howard, Nightingale, & Ellis, 1998). For example, Lambon-Ralph et al. presented the case of IW, who showed significant problems processing visual information but no associated category-specific deficit in name comprehension. As shown in Table 17.4, IW performed significantly worse when asked to select the name (from 5 choices) when given perceptual information as compared to selecting the name when given nonperceptual information, but no associated category effect was observed. IW was also much better with nonperceptual information when asked questions about items and provided much more nonperceptual information when asked to define items. On none of these tasks did she show category-specific effects; that is, she performed equally with living and nonliving items.

### Table 17.4
Deficit to Visual Knowledge without a Corresponding Living Things Deficit (Proportion Correct)

<table>
<thead>
<tr>
<th></th>
<th>Perceptual Definition</th>
<th>Nonperceptual Definition</th>
<th>Total</th>
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</thead>
<tbody>
<tr>
<td><strong>Animals</strong></td>
<td>8/16 (.50)</td>
<td>13/16 (.81)</td>
<td>21/32 (.66)</td>
</tr>
<tr>
<td><strong>Artefacts</strong></td>
<td>5/12 (.42)</td>
<td>9/12 (.75)</td>
<td>14/24 (.58)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>13/28 (.46)</td>
<td>22/28 (.79)</td>
<td></td>
</tr>
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</table>
These cases pose a strong challenge to the first prediction from the sensory/non-sensory hypothesis of semantic knowledge organization. We argued previously (Caramazza & Shelton, 1998) that the associated patterns of category impairments (e.g., living things and musical instruments) reported in the early studies may have reflected influences of familiarity (either instead of or in addition to deficits to a specific category). Thus, when familiarity and other factors are controlled, deficits to associated categories disappear (see Bunn, Tyler, & Moss, 1998 for a demonstration of this with the classic patient JBR).

The Influence of Familiarity on Processing Visual Information about Animals

The second prediction of the modality-specific theory, that category and modality-specific deficits should co-occur and, ultimately, that there should be a category X modality interaction, has not been found when the familiarity of the stimuli was controlled. Stewart et al. (1992) demonstrated that normal subjects were significantly slower in verifying visual/perceptual attributes than nonperceptual attributes of living things. They argued this demonstrates that perceptual attributes of living things are less familiar than their nonperceptual attributes (Experiment 5). As shown in Table 17.5, their patient, HO, performed much worse on a naming-to-definition task with perceptual than nonperceptual information; however, when visual and nonvisual judgments were matched for familiarity, the difference in performance disappeared (Experiment 6). Stewart et al. clearly demonstrated that their patient's putative category-specific deficit and expected patterns of performance predicted by the modality-specific semantics hypothesis emerged solely because of the influence of familiarity on HO's performance. This result raises questions regarding the findings reported for cases in which the stimuli used were not controlled for familiarity, a problem associated with many of the early reports of category-specific effects.

In recent years, researchers have controlled for familiarity in their stimuli and have assessed

| Table 17.5 |
| Performance on Perceptual and Nonperceptual Attributes |

<table>
<thead>
<tr>
<th></th>
<th>Perceptual</th>
<th>Nonperceptual</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stewart et al., 1992 Patient HO</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experiment 5 (items NOT matched on familiarity)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Naming to definition (proportion correct)</td>
<td>46%</td>
<td>79%</td>
</tr>
<tr>
<td>HO</td>
<td>76%</td>
<td>99%</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reaction times for control subjects verifying perceptual and nonperceptual statements</th>
<th>Perceptual</th>
<th>Nonperceptual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perceptual 1769 ms</td>
<td>1699 ms</td>
<td></td>
</tr>
<tr>
<td>Experiment 6: (items matched on familiarity; proportion correct)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perceptual 27/32 (.84)</td>
<td>26/32 (.81)</td>
<td></td>
</tr>
<tr>
<td>Nonperceptual</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Caramazza & Shelton, 1998: Patient EW |            |               |
| Performance on perceptual and nonperceptual attribute questions | Perceptual | Nonperceptual |
| Animate 202/301 (.67) | 223/300 (.74) |            |               |
| Inanimate 217/236 (.96) | 217/219 (.99) |            |               |

*Note. Error rates for reaction time data were very low (< 1%)*
the expectation of a co-occurrence of category and modality-specific deficits and a category by modality interaction (e.g., Caramazza & Shelton, 1998; Laiacena et al., 1997; Lambon-Ralph et al., 1998; Sheridan & Humphreys, 1992). For example, our patient EW was tested on a very large number of items and attributes matched on familiarity. Questions about perceptual and nonperceptual attributes were matched on familiarity by having elderly control subjects rate how familiar they were with the information being asked in each question. EW showed no difference in performance with perceptual and nonperceptual attributes of animals, and no difficulty in performance with perceptual attributes of nonanimals (see Table 17.5). That is, contrary to the predictions derived from the modality-specific semantic hypothesis, EW showed only a main effect of category and no interaction between category and modality.

