COGNITIVE NEUROPSYCHOLOGY, 2003, 20 (3/4/5/6), 433–450

CONSTRAINING QUESTIONS ABOUT THE ORGANISATION AND REPRESENTATION OF CONCEPTUAL KNOWLEDGE

Bradford Z. Mahon and Alfonso Caramazza
Harvard University, Cambridge, USA

In this article we assume a domain-specific organisation of conceptual knowledge and consider two questions: How does this architecture constrain further assumptions that might be made regarding (1) the organisation of conceptual knowledge in the brain, and (2) the representation of conceptual knowledge in the brain? Data from category-specific semantic deficits, functional neuroimaging, and apraxia are recruited in attempt to clarify these questions. It is shown that the domain-specific hypothesis can account for the extant facts. Furthermore, we outline one possible theoretical framework that imposes empirical constraints on proposals that might be advanced in response to the two questions raised above.

INTRODUCTION

The patterns of differential impairment/sparing of cognitive function subsequent to brain damage can provide strong constraints on theories of the organisation and representation of cognitive systems in the brain. As the articles in this Special Issue of *Cognitive Neuropsychology* attest, the phenomenon of category-specific semantic[1] deficit is a compelling case in point. One well-iterated demonstration of the types of constraints imposed on theories of cognitive organisation is provided by recent evaluations of a widely received explanation of category-specific semantic deficits: the sensory/functional theory (e.g., Warrington & McCarthy, 1983, 1987, 1994; Warrington & Shallice, 1984). This theory assumes that category-specific semantic deficits emerge as a result of damage to a type or modality of information (e.g., visual/perceptual vs. functional/associative) upon which successful recognition/naming of objects from the impaired category differentially depends (i.e., living things vs. nonliving things, respectively). However, a nearly exhaustive review of the literature on category-specific deficits (Capitani, Laiacona, Mahon, & Caramazza, 2003-this issue) establishes the *fact* that the majority of patients with such impairments *do not* present with a disproportionate deficit for a type or modality of knowledge. From this fact it can be concluded that the cause of category-specific semantic deficits cannot be damage to a type or modality of information. This conclusion

[1] In this article we use the terms “semantic” and “conceptual” interchangeably.

Requests for reprints should be addressed to Alfonso Caramazza, Department of Psychology, William James Hall, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA (Email: caram@wjh.harvard.edu).

Preparation of this manuscript was supported in part by NIH grant DC 04542 to Alfonso Caramazza. The authors are grateful to Laurel Buxbaum and Alex Martin for their comments on an earlier version of this manuscript. We would also like to thank Lauren Moo for her insights into the functional neuroimaging data that have been reviewed.

http://www.tandf.co.uk/journals/pp/02643294.html DOI:10.1080/02643290342000014

implies the rejection of the sensory/functional theory as a viable theoretical framework with which to explain the existence of category-specific semantic deficits (see also Caramazza & Shelton, 1998).

How, then, does one account for the facts of category-specific semantic deficits? Perhaps the most straightforward proposal is that the organisation of conceptual knowledge in the brain is subject to domain-specific principles (Caramazza & Shelton, 1998). In this article, we assume a domain-specific organisation of conceptual knowledge, and ask two questions: If we assume a domain-specific architecture, (1) what constraints are placed on further theoretical assumptions that might be made regarding the organisation of conceptual knowledge in the brain, and (2) what constraints are placed on assumptions about how conceptual knowledge is represented? Relevant neuropsychological and functional neuroimaging data, as well as alternative theoretical proposals, are recruited in an attempt to clarify these two questions.

Clues from category-specific semantic deficits

The central assumption of the domain-specific hypothesis (Caramazza & Shelton, 1998) is that evolutionary pressures have resulted in specialised (and functionally dissociable) neural circuits dedicated to processing, perceptually and conceptually, different categories of objects. In this way, the domain-specific hypothesis provides a principled way of specifying what constitutes a conceptual category in the brain, since it is restricted to only those categories for which rapid and efficient identification could have had survival and reproductive advantages. Plausible candidates are the categories "animals," "plant life," "conspecifics," and possibly "tools."[2] The plausibility of the domain-specific hypothesis is established by the fact that the grain of category-specific deficits is as fine as the above-mentioned evolutionarily salient object domains (see, e.g., Crutch & Warrington, 2003-this issue; Samson & Pillon, 2003-this issue; for review see Capitani et al., 2003-this issue).

The domain-specific hypothesis generates several predictions: First, at a functional level, the prediction is made that there will not be a necessary association between a deficit for a type or modality of knowledge and a conceptual deficit for a specific category of objects. This prediction follows from the assumption that processes/information are not *functionally* organised within object domain. In line with this prediction,[3] the majority of cases that presented with a disproportionate deficit for living things also presented with *equivalent* impairments for visual/perceptual and functional/associative knowledge. For instance, cases EA (Barbarotto, Capitani, & Laiacona, 1996; Laiacona, Capitani, & Barbarotto, 1997), EW (Caramazza & Shelton, 1998), FM (Laiacona, Barbarotto, & Capitani, 1993), Jennifer (Samson, Pillon, & De Wilde, 1998), and SB (Sheridan & Humphreys, 1992) all had disproportionate semantic deficits for living things compared to nonliving things, but *equivalent* deficits to visual/perceptual and functional/associative knowledge of living things (for review, see Capitani et al., 2003-this issue).

A second prediction made by the domain-specific hypothesis is that there should be relatively poor recovery of lost function for impaired categories. This prediction receives striking support from a recent case study (Farah & Rabinowitz, 2003-this issue) of a patient, Adam, who suffered a bilateral posterior cerebral artery infarction at age 1 day. When tested at age 16 years, Adam was disproportionately impaired at naming pictures of living

[2] For discussion of the domain-specific hypothesis in developmental psychology and comparative work with nonhuman primates, see, e.g., Carey (2000); Carey and Markman (1999); Keil (1989); Santos and Caramazza (2002); Santos, Hauser, and Spelke (2002).