The recent results from patients with category-specific effects cast strong doubt on the original interpretations of the co-occurrence of modality-and category-specific deficits, reported in the early studies of patients with category-specific deficits. Thus, there now appears to be little support from the neurological literature to suggest that semantic knowledge is organized according to modality of information—specifically, along a perceptual/nonperceptual dichotomy. However, there are other areas of research cited in support of modality-specific semantic organization of knowledge, which we now evaluate to determine the support these data provide for modality-specific theories of semantic knowledge organization.

Computational Models of Modality-Specific Semantics and Problems with the Underlying Assumptions of the Models

Farah and McClelland (1991) developed a computer model of semantic memory in which perceptual ("visual") and nonperceptual ("functional") information is represented in separate but interconnected networks. An item was represented by the sum of its features, and to accommodate the assumption that is necessary for a modality-specific theory to account for category-specific effects, living items had a large number of perceptual features and nonliving items had a large number of functional features. The ratio of visual and functional features for living and nonliving items was determined empirically by having subjects classify information in the dictionary definition of each item as either visual ("what it looks like") or functional ("what it is used for"). Based on these data, the ratio of visual to functional features was set to 16.1:2.1 for living things and 9.4:6.7 for nonliving things. Because the model is interactive, when visual information is activated, functional features related to that item are activated as well and vice versa. Farah and McClelland (1991) damaged the perceptual network and found that damage to visual features resulted in worse performance on living things. Thus, if visual features are more numerous for living things, damage to these features will result in difficulties with living things.

However, Caramazza and Shelton (1998) argued that there was little empirical support for the notion that certain categories of items rely more heavily on perceptual attributes for identification, and questioned the results obtained by Farah and McClelland (1991) regarding the ratios of perceptual and nonperceptual knowledge for living and nonliving things. In Farah and McClelland's study, subjects were instructed to identify nonsensory properties on only one dimension, their function ("what it is for"), which omits such important nonsensory information concerning what an animal might eat, where it lives, how it reproduces, how it moves, etc. However, this is the exact information that is termed "functional" information in studies examining category-specific deficits. Using the exact stimuli and definitions as Farah and McClelland, we asked subjects to identify either sensory properties or nonsensory properties (i.e., not limiting nonsensory properties to only functional information). When we changed the

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8This dimension of the model makes the prediction that there should be a category-by-modality interaction, which we have already argued is not found in patients with category-specific deficits.
instructions to include all nonsensory information, the resulting sensory to nonsensory attribute ratios were 2.9:2.5 for living things and 2.2:3.3 for nonliving things. Thus, there is little evidence of a strong bias of sensory attributes for living things if we include all nonsensory information from the definitions. Given these ratios, a model of the structure proposed by Farah and McClelland cannot produce category-specific effects if damage were restricted either to sensory or nonsensory attribute knowledge.

Similar results have been found by McRae, de Sar, & Seidenberg et al. (1997). In their study, 300 subjects listed features of items that referred to physical properties, functional properties and encyclopedic facts. The results demonstrated that the frequency of functional features was much greater for nonliving things but that the overall number of physical properties was quite similar between the two categories. And, encyclopedic information was equally frequent for living and nonliving things. Taken together, the results from these two studies suggest that the intuition first proposed by Warrington and colleagues regarding the importance of physical properties for our understanding of certain categories, especially living things, has little empirical support. Without this assumption, it is unclear exactly how a modality-specific theory of semantics could account for category-specific deficits.

Normal Studies of Semantic Priming: Tests of the Modality-Specific Hypothesis

With regard to studies of normal populations, proponents of modality-specific semantics have argued that support for this theory comes from semantic priming studies reported by Flores d'Arcis, Schreuder, and Glazenberg (1985) and Schreuder, Flores d'Arcis, and Glazenberg (1984). In these studies, priming effects were examined for word pairs that shared a perceptual dimension but were not conceptually related. For example, PAINTBRUSH and CARROT are visually similar in shape and contour but do not share any meaning with regard to function or natural category. The authors hypothesized that if information is organized/represented only by modality (i.e., is distributed according to type of information), priming should obtain for word pairs that are perceptually similar but are not conceptually related. In fact, this is what they found and they proposed a model of semantic memory in which information is organized into perceptual and nonperceptual subsystems.

However, a recent study suggests that methodological problems with the experiments by Schreuder et al. (1984) and Flores d'Arcis et al. (1985) may have been responsible for the effects reported by those authors. When the experiments are conducted properly, there is no evidence of priming for perceptually related, conceptually unrelated word pairs (e.g., paintbrush-carrot). Pecher, Zeelenberg, and Raaijimakers (1998) re-examined priming for perceptually related (e.g., pizza-coin) and conceptually related (e.g., pizza-hotdog) items. In the earlier studies by Flores d'Arcais and colleagues, target items were presented four times, once in each condition, to a single subject and the prime remained on the screen while the target was presented for either lexical decision or naming. Pecher et al. (1988) argue that under these conditions subjects are made overly aware of the perceptual relationships between the prime and target and may use this information to perform the task. Pecher et al. corrected these methodological problems and found no evidence of priming for perceptually-related word pairs and only found priming for conceptually related word pairs.

Conclusion: Little Support for Modality-Specific Theories and Problems Defining Perceptual and Nonperceptual Knowledge

It appears then that there is little support from any sector for the division of semantic knowledge on the basis of modality. Early support for this distinction, which came from several areas of research, has been shown to suffer from methodological problems. Moreover, the specific
predictions made by theories which suggest that knowledge is organized according to sensory/non-sensory information have not been upheld. Reports of patients who show selective deficits to narrow categories of knowledge and show the same pattern of performance for types of knowledge within the spared and impaired categories pose great challenges to modality-specific theories of semantic memory.

Moreover, the theory is vague as to how semantic memory is organized and how properties of items become differentiated between perceptual and nonperceptual information. How do we determine if something is a perceptual or a nonperceptual feature? Why are the features of a horse such as “four legs,” “mane,” or “tail” considered perceptual features but “runs fast,” or “is ridden” considered nonperceptual features? What is it about each of those features that makes them one type of feature and not the other, especially since they can both be experienced only perceptually, only through nonperceptual input, or both ways? For example, if we have never seen a certain type of animal (e.g., wombot) we may still know many things about it that are perceptual (e.g., color, shape, size) and nonperceptual (e.g., where it lives, what it eats, how it reproduces). How does each of these specific types of information get encoded properly? The same questions can be asked about learning the functionality of objects. We often learn to use items by watching someone else use them (e.g., forklift) yet this information is not coded with perceptual information but rather with nonperceptual information. The idea of a perceptual/nonperceptual knowledge distinction can only be useful if we establish exactly what is meant by these terms and how knowledge is acquired and organized based on this distinction.

Having shown that modality-specific semantic theories suffer from a number of problems that limit their usefulness, we turn now to consider another type of feature-based theory of semantic memory.

IS SEMANTIC KNOWLEDGE ORGANIZED BY INTERCORRELATIONS AMONG FEATURES?

In this section, we discuss studies of category-specific effects in dementia, a disease that often results in diffuse brain damage, as well as studies of category-specific effects in stroke and other instances of trauma. We also discuss attempts at developing feature-based computer models of semantic memory, their usefulness in explaining category-specific effects, and the problems with these approaches. We conclude that feature-based theories provide a better means of capturing some aspects of the neuropsychological data but there are still limitations.

The Development of Computerized Models and Initial Support from Patients with Dementia

Studies have shown that there are systematic relationships among properties of members of a category (a “natural” category such as animals, furniture, vehicles, flowers). For example, Malt and Smith (1984) had subjects rate properties as belonging to a certain category (e.g., if beak was related to bird) and found that within categories, properties tended to correlate. Within the category “bird,” for example, the properties “large,” “beak,” “large wings,” and “eats fish” were correlated to one another. Within the category “furniture,” for example, the properties “springs,” “cushions,” “sit on,” “comfortable,” and “soft” were correlated to one another. The results suggest that the properties of members of a certain category tend to be related to one another such that the likelihood of a member having a certain property, A, increases if they also have property B.