[3] Early reports seemed contrary to this prediction: Patients were reported with deficits for living things who were also disproportionately impaired for the visual attributes of objects compared to functional/associative attributes (Basso, Capitani, & Laiacona, 1988; Farah, Hammond, Mehta, & Ratcliff, 1989; Silveri & Gainotti, 1988). However, these studies have been criticised methodologically on the grounds that the tasks accessing visual and functional/associative knowledge were not matched for difficulty (see Caramazza & Shelton, 1998).

things (40% correct) compared to nonliving things (75% correct). Furthermore, Adam's deficit for living things affected all types of semantic information investigated: The patient was at chance for both visual/perceptual and functional/associative knowledge for living things (visual/perceptual = 40%; functional/associative = 45% correct), while performance was within the normal range for both types of knowledge for nonliving things (visual/perceptual = 78%, normal range = 70–90%; functional/associative = 72%, normal range = 73–92%).

A third prediction made by the domain-specific hypothesis follows from the assumption that relatively early (i.e., pre-semantic or perceptual) stages of object processing will be organised by domain. With respect to the visual modality, this hypothesis generates the prediction that the structural description system will be functionally organised by object domain. Perhaps the strongest evidence consistent with this prediction is provided by the performance of patient Michelangelo (Sartori, Coltheart, Miozzo, & Job, 1994; Sartori & Job, 1988; Sartori, Miozzo, & Job, 1993b). Michelangelo was disproportionately impaired for the category "living things" and was also disproportionately impaired on an object decision task for living things compared to nonliving things (see also, for example, patient EW, Caramazza & Shelton, 1998; Capitani et al., 2003-this issue, Table 3).

Another aspect of Michelangelo's profile of category-specific deficit for living things is that he was disproportionately impaired for visual/perceptual knowledge of living things compared to functional/associative knowledge (see also patient Giulietta: Sartori, Job, Miozzo, Zago, & Marchiori, 1993a). If we take these data to be a fact of category-specific deficits (but see Capitani et al., 2003-this issue), these data could suggest that object domain is not the only constraint on the organisation of conceptual knowledge in the brain. Specifically, one possibility would be to adopt the domain-specific hypothesis (in order to account for the data from category-specific semantic deficits) but *not* dispose of the modality-specific assumption.

To be clear: It is an established fact that the majority of patients who have presented with category-specific semantic deficits have not presented with a disproportionate impairment to a modality or type of knowledge. The conclusion that follows from this fact is that it cannot be assumed that the *cause* of category-specific semantic deficits is damage to a type (i.e., modality) of knowledge upon which successful recognition/naming differentially depends. However, this conclusion is silent with respect to the possibility that one organising constraint on the physical distribution of conceptual knowledge in the brain is modality or type of information. The conjunction of the domain-specific hypothesis with the modality-specific assumption would imply that, within for instance the visual modality, information would be organised by object domain.

The assumption that conceptual knowledge corresponding to visual/perceptual properties of objects is stored in a different area of the brain from knowledge about the functional/associative properties of objects must be distinguished from the claim that there are modality-specific semantic subsystems specialised for processing a specific type of information. In the context of the domain-specific hypothesis, there are two reasons why it would not be theoretically coherent to refer to the "system" that stores information about the visual properties of objects as a "modality-specific semantic subsystem." First, information internal to such a "system" would be functionally organised (and thus functionally dissociable) by object domain. Second, information across these "modality-specific semantic subsystems" would be functionally unitary within any given object domain. In other words, we would no longer have functionally defined modality-specific semantic subsystems, but rather neuroanatomically defined modality-specific semantic subsystems. In order to avoid confusion, we will refer to the "systems" that represent/process conceptual knowledge of a given type (e.g., visual/perceptual vs. functional/associative) as modality-specific semantic *stores* (for further discussion of these issues, see Caramazza, Hillis, Rapp, & Romani, 1990; and Mahon & Caramazza, in press).

Modality-specific semantic stores must be further distinguished from modality-specific input/output representations. For instance, with respect to visual knowledge, we will adopt as a working assumption a distinction between the modality-specific semantic store that represents/processes conceptual knowledge about the visual properties of objects and the structural description system. Representations contained in the structural description system are pre-semantic, and thus provide one route for *accessing* information contained in the visual modality-specific semantic store. Assuming the validity of this distinction for discussion amounts to a strong (and by no means uncontroversial) claim about the independence of conceptual knowledge from modality-specific input/output representations. We will return to an evaluation of this distinction in our Conclusion in light of the empirical evidence to be discussed below.

Distinguishing between modality-specific semantic stores and modality-specific input/output representations requires some specification of why information in a modality-specific semantic store is modality-specific. In other words: What is *visual* about "visual" semantic knowledge? At least three (nonmutually exclusive) possibilities could be envisioned. First, it could be argued that what makes "visual" semantic information *visual* is that it is stored in a visual *format*. Second, it could be argued that what makes this information *visual* is that it is *about* the visual properties of objects. Third, it could be that what is *visual* about "visual" knowledge is that it was *learned* or *acquired* through the visual modality. These are questions for future research (see Caramazza et al., 1990, for extended discussion). Our present interest is not in arguing *for* the architecture just described, but rather is of the form: *If* we were to assume such an organisation, then what further expectations might we have regarding the neuroanatomical organisation and representation of conceptual knowledge?

In the next section, we approach the question of whether conceptual knowledge is organised by object domain within the visual modality from the perspective of functional neuroimaging.

Clues from functional neuroimaging

If we assume that conceptual knowledge is organised by domain-specific constraints within neuroanatomically defined modalities, then the strongest prediction that can be made is that there will be spatial segregation of processes/information by semantic category *within* modality. We limit our discussion to functional neuroimaging studies that have investigated category-specific patterns of activation in inferior and lateral temporal areas, as these neural areas correspond to (at least part of) the "visual modality."

A number of investigators have observed differential activation in the ventral object processing stream for different categories of objects. For instance, Chao, Haxby, and Martin (1999a) reported activation in the medial aspect of the fusiform gyri bilaterally across viewing, naming, and matching tasks involving pictures of "tools," as well as for a task in which subjects were reading the names of "tool" stimuli. In the same study, activation was reported in the lateral aspect of the fusiform gyri for the same tasks conducted over "animal" stimuli. A similar pattern of results has been found when contrasting the activation produced by "face" stimuli and "house" stimuli: Compared to houses, faces activated more lateral regions of the fusiform gyrus (e.g., Haxby, Ungerleider, Clark, Schouten, Hoffman, & Martin, 1999; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), whereas the reverse comparison (houses–faces) yielded disproportionate activation in more medial regions of the fusiform gyrus (Aguirre, Zarahn, & D'Esposito, 1998) as well as in parahippocampal cortex (Epstein & Kanwisher, 1998). To sum up, differential and spatially dissociable (although overlapping) foci of activation have been found for each of the categories "animals," "tools," "houses," and "faces" (Chao et al., 1999a; Chao, Martin, & Haxby, 1999b; see Martin & Chao, 2001).[4]

Similar patterns have been observed in lateral temporal cortex. Items corresponding to "living

[4] Not all investigators have observed category-specific effects with functional neuroimaging. For instance, Devlin et al., (2002) did not find reliable category-specific foci of activation for the categories "animals," "fruit," "tools," and "vehicles."

things" differentially activated the superior temporal sulcus (faces: Chao et al., 1999a, 1999b; Haxby et al., 1999; Hoffman & Haxby, 2000; Kanwisher et al., 1997; animals: Chao et al., 1999a, 1999b). In contrast, activation associated with identifying pictures of tools activated more inferior regions centred on the left middle temporal gyrus (e.g., Chao et al., 1999a; Martin, Wiggs, Ungerleider, & Haxby, 1996). Furthermore, lateral temporal cortex seems to be specialised for processing object-associated motion. In a recent study, Beauchamp, Lee, Haxby, and Martin (2002) found that the superior temporal sulci and gyri responded differentially to biological motion (right ≫ left) while the middle temporal gyri and inferior temporal sulci responded differentially to tool associated-motion (left ≫ right) (see also Senior et al., 2000, for related findings; see Beauchamp et al., 2002, for review and discussion).

Taken together, these data would seem to provide strong prima facie support for the hypothesis that conceptual knowledge is organised by object domain within inferior and lateral temporal areas. However, a reductio counterargument that has been raised against a domain-specific interpretation of these data is based on the observation (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999) that "chair" stimuli activated an area in inferior temporal cortex lateral to that elicited by faces. In other words: Why would the category "chairs" elicit a discrete area of activation, since this category clearly does not constitute an evolutionarily significant object domain? In the context of this argument, Martin and Chao (2001, p. 196) propose that these data are consistent with the notion that conceptual representations are distributed over features: "A feature-based model can accommodate the observation that an arbitrary category such as chairs elicited a pattern of neural activity distinct from other object categories (i.e., faces and houses). Clearly, it would be difficult, as well as unwise, to argue that there is a 'chair area' in the brain." The premise upon which this argument is based is that a feature-based model *could* accommodate the results reported by Ishai and colleagues (1999). But wouldn't a feature-based model face the same dilemma that the domain-specific hypothesis purportedly faces? In other words, if conceptual knowledge is organised by the features that define objects, so that the conceptual representations of objects that share features are stored in adjacent neural areas, then why would "chair" stimuli activate an area next to an area that has previously shown disproportionate activation for "animal" stimuli? What features are shared between the conceptual representations of exemplars from the categories "chairs" and "animals?" Is the claim that animals and chairs share the feature "legs?" Would this still be the claim if the word referring to the feature [+LEG$_{[animal]}$] was not homonymous with the feature [+LEG$_{[chair]}$]? What about the feature [+ARM$_{[human]}$] and [+ARM$_{[chair]}$]: Are these the same feature too because the word referring to each is the same?

Data from a recent functional neuroimaging study (Martin & Weisberg, 2003) lends some support to the argument that the patterns of differential activation by object category in inferior and lateral temporal areas are driven by domain-specific processes, and not object-specific features. The authors compared the activation produced when subjects viewed the *same physical stimuli* (e.g., coloured triangles) depicting either social or mechanical motion. When these two conditions were compared, activation associated with social motion (e.g., scaring, sharing etc.) was observed in the lateral fusiform gyrus and superior temporal sulcus, while activation associated with mechanical motion (e.g., bowling, conveyor belt, etc.) was observed in the medial aspect of the fusiform gyrus and the left middle temporal gyrus.[5] These data indicate that seemingly category-specific patterns of activation can be invoked by stimuli that must be *interpreted* (at a relatively abstract level) as pertaining to one or another semantic domain. Crucially, this level of interpretation must be more abstract than the level at which the physical properties of stimuli are represented, since the stimuli in the mechanical and social conditions were physically identical.

[5] Activation associated with social motion was also found in the amygdala and ventromedial prefrontal cortex (Martin & Weisberg, 2003-this issue; see also Castelli, Frith, Happé, & Frith, 2002; Castelli, Happé, Frith, & Frith, 2000).