Building on this idea, McRae et al. (1997) developed a computer model of semantic memory that captures the correlational aspect among semantic features. In their model, correlated features were more prominent for living things than for artefacts, and the larger number of
correlations among features of living things was responsible for a dissociation in processing between living and nonliving items. This is the basic assumption of other models of semantic memory that rely on correlated features to explain category-specific semantic deficits in Alzheimer’s disease (e.g., Devlin, Gonnerman, Andersen, & Seidenberg, 1998). In Devlin et al.’s model, living things have a high number of intercorrelated properties (i.e., few distinctive features) and the degree of correlation between these properties is higher for living things and nonliving things. The authors demonstrated that with mild damage, nonliving things were impaired but as damage became more severe, living things were more impaired. These computational results were supported by behavioral data from Gonnerman, Andersen, Devlin, Kempler, and Seidenberg (1997). They showed that patients with probable Alzheimer’s disease who were mildly impaired showed more difficulty with nonliving things and as the severity increased, the impairment shifted to a deficit with living things.

Moss, Tyler, Durrant-Peatfield, and Bunn (1998) propose a slightly different account of semantic memory and make several basic assumptions in developing their computer model (see also Durrant-Peatfield, Moss, & Tyler, 1998). The first assumption is that the distribution of distinctive versus shared properties differs between living and nonliving things such that living things have many more shared properties and these shared properties tend to be correlated with one another (similar to Devlin et al.’s, 1998, proposal). For example, animals fall into well-defined categories such as mammals, birds, or reptiles but man-made things do not, and the boundaries between artefact categories are less clear, e.g., vehicles, toys, household objects. The second assumption, which differentiates this model from the Devlin et al. model, is that “functional” properties are important for both living and nonliving things, but “function” for living things involves biological motion rather than a specific use. And, function for living things tends to be shared among many members of the category whereas function for artefacts tends to be specific to a particular item. Moss et al.’s (1988) model stresses the importance of functional semantic properties, resulting in great overlap between both perceptual and functional properties for living things. This results in many features being intercorrelated for living things across different types of semantic properties. Moreover, semantic properties of nonliving things have few intercorrelated properties but strong correlations between specific perceptual and functional features associated for individual items (e.g., has a blade—used for cutting).

Although these models make some differences in their basic assumptions, the structure of all these models makes very clear predictions regarding when category-specific deficits should emerge. Because of the strong sharing of properties among living things (regardless of the type of property), the Devlin et al. (1998) model predicts only severe damage would result in specific deficits to the living things category. However, when the damage is mild, deficits should arise for artefacts. The reasoning is that mild damage should impair distinctive features (which are more prevalent for nonliving things) since damage to a shared feature of an item can be compensated by the undamaged features. The Moss et al. (1998) model predicts that living things will be affected at any level of damage, except severe, since the individual features of animals are more unique and therefore more likely to be damaged. However, artefacts are impaired only at more severe levels of damage since the distinctive relationship between form and function is strongly correlated and therefore robust to brain damage. Thus, these computer models demonstrate that using the basic structure of correlated features, category-specific deficits can emerge based on the severity level of the damage to the system. These models also account for the fact that when familiarity is controlled, patients do not show any specific problems with a certain type of knowledge within a category (i.e., co-occurrence of category-and modality-specific deficits and/or a category-by-modality interaction).

* However, Moss et al. (1988) also allow that artefacts may also be impaired at mild levels of damage if the specific form-function features are damaged. It is unclear how this prediction is instantiated in their model and what it implies about the organisation of distinctive features for artefactual concepts.
Challenges to the Theories

One important problem is that the original results of Gonnerman et al. (1997) with dementia patients have not been replicated. Garrard, Patterson, Watson, and Hodges (1998) examined naming and comprehension performance in a group of patients with probable Alzheimer’s disease and investigated whether or not severity of the disease related to performance with different categories of knowledge. Garrard et al. (1998) failed to find a relationship between disease stage and the direction of the category-specific dissociation. In general, their patients as a whole showed a deficit to living things, regardless of the degree of the severity of the disease.