Interim summary and directions

To this point, we have been discussing issues concerning the organisation of conceptual knowledge from two perspectives: category-specific semantic deficits (for review, see Capitani et al., 2003-this issue) and the patterns of differential activation observed for stimuli from different semantic categories in functional neuroimaging (see Joseph, 2001; Martin & Chao, 2001; Price & Friston, 2002; Thompson-Schill, 2002, for recent reviews). Both methods provide evidence in line with the basic expectations that follow from the assumption that conceptual knowledge is organised by the domains of "animals," "fruit/vegetables," "conspecifics," and possibly "tools." Furthermore, the data from category-specific semantic deficits lend tentative support to the possibility that there are two orthogonal constraints on the organisation of conceptual knowledge: domain and modality. This architecture receives independent support from the functional neuroimaging data that have been reviewed. For instance, differential effects of object category have been observed in inferior temporal cortex, which is specialised for processing visual information. A domain-specific interpretation of these differential effects of semantic category in inferior temporal regions is consistent with either of two possibilities regarding the nature of the information stored in these regions. First, it could be that these data reflect the activation of modality-specific visual structural descriptions of objects (see Whatmough, Chertkow, Murtha, & Hanratty, 2002, for discussion). In this case, these data would be consistent with the view that even at relatively low (i.e., pre-semantic) levels of representation, processes/information are organised by object domain. Second, these data could reflect semantic processing of the visual properties of objects. If this were the case, these data would be consistent with the proposal that conceptual knowledge is organised by object domain within neuroanatomically defined modality-specific semantic stores.[6]

A domain-specific interpretation of category-specific patterns of activation in functional neuroimaging is by no means the received view. In fact, the received view assumes that differential effects of object category reflect the activation of object-specific features, but that these features are not explicitly organised by object domain (e.g., Bookheimer, 2002; Gerlach, Law, Gade, & Paulson, 2000; Ishai et al., 2000; Kraut, Moo, Segal, & Hart, 2002; Martin & Chao, 2001; Moore & Price, 1999; Mummery, Patterson, Hodges, & Price, 1998; Perani et al., 1995; Thompson-Schill, 2002; but see, e.g., Kanwisher, 2000). The primary empirical motivation for this proposal is the observation that the same brain regions are activated by objects from different categories (e.g., Martin & Chao, 2001). For instance, in inferior temporal cortex, the areas of activation observed for animals, tools, houses, and faces were differential and not selective.[7]

There may be methodological limitations regarding this inference: Many functional neuroimaging studies first identify regions of interest (ROIs) that are activated by objects from all of the categories being investigated. For instance, Chao et al. (1999a) first identified ". . . brain regions that responded to visually presented objects . . ." (p. 918) and then looked within those areas for differential effects of object category, in this case "animals" vs. "tools" and "houses" vs. "faces." This methodological approach is biased against the possibility of observing patterns of activation that are "selective," and it is perhaps, then, not surprising that there is substantial overlap between the

[6] It is a separate question as two *why* inferior temporal areas are activated: Are they activated by object-specific properties or is activation in these regions driven (in part) by higher-level processes organised by domain-specific constraints (e.g., see above discussion of Martin & Weisberg, 2003-this issue)?

[7] The assumption that conceptual knowledge is represented as features or conceptual primitives is not in itself contrary to the domain-specific hypothesis: This hypothesis is aimed at articulating the organization of information at the level of domain, and is thus silent with respect to whether or not concepts are assumed to decompose into conceptual primitives or features (for further discussion, see Mahon & Caramazza, in press).

activation produced by objects from different categories. For discussion we will set this methodological concern aside (for further discussion, see Joseph, 2001).

The most articulated version of the proposal that conceptual knowledge is represented in the brain in terms of the features that define objects is the sensory/motor theory of Martin, Chao, and colleagues (e.g., Martin & Chao, 2001; Martin, Ungerleider, & Haxby, 2000). There are two important differences between the sensory/motor theory and the sensory/functional theory. First, whereas the sensory/functional theory assumes that conceptual knowledge and *modality-specific representations* are functionally and physically dissociable, the sensory/motor theory assumes that *conceptual knowledge is distributed over* modality-specific representations. The second way in which the two theories diverge is that, whereas the sensory/functional theory assumes that functional/associative information is crucial for recognising/naming tools, the sensory/motor theory assumes that information about how tools are physically manipulated is required in order recognise/name tools. We can thus evaluate our working assumption that a distinction is required between conceptual information and modality-specific input/output representations by considering whether or not the sensory/motor theory can account for the extant facts. Specifically, we can evaluate the assumption that conceptual knowledge is distributed over modality-specific representations by asking whether this is a plausible assumption for the category "tools." In the next section we briefly outline the functional neuroimaging data that have been marshalled in support of the sensory/motor theory. Empirical predictions are generated from the assumption that conceptual knowledge of tools is distributed over modality-specific representations and these predictions are evaluated with neuropsychological data. We argue that the sensory/motor theory is not tenable in light of the reviewed data. We conclude by considering the implications of the data reviewed in this article for the two questions with which we began.

The sensory/motor theory

Over what is conceptual knowledge of tools distributed?

The distinguishing assumption of the sensory/motor theory is that conceptual knowledge of manipulable artifacts and information about the correct motor movements associated with their use are distributed over the same features.[8] For instance, Martin et al. (2000; p. 1028) write: "…[T]he position proposed here is that the information about object function *needed* to support tool recognition and naming is information about the patterns of visual motion and patterns of motor movements associated with the actual use of the object [emphasis added]." If information regarding the correct use of a tool, or the visual motions associated with its use, is *needed* to identify the object, then how is such information accessed? None of this information is transparent in the visual presentation of the object. In other words, a plausible processing story is required of how the information about object use *specific* to the object being recognised is accessed, *given that the object has not yet been recognised*. One possibility is that there are systematic mappings from the structural description system to information encoding the ways in which objects are manipulated (for proposals in line with this, but which also assume a unitary-amodal semantic system, see Caramazza et al., 1990; Plaut, 2002; Riddoch, Humphreys, Coltheart, & Funnell, 1988).