Equally important, the models have difficulty accounting for two well-established patterns of performance. First, the model(s) cannot account for selective deficits to narrowly defined categories; for example, how would diffuse damage result in a deficit only to animals (e.g., Caramazza & Shelton, 1996; Hart & Gordon, 1992; Hillis & Caramazza, 1991) or only to fruits and vegetables (e.g., Farah & Wallace, 1992; Hart, Bendt, & Caramazza, 1985) or only to body parts (e.g., Goodglass et al., 1966; Semenza & Goodglass, 1985; see also Shelton et al., 1998). The assumptions about the number and degree of intercorrelated properties is relevant to all living things, which includes animals, plant life, fruits, and vegetables. Second, a potentially more serious problem concerns the idea of severity level and how it relates to the type of category-specific deficit that will emerge. The two patients reported by Hillis and Caramazza (1991) described earlier have similar levels of performance and yet show complementary deficits to living and nonliving categories (see Table 17.6). For example, at 13 months post-onset, JJ was impaired in naming nonliving objects (69% correct) as compared to animals (100% correct) whereas PS was impaired in naming animals (62% correct) as compared to nonliving objects (92% correct). Note the comparable levels of performance for the impaired category. These patients demonstrate quite clearly that severity level is not related to the nature of the category-specific deficit, as would be predicted by the Devlin et al. and Moss et al. models of semantic memory.

The Organized Unitary Content Hypothesis

Another model of semantic memory that relies on intercorrelated features (but has not been simulated) is the Organized Unitary Content Hypothesis (OUCH; Caramazza, Hillis, Rapp, & Romani, 1990; Caramazza, Hillis, Leek, & Miozzo, 1994). This model makes two assumptions: 1) members of a semantic category tend to share attributes (e.g., animals breathe; they are

<table>
<thead>
<tr>
<th>Table 17.6</th>
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<tbody>
<tr>
<td>Similar Accuracy Levels in Patients with Contrasting Category-Specific Deficits (Percentage Correct)</td>
</tr>
<tr>
<td>Hillis &amp; Caramazza, 1991: Patients JJ and PS</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Oral Naming</th>
<th>Written Naming</th>
<th>Auditory Comp.</th>
<th>Visual Comp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>JJ</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>animals</td>
<td>46</td>
<td>91.3</td>
<td>70.0</td>
<td>91.3</td>
<td>97.8</td>
</tr>
<tr>
<td>inanimate</td>
<td>86</td>
<td>20.4</td>
<td>15.3</td>
<td>60.2</td>
<td>42.9</td>
</tr>
<tr>
<td>PS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>animals</td>
<td>46</td>
<td>39.1</td>
<td>34.8</td>
<td>93.5</td>
<td>89.1</td>
</tr>
<tr>
<td>vegetables</td>
<td>12</td>
<td>25.0</td>
<td>33.3</td>
<td>61.7</td>
<td>83.3</td>
</tr>
<tr>
<td>inanimate</td>
<td>86</td>
<td>52.5</td>
<td>76.7</td>
<td>100.0</td>
<td>83.7</td>
</tr>
</tbody>
</table>

Note. Levels of performance at 6 months post-onset.
made of certain kinds of substances, etc.), and 2) core semantic properties of an object tend to be highly intercorrelated (e.g., objects that breathe also tend to be made of certain kinds of stuff). An implication of these assumptions is that semantic space will be "lumpy" in the sense that members of semantic categories will cluster closely together in feature space. For example, a horse has a mouth, which is related to its ability to eat, move, and breathe, or a chair has a flat surface for sitting, which is related to it's material (e.g., wood), inertness, and inability for self-initiated motion. Category-specific deficits result from brain damage to a lumpy region of semantic space. Thus, for example, damage to a region of the brain that represents the highly intercorrelated features shared by living things would result in a category-specific deficit for living things.7

Unlike the models reviewed above, OUCH naturally accounts for the finer-grained distinctions within the categories of living things (e.g., impairment only to animals). This is because the model assumes that the "lumpiness" in semantic space directly reflects the shared properties of category members and therefore we expect that animals will cluster closely together and separately from fruits and vegetables, say. However, a weakness of the model is that it is too unconstrained—any tightly correlated set of features is a candidate for a category-specific deficit. Furthermore, as it stands, it is not clear which semantic categories are sufficiently compactly represented to allow for selective damage (see Caramazza & Shelton, 1998, for further discussion).

Conclusions

The intercorrelated features models of Devlin et al. (1998) and Moss et al. (1998) are based on the established empirical fact that many more features are correlated to a stronger degree within the categories of living things. These models can capture the distinction between the broad categories of living and nonliving things and thus, explain reports of patients who demonstrate better performance with nonliving things as compared to living things (and the opposite dissociation). However, neither model can readily capture the finer-grained dissociations which have been demonstrated, nor can they explain the fact that types of semantic category-specific deficits do not depend on severity level. The OUCH model can in principle account for fine-grained categorical distinctions at all levels of severity, but is currently too unconstrained.

IS SEMANTIC KNOWLEDGE ORGANIZED BY NATURAL DOMAINS?

The idea that the organization of knowledge in the brain honors some natural categorical distinctions has been rejected outright (but see Laiacona, Barbarotto, & Capitani, 1993; Warrington, 1981). Instead, as reviewed above, most researchers have sought alternative explanations for category-specific knowledge deficits that reduce the distinctions among categories to the differences in underlying representations or the type of knowledge important for each category.

The Domain-Specific Knowledge Hypothesis

Recently, we have reviewed the literature and presented 2 case studies that motivated us to propose a "categorical" organization of evolutionarily important knowledge—the domain-specific knowledge hypothesis (Caramazza, 1998; Caramazza & Shelton, 1998; Shelton & Caramazza, 1999; Shelton et al., 1998). According to this hypothesis, knowledge is organized into broad

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7The difference between this model and the Moss et al. (1998) and Devlin et al. (1998) models is that OUCH does not make assumptions regarding the nature of the features important for living or nonliving categories. That is, the other models assume that the categorical deficits (at the broad level of living-nonliving) emerge due to the featural properties important to the items within those categories.
domains (categories) reflecting evolutionarily salient distinctions in semantic knowledge; thus, we propose that there are specialized neural mechanisms for recognizing and understanding certain categories of knowledge. The assumption is that the categories of animals, plant life, and conspecifics are important for survival. Animals are predators and prey; plant life provides food and medicine, and the recognition of conspecifics is important for physical and social needs.

This proposal was made as a way to account for the highly selective categorical deficits that have been reported. As mentioned earlier, patients have been reported to have selective deficits/sparing to just animals (e.g., Caramazza & Shelton, 1998; Hillis & Caramazza, 1991), to just fruits and vegetables (Farah & Wallace, 1992; Hart et al., 1988) or a selective deficit to vegetables in comparison to animals (Hillis & Caramazza, 1991). Many patients show deficits to body parts (e.g., Goodglass et al., 1968; Semenza & Goodglass, 1985) and there is recent evidence for the selective sparing of body part processing (Shelton et al., 1998). Our patient, IOC, was severely impaired at naming and showed mild-to-moderate comprehension problems, but what was striking about her performance was her preserved ability to process body parts (see Table 17.7). This result complements the previously reported cases of impairment to body parts (e.g., Semenza & Goodglass, 1985) and suggests that body parts can be a selectively impaired category of semantic knowledge.

Data from developmental studies also converge with the findings from neurological studies to suggest that the brain respects categorical knowledge distinctions. Infants make fundamental distinctions very early on between biological and nonbiological entities (e.g., Carey, 1995). For example, infants as young as three months old can distinguish between biological and nonbiological motion (Berenthal, 1998; Berenthal, Proffitt & Cutting, 1984). And, nine month old infants can correctly categorize animals and nonanimals even when items from different categories are more perceptually similar than items from the same categories (Mandler, 1995; Mandler, Bauer, & McDonough, 1991; Mandler & McDonough, 1993). Other evidence suggests that within the biological domain further distinctions should be made between animate and

### Table 17.7

<table>
<thead>
<tr>
<th>Picture Naming (from Snodgrass &amp; Vanderwart set)</th>
<th>Category</th>
<th>Proportion Correct</th>
<th>Category</th>
<th>Proportion Correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body Parts</td>
<td>11/12 (.92)</td>
<td>Musical Instruments</td>
<td>0/9 (.00)</td>
<td></td>
</tr>
<tr>
<td>Animals</td>
<td>6/48 (.13)</td>
<td>Tools</td>
<td>1/12 (.08)</td>
<td></td>
</tr>
<tr>
<td>Appliances</td>
<td>5/14 (.36)</td>
<td>Vegetables</td>
<td>0/15 (.00)</td>
<td></td>
</tr>
<tr>
<td>Clothing</td>
<td>14/19 (.74)</td>
<td>Vehicles</td>
<td>1/10 (.10)</td>
<td></td>
</tr>
<tr>
<td>Fruit</td>
<td>4/11 (.36)</td>
<td>Other</td>
<td>22/98 (.22)</td>
<td></td>
</tr>
<tr>
<td>Furniture</td>
<td>3/14 (.21)</td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Picture-Word Verification</th>
<th>Category</th>
<th>Proportion Correct</th>
<th>Category</th>
<th>Proportion Correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body Parts</td>
<td>11/12 (.92)</td>
<td>Musical Instruments</td>
<td>8/8 (.97)</td>
<td></td>
</tr>
<tr>
<td>Animals</td>
<td>30/48 (.63)</td>
<td>Tools</td>
<td>8/12 (.67)</td>
<td></td>
</tr>
<tr>
<td>Appliances</td>
<td>9/14 (.64)</td>
<td>Vegetables</td>
<td>10/13 (.77)</td>
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</tr>
<tr>
<td>Clothing</td>
<td>15/19 (.79)</td>
<td>Vehicles</td>
<td>8/10 (.80)</td>
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</tr>
<tr>
<td>Fruit</td>
<td>8/11 (.73)</td>
<td>Other</td>
<td>79/98 (.81)</td>
<td></td>
</tr>
<tr>
<td>Furniture</td>
<td>8/14 (.57)</td>
<td></td>
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</table>