The sensory/motor theory has been motivated by two well-established results in the functional neuroimaging literature: It has been found that (for instance, naming) tasks performed over tool stimuli (compared to animal stimuli) differentially activated (1) the left middle temporal gyrus (e.g.,

[8] Note the similarity between the sensory/motor theory of object recognition and the motor theory of speech perception (e.g., Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967): Both theories assume that information required for production (i.e., motor engrams for using tools or producing speech sounds) must be retrieved in the course of successful recognition (of tools or speech sounds, respectively).

Chao et al., 1999a; Martin et al., 1996; Moore & Price, 1999; Mummery et al., 1998; Perani, Schnur, Tettamanti, Gorno-Tempini, Cappa, & Fazio, 1999), and (2) left premotor cortex (e.g., Chao & Martin, 2000; Chao, Weisberg, & Martin, 2002; Grabowski, Damasio, & Damasio, 1998; Martin et al., 1996). Relevant to these findings is the observation that the area activated in the left middle temporal gyrus is at most 8 mm away from an area assumed to store information about object movement (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; see also Beauchamp et al., 2002). Likewise, Martin and colleagues interpret the differential activation observed in left premotor cortex in the context of the observation that this area is activated when subjects are asked to imagine grasping objects, but not to actually do so (Decety et al., 1994).

Because the sensory/motor theory assumes that conceptual knowledge is distributed over modality-specific representations, this proposal is a species of a broader theoretical view which holds that conceptual knowledge does not constitute (physically) distinct information from modality-specific input/output representations.[9] The question is: Does the sensory/motor theory make empirically tractable predictions?

In order to generate empirical predictions from the sensory/motor theory we will interpret this theory in its strongest form. The reason for this is straightforward: It is not clear in what ways the theory might be "weakened" while remaining empirically distinguishable from other theoretical alternatives. For instance, a weaker version of the theory might propose to combine a unitary-amodal account of semantic memory with the assumption that different types of knowledge are differentially important for different categories of objects and/or tasks. This was the route taken by Plaut (2002). The author presented a model of optic aphasia in which a central semantic store received input from two modalities, vision and touch, and made two types of output projections: action naming and object naming. This architecture was implemented in a distributed connectionist model, in which there was a topographic learning bias favouring short connections between semantic representations and modality-specific representations. When focal areas of semantic space were lesioned, the model demonstrated what Plaut referred to as a *graded degree of modality-specific functional specialisation within semantics*. However, the theory and the implemented model are indistinguishable from an amodal account of semantic memory in which there is a privileged relationship between the semantic representations of a certain class of objects and the information contained in a certain type of modality-specific input or output representation (for discussion, see Caramazza et al., 1990).[10]

Assuming the sensory/motor theory in its strongest form, it is important to be clear about what is meant by "information about the visual motion and patterns of motor movements associated with the actual use of the object." We reason as follows: Since modality-specific input/output representations and conceptual knowledge are distributed over the *same* features, this information *must* be modality-specific. Following conventions of the literature regarding modality-specific representations encoding information about how to manipulate objects, we refer to such representations as "sensorimotor representations" (these can also be referred to as visual/kinaesthetic representations). Two straightforward empirical predictions follow from the basic assumptions of the sensory/motor theory. *Prediction 1:* A deficit for conceptual knowledge of manipulable artefacts will be associated with damage to modality-specific input/output representations (i.e., sensorimotor knowledge); and *Prediction 2:* Damage to sensorimotor representations will *necessarily* be associated with a deficit for conceptual knowledge of manipulable artefacts. Note that the structure of these predictions, and the empirical arguments to be developed below, exactly

[9] For instance, Allport (1985) sums up this position as follows: "The essential idea is that the *same* neural elements that are involved in coding the sensory attributes of a (possibly unknown) object presented to eye or ear also make up the elements of the auto-associated activity patterns that represent familiar object-concepts in 'semantic memory'" (p. 53).

[10] We thank Laurel Buxbaum (personal communication) for raising this issue.

parallel recent evaluations of the sensory/functional theory (e.g., see Capitani et al., 2003-this issue; Caramazza & Shelton, 1998).

Empirical evaluation of Prediction 1

A deficit for conceptual knowledge of manipulable artefacts will be associated with damage to modality-specific input/output representations (i.e., sensorimotor knowledge).

Consider the performance of patients FB (Sirigu, Duhamel, & Poncet, 1991) and DM (Buxbaum, Schwartz, & Carew, 1997), who could indicate the correct use associated with an object despite being impaired for semantic knowledge of manipulable objects. For example, when FB was asked to verbally provide both function information (what an object is used for) and manipulation information (how an object is used) in response to a safety pin (presented visually), he responded: "You open on one side, stick something on it, close it, and it stays in. I can tell you how it works, but I don't see its exact use. I don't think I have seen one like this before, it is not a very common object (Sirigu et al., 1991, p. 2555). It seems, from this example, that the patient has knowledge of *how* a safety pin is used, but no knowledge of what it might be *used for*.

Similarly, patient DM presented with impaired conceptual knowledge of objects but relatively intact ability to use objects. For instance, on a function matching test, the patient was asked to match two pictures out of three that are used for similar purposes (e.g., given pictures of a can opener, a hand mixer, and an electric mixer, the latter two would be the correct choice). The unrelated foil on this task was always visually similar to one of the two target items, and on many trials, all three items were associated (e.g., in the above example, all of the items are found in a kitchen). DM's performance was impaired on this task (61%; 22/36) compared to normal control subjects (94%; 34/36; range: 29–36/36). In contrast, DM's performance was flawless on a task in which real objects were presented in both the visual and tactile modalities and the patient was asked to demonstrate the correct use associated with the object. Crucially, DM's performance was also very good (91%; 10/11) at demonstrating the correct use associated with objects when they were presented only in the visual modality (and the patient was not allowed to touch them). This last result indicates that visual information alone was sufficient to support relatively unimpaired performance on a task requiring objects to be used, but the same information (provided in pictures) was not sufficient to support performance on a function matching task.

The performance of patients FB and DM indicates that (1) there is a dissociation between function knowledge (what an object is for) and manipulation knowledge (how an object is used); and (2) it is possible to observe, within the same patient, a *semantic* impairment for tools without an associated impairment in *using* tools. These data would seem to indicate that it can't be the case that conceptual knowledge of tools is distributed over the same features as knowledge of how tools are used, since these patients could access knowledge of how tools are used but were impaired at accessing conceptual knowledge about tools. However, the strength of this conclusion is mitigated by the alternative hypothesis that patients such as FB and DM are succeeding on object use tests through general mechanical problem-solving abilities and not through accessing stored representations of the correct gestures associated with objects (e.g., Goldenberg & Hagmann, 1998; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000; Hodges, Spatt, & Patterson, 1999).

In the case of FB, support for this alternative hypothesis is provided by the fact that on an object decision task, the patient accepted nonobjects that were not functionally anomalous as real objects, suggesting that the patient was not accessing stored representations but was making judgements based on the extraction of object properties. Furthermore, neither FB nor DM were tested on a novel tool use task, which is generally regarded as informative of a patient's ability to infer the function of a tool from its physical structure. Finally, it could also be noted that neither FB nor DM had lesions extending into the parietal lobes, and that parietal lobe lesions have been associated with impairments in novel tools selection tasks (Goldenberg & Hagmann, 1998).

The possibility that FB and DM are succeeding on object use tests through general mechanical problem-solving skills raises an important theoretical question: On the assumption that part of the conceptual representation of a tool includes knowledge of how to use that tool, a distinction is required between the semantic system *storing* such information and the semantic system *reading* this information from sensorimotor engrams (see, e.g., Sirigu et al., 1991; and Buxbaum, Veramonti, & Schwartz, 2000, for discussion). That is, how might we distinguish between the semantic system storing the information that a hammer is used by swinging the hand in an arc from the semantic system retrieving this information by reading a modality-specific sensorimotor engram? It is the burden of those theories for which knowledge of the ways in which objects are manipulated figures critically in the conceptual representations of those objects to give a principled account of how these two possibilities might be empirically distinguished.

Empirical evaluation of Prediction 2

Damage to sensorimotor representations will *necessarily* be associated with a deficit for conceptual knowledge of manipulable artefacts.

We turn now to the second, and *determining* prediction made by the sensory/motor theory: There *cannot* be patients who are impaired at using tools but can nevertheless access intact semantic information about tools and/or recognise/name tools. If there were to be a patient whose performance was contrary to this prediction, then we could conclude that it is not the case that conceptual knowledge of artefacts is distributed over the same features that constitute sensorimotor knowledge. In fact, there are a number of such patients reported in the literature (Buxbaum et al., 2000; Hodges et al., 1999; Montomura & Yamadori, 1994; Ochipa, Rothi, & Heilman, 1989; Rumiati, Zanini, Vorano, & Shallice, 2001). For instance, Ochipa and colleagues reported the performance of a patient who was relatively unimpaired at naming tools (17/20 correct) as well as pointing them out to name (19/20). However, he was severely impaired at (1) pointing to a correct tool when given its function (7/20); (2) verbally describing the function of a visually presented tool (3/20); (3) verbally identifying a tool described by its function (3/10); (4) pantomiming the use of a tool to a verbal command (0/20); and (5) demonstrating tool use when holding a tool (2/20). Crucially, the same 20 tools were used for all tasks with this patient, and yet he was able to name and identify tools but was not able to use them or identify them based on their function (see Figure 1).

The patient reported by Ochipa and colleagues (1989) was also impaired at imitating symbolic gestures (4/20); symbolic gestures are learned manual movements, such as making the "peace sign" or the "hitch-hiking fist." Based on this deficit for symbolic gestures, it might be argued that the patient had an uninteresting production deficit that did not compromise sensorimotor representations. However, the patient reported by Montomura and Yamadori (1994) was unimpaired at making symbolic gestures to command, imitating symbolic gestures, pantomiming tool use to command, and pantomiming tool use to imitation, indicating that the inability of the patient to use the same tools correctly cannot be dismissed in terms of a motor deficit. This patient was impaired at imitating and pantomiming to command "meaningless" gestures (i.e., manual gestures that do not have a conventional meaning). This pattern of performance suggests damage to a mechanism for directly converting observed hand movements to motor commands, without accessing stored representations of what those movements mean; see Rothi, Ochipa, and Heilman (1991) and Cubelli, Marchetti, Boscolo, and Della Sala (2000) for discussion.

The performance of the patient reported by Ochipa and colleagues (1989) seems to indicate

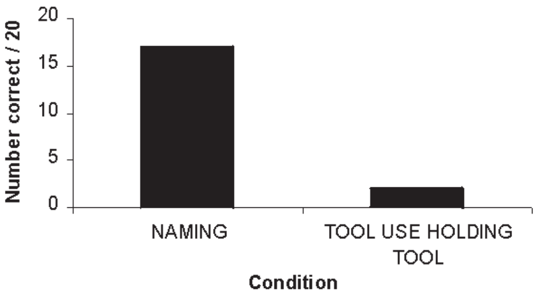

Figure 1. *Dissociation of tool use from tool naming (Ochipa et al., 1989).*

that the ability to recognise/name objects does not require that either functional knowledge (what an object is used for) or manipulation knowledge (how an object is used) must be intact and/or accessible. However, it might be argued that it has not been demonstrated that the patient reported by Ochipa and colleagues had damage to stored knowledge of how tools are used. Specifically, it might be argued that this patient was impaired at producing the correct actions associated with a tool, but the patient was nevertheless able to access stored knowledge of the movements associated with objects in order to succeed at naming tasks; this position entails the hypothesis that the damage in Ochipa and colleagues' patient was to the *connections* between sensorimotor engrams and the production system. A similar position has been advanced by Buxbaum et al. (2000) to distinguish between what the authors term "central" and "peripheral" apraxics: Central apraxics can neither recognise nor produce gestures, while peripheral apraxics are only impaired at producing the correct gesture associated with an object. It is assumed that central apraxics have damage to sensorimotor representations, while peripheral apraxics have damage to the connections between sensorimotor representations and the production system. The question is: Are there any central apraxics (i.e., patients with impairments in both recognising and producing gestures) who can nevertheless access intact semantic information about objects?