*Note: Familiarity had a strong effect on IOC’s performance but, for naming, category effects still emerged even after familiarity was controlled. For comprehension, category effects emerged on some tasks but not others after familiarity was controlled. Since comprehension was fairly good, these tasks may not have been sufficiently demanding to uncover a deficit to specific categories. Data from "The Selective Sparing of Body Part Knowledge: A Case Study," by J. E. Shelton, E. Fouch, & A. Caramazza, 1998, Neurocase, 4, pp. 343-345."
inanimate concepts. For example, research has demonstrated that the notion of self-propelled motion is important for the infant's concept of "human" (e.g., Mandell, 1992; Spelke, Phillips, & Woodward, 1995). That is, infants appreciate the distinction between self-initiated movement and movement caused by another object (e.g., Spelke et al., 1996).

The domain-specific hypothesis readily accounts for the established patterns of observed deficits and can accommodate the data from the developmental literature. The problem with this hypothesis is the lack of specificity regarding how knowledge within categories is represented. Although the hypothesis speaks to broad distinctions of domains in the brain, the representation and organization of that knowledge within the domains is unspecified. Thus, we can ask whether or not further structure exists within, for example, the biological domain. Since it has been established that plant life and animals can be damaged independently of each other, we know there must be further differentiation within the biological domain.

We make the distinction between animals and plant life and artefacts as a means of accounting for the highly selective deficits shown by some patients, deficits that do not respect the broad distinction living/nonliving things. We have hypothesized that there may have been important survival reasons in the evolution of humans for the brain to honor distinctions among these categories, specifically respecting distinctions between the animal and plant life categories. Although items in both categories are living, there are few other shared features between the two. The ability to recognize and identify those things that are capable of attacking and killing (animals) versus those things that are not (plants) would be important for survival. Further, identifying a dangerous (poisonous) plant would rely on highly specific features that are quite different from those features involved in identifying a dangerous animal. Although these two categories both represent living items, there is little other similarity between the two. Thus, there is no reason to suppose that brain damage would necessarily affect both categories of living things.

When we initially proposed the domain-specific knowledge hypothesis, we treated the artefacts category as the default category for nonbiological concepts. But, there may be certain domains of nonbiological knowledge that have crucial dimensions that may have led to the development of neural areas dedicated to processing these domains. For example, in several papers we have suggested that "tools" may form an evolutionarily important category (Caramazza & Shalton, 1998; Shelton & Caramazza, 1999), a position that has recently been discussed by Hauser (1997) in relation to nonhuman primate data. It is not inconceivable that the ability to use tools may have conferred a distinct survival advantage that could have led to specialized mechanisms for the recognition and use of such objects. Thus, some artefactual categories may have evolved into separate domains, implying that these categories of items could dissociate from other categories following brain damage.

But other than outlining the reasons for the broad distinctions between animals, plants, and artefacts (and perhaps tools), the domain-specific knowledge hypothesis provides little detail about the nature of the representation of information within categories. That is, why do the objects in each of these categories cluster together? What is the nature of the knowledge representation such that animals, for example, form a category that differs from plants? We hypothesize that a featural hypothesis, such as OUCH, could provide the framework for understanding how information is represented within categories. This hypothesis states that items within categories share many properties and that core properties tend to be intercorrelated. So, animals tend to share many properties (e.g., related to movement, digestion, number of legs, eyes, mouth, ferocity, etc.) that are intercorrelated (e.g., mouth implies ingestion) and these properties are not likely to be shared with plants (e.g., plants have few of the above properties which are central to our understanding of animals). Therefore, the featural proper-

*Note that the lack of similarity between the features shared between animals and plants is a different assumption than that made by the Moss et al. (1998) and Devlin et al. (1998) theories, which assume all living things have many shared, intercorrelated features.
ties for defining animals and plants are quite different, a difference that is captured at a broad level by assuming domain-specificity and at a more specific level by assuming that members of a given domain share certain properties important for defining most members of that category.