Further empirical evaluation of Prediction 2

Damage to sensorimotor representations will *necessarily* be associated with a deficit for conceptual knowledge of manipulable artefacts.

Patient WC (Buxbaum et al., 2000) presented with an impairment for knowledge of how objects are manipulated but perfect performance on a number of tasks requiring access to conceptual knowledge of objects. For instance, WC was impaired at choosing the correct object out of four to match an observed gesture, indicating an impairment in recognising gestures (80%; control mean 97%). WC was also impaired in using actual objects presented in the visual and tactile modalities, indicating an impairment in producing the correct gestures associated with an object (73%; control mean 99%). The combination of a deficit in both gesture production and recognition indicates that there is damage to stored sensorimotor representations of the correct gestures associated with objects (Buxbaum et al., 2000). Perhaps even more convincing that the impairment in WC was to the knowledge (per se) of how to manipulate objects is the patient's contrasting performance on picture matching tasks requiring objects to be matched based on either their function or their manner of manipulation. In this task, the patient is presented with three pictures and must choose the two that are most similar. In the manipulation condition, all three items on a given trial differ in terms of their function, while two of the three are similar in their manner of manipulation (for instance, given pictures of a piano, typewriter, and stove, the correct response would be to choose piano and typewriter). For this manipulation condition, WC was severely impaired (50%; control mean 96%). Contrastively, for the function condition, all three items on a given trial differ in their manner of manipulation, and the patient must pick the two pictures out of three that have similar functions (i.e., given radio, record player, and telephone, the correct response would be to select radio and record player). WC was at ceiling (100%) on this task. WC was also administered semantic probe questions testing his knowledge of specific conceptual properties of tools. For instance, given a picture of, for instance, a knife, the patient might be asked: "Is it used for tightening or for cutting?" WC was at ceiling (100% correct) for answering semantic probe questions about tools.

Refuting the sensory/motor theory

A final aspect of WC's profile should be noted: WC presented with severe anomia. This aspect of the patient's performance seems to indicate, at least at first glance, that an impairment to knowledge of how to use objects is associated with a naming deficit. However, we know from the performance of the patient reported by Ochipa and colleagues (see Figure 1) that this association of impairments is not necessary. Regardless, even setting aside Ochipa and colleagues' patient, the association of anomia and an impairment for using tools is not relevant to an evaluation of the assumption that conceptual knowledge of tools is distributed over modality-specific sensorimotor representations.[11] It is this assumption that is under evaluation.

Patient WC was at ceiling on several tasks requiring access to conceptual knowledge of tools and at the same time disproportionately impaired for knowledge of how to use tools. On the assumption that WC had damage to sensorimotor representations that store information about the ways in which objects are used, it would not be possible, given the assumptions of the sensory/motor theory, to account for the ceiling performance of this patient on several tasks requiring access to conceptual knowledge.[12] Furthermore, recall that the sensory/motor theory also appealed to knowledge of the visual movements associated with using tools: The performance of WC speaks to this assumption as well, as the patient was impaired at recognising the correct gestures associated with the use of tools. The performance of patient WC refutes the hypothesis that conceptual knowledge of manipulable objects is distributed over the same modality-specific representations that are active when such objects are being used. Given that this is the central (and distinguishing) assumption of the sensory/motor theory, the theory as a whole can be provisionally rejected.[13] Our conclusion is *not* that conceptual knowledge of artefacts does not include knowledge of the ways in which artifacts are used. Rather, we have been arguing against the claim, in the terms in which it has been proposed, that conceptual knowledge of artefacts is distributed over modality-specific sensorimotor representations.

One possible counterargument to our conclusion is the following: It might be argued by a sensory/motor theorist that while WC had damage to sensorimotor representations, this damage was not so extensive as to cause a deficit for the conceptual knowledge that is distributed over these representations. There is an empirical argument against this: If there were patients with disproportionate conceptual deficits for artefacts compared to other categories of objects, then we could infer (based on the sensory/motor theory) that these patients must also have presented with disproportionate deficits for the type of conceptual knowledge that is hypothesised to be distributed over sensorimotor representations. Specifically, the prediction is the same as is made by the original formulation of the sensory/functional theory: Patients with disproportionate deficits for artefacts will also have disproportionate deficits for functional/associative knowledge compared to visual/perceptual knowledge. Contrary to this prediction is the performance of patients PL (Laiacona & Capitani, 2001), CN98 (Gaillard, Auzou, Miret, Ozsancak, & Hannequin, 1998), and ES (Moss & Tyler, 1997, 2000). These patients presented with disproportionate deficits for artifacts, but *equivalent* impairments for perceptual and functional/associative knowledge of artifacts. Furthermore, the structural description system was spared in patient PL, indicating that the impairment to visual/perceptual knowledge of nonliving things was not an artefact of having damage to the structural descriptions of those objects. Even more striking is the performance of patient IW (Lambon Ralph, Howard, Nightingale, & Ellis, 1998) who presented with a

[11] Data is not reported on WC's naming performance by semantic category. However, on a triplet matching task, the patient was presented with three words, and had to choose the two that were most semantically similar (e.g., given hammer, mallet, and saw, the correct answer would be hammer and mallet). Contrary to what would be predicted by the sensory/motor theory, WC's performance on this test was actually slightly *better* for tool triplets (94%) than for animal triplets (83%).

[12] Another task administered to WC investigated whether he could choose the correct object corresponding to a given tool. For instance, when presented with a hammer, WC had to choose between a nail and screw as the correct object to use with a hammer. WC was just below ceiling on this task (96%); however, when WC was asked to demonstrate the use of the *same* tools on the *same* objects that the patient had just selected, the patient was severely impaired (58%). For instance, on the trial with a hammer and nail, after selecting the nail, WC grasped the hammer at the wrong end and pounded the nail with the hammer's handle.

[13] The "other half" of the theory concerns living things. The assumption here is the same made by the sensory/functional theory: The ability to recognise living things differentially depends on visual/perceptual information. (But see Capitani et al., 2003-this issue; Humphreys & Forde, 2001; Mahon & Caramazza, 2001.)

disproportionate (albeit small) impairment for nonliving things compared to living things (33% and 42% respectively). In direct contrast to what would be expected based on the assumption that functional/associative knowledge is needed to support correct recognition/naming of artefacts, this patient was disproportionately impaired for visual/perceptual knowledge compared to functional/associative knowledge for both living and nonliving things. At this point, it seems the only option left for a sensory/motor theorist is to assume that visual/perceptual knowledge is what is crucial for recognising/naming artifacts, and that it is *this* knowledge that is distributed over sensorimotor engrams. However, at this point, the theory cannot explain the cause of category-specific deficits, since both living things and artefacts would be hypothesised to depend on visual/perceptual knowledge.

One way in which the sensory/motor theory might be modified in an attempt to account for the neuropsychological evidence that has been reviewed would be to drop the assumption that conceptual knowledge of manipulable artefacts is distributed over the same representations that are active when such objects are being used. In other words, it could be that sensorimotor knowledge is functionally (and physically) dissociable from conceptual knowledge, but that sensorimotor information is nevertheless required in order to perform correctly on naming and recognition tasks. Note that the revised sensory/motor theory *must* assume that knowledge of the ways in which objects are used is required, or at least differentially important, for recognising tools; if the theory does not assume sensorimotor knowledge is (at least) differentially important for recognising/naming tools, then it would not have provided an explanatory account of the cause of category-specific semantic deficits.

However, even on the basis of the neuropsychological evidence that has already been reviewed, it is clear that revising the sensory/motor theory in this way will not be sufficient to save it. For instance, if knowledge of the ways in which objects are manipulated is required (or differentially important) in order to recognize/name objects, then one cannot account for the performance of the patient reported by Ochipa and colleagues (1989). Recall that this patient was relatively unimpaired at naming tools (17/20 correct) but was severely impaired at demonstrating the use of the same tools (2/20) (see Figure 1).

Another version of the sensory/motor theory stresses the contexts in which different types of information are recruited:

> Consistent with the notion of 'privileged access' to various kinds of stored information (e.g., sensorimotor versus verbal/propositional) according to the modality of the task (e.g., action versus verbal), it may be that on naturalistic action tasks, manipulation nodes for objects are the most strongly and rapidly activated, whereas on verbal tasks concerned with man-made objects, function nodes receive greater and/or more rapid activation. The hypothesized privileged role of manipulation knowledge in naturalistic action may explain why JD [reported in Buxbaum et al., 2000] and WC are unable to use their relatively intact function knowledge to prevent object misuse errors in naturalistic action (Buxbaum et al., 2000, p. 94).

It is not clear what work the notion of "privileged access" could be doing, unless the proposal is that there is an amodal semantic system. In other words, if the semantic system is assumed to be modality-specific, then there would be no need for the assumption of a *privileged* relationship between a certain type of semantic information and a certain type of modality-specific input/output representation, since the semantic representations themselves would *already be* modality-specific. However, if an amodal semantic system is assumed, then this is not a "weaker" version of the sensory/motor theory, but rather an amodal account of the organisation of semantic knowledge that stresses the importance of different types of semantic information as a function of task demands (see, e.g., Caramazza et al., 1990, and above discussion of Plaut, 2002).[14]

In this section we have critically evaluated two assumptions: First, we have shown that the assumption that conceptual knowledge of manipulable artefacts is distributed over modality-specific sensorimotor representations is contrary to the performance of patient WC. Second, we have shown that the (weaker) assumption that in order to name/recognise tools, information about their use

[14] We are grateful to Laurel Buxbaum (personal communication) for bringing these issues to our attention.

must be accessible, is contrary to the performance of patients such as the one reported by Ochipa and colleagues (1989). In the next section we consider how the data reviewed in this article constrain questions about the organisation and representation of conceptual knowledge.

CONCLUSION

The structure of the argument that has been developed against the sensory/motor theory is not new: Arguments of the same structure have been articulated against the basic assumptions of the sensory/functional theory by a number of authors. For example, some sensory/functional theorists have proposed that the specific type of visual/perceptual information required in order to recognise fruit/vegetables consists of knowledge of their colour (e.g., Humphreys & Forde, 2001). If we interpret this claim literally and in its strongest form, the prediction is made that a deficit for knowledge of object colour must be associated with a disproportionate deficit for fruit/vegetables. Notice that any weaker interpretation of the proposal renders it unable to account for a category-specific deficit for fruit/vegetables. Evidence contrary to this proposal has been reported by Miceli, Fouch, Capasso, Shelton, Tomaiuolo, and Caramazza (2001): Patient IOC presented with intact colour perception but impaired knowledge of the colours associated with objects. IOC did not present with a disproportionate deficit for fruit/vegetables compared to other semantic categories. These data indicate that the existence of category-specific deficits for fruit/vegetables cannot be explained in terms of an impairment to knowledge of object colour. Similarly with respect to the sensory/motor theory: Patient WC was impaired for both producing and recognising the correct movements associated with the actual use of objects, but was unimpaired for conceptual knowledge of objects across a wide range of tests