In light of the above considerations it could be assumed that same category items are represented in close neural areas dedicated to processing items within a specific category, represented by features important for the definition of those items (and perhaps the category itself). This does not imply, however, that specific features are represented redundantly between categories. For example, the feature "move" could be represented in the animal category but could also be represented in other categories such as plants or vehicles. However, the meaning of "move" is very different for each category and would not be expected to be represented by a single feature "move." There might be exceptions to this, but we suggest that there is very little redundancy in the features represented between categories.

Conclusions
The domain-specific knowledge hypothesis provides a natural way of accounting for the dissociations in processing observed in patients demonstrating category-specific semantic deficits. Data from developmental studies also provide support for the notion that there may be neural mechanisms dedicated to processing specific classes of objects corresponding to the broad domains of biological and nonbiological concepts. Further distinctions may be found within these categories, such as plants, animals, body parts, and perhaps tools. There are likely to be multiple levels of organization of semantic knowledge and this hypothesis is one way in which to conceptualize the organization of semantic knowledge at a broad level.

NEUROANATOMICAL CONSIDERATIONS: ARE CERTAIN BRAIN AREAS DEDICATED TO PROCESSING SPECIFIC CATEGORIES OF KNOWLEDGE?

When examining lesion sites reported for cases with category-specific knowledge deficits, the clearest picture comes from those patients showing selective deficits to living things (see Gainotti et al., 1995, and Saffran & Schwartz, 1994, for reviews). Most patients with deficits to living things have sustained damage to the left temporal lobe and in some cases to the right temporal lobe as well although some have been reported to have only right temporal lobe damage (Barbarotto et al., 1995; Laws et al., 1995). Furthermore, some cases with a deficit to living things have sustained damage to the frontal and inferior parietal areas (Caramazza & Shelton, 1998; Hillis & Caramazza, 1991; Laiacona et al., 1993) while other cases have sustained widespread damage due to traumatic brain injuries (e.g., Farah et al., 1989; Laiacona et al., 1993; Samson, Pillon, & De Wilde, 1998).

There is even less agreement when we examine lesion sites reported for cases with selective deficits to artefacts. Some cases have sustained damage to the left temporal lobe and basal ganglia (Hillis & Caramazza, 1991) or just the left temporal lobe (Cappa et al., 1998). Other cases have sustained damage to left frontal and parietal areas (Sacchett & Humphreys, 1992; Warrington & McCarthy, 1983, 1987).

Several neuroimaging studies (using PET) have examined normal understanding of living and nonliving things (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1998; Martin, Wiggs, Underleider, & Harvey, 1996; Perani et al., 1995) and shown different brain areas involved in processing the two categories. All the studies found activation in the inferior temporal lobe for processing living things/animals, either bilaterally (Perani et al., 1995) or in the left hemisphere only (Damasio et al., 1996; Martin et al., 1996). Both Martin et al. and Perani et al. also found activation bilaterally in the occipital lobes for processing of living things. There was little agreement among the studies in the activation of the brain areas involved in normal understanding of nonliving things. Damasio et al. found activation in the posterior middle and
in inferior temporal gyr; Martin et al. found activation in the fusiform gyri of the temporal lobes and left inferior frontal region; Perani et al. found activation in the lingual, parahippocampal gyr, middle occipital gyrus, and dorsolateral frontal regions.

Thus, some evidence suggests that there may be nonoverlapping areas of the brain that are important for processing different categories of items. The inferior areas of the temporal lobe appear to be especially important for processing living things and the posterior area of the temporal lobe and fronto-parietal areas appear more important for processing nonliving things.

CONCLUSIONS

We have examined three hypotheses regarding semantic knowledge organization: 1) the modality-specific semantic hypothesis, 2) the feature-intercorrelation hypothesis, and 3) the domain-specific knowledge hypothesis. At least as currently formulated, there is little support for the hypothesis of modality-specific semantics. Well-controlled studies of normal processing and patient performance have provided little support for a theory of semantics that divides knowledge into two broad categories of perceptual and nonperceptual knowledge. We have proposed that one aspect of the overall organization of semantic memory is the domain-specific knowledge hypothesis and that other principles of organization can exist within each of the domains.

Further structure within each of the domains may be provided by other theories of knowledge organization, such as OUCH.

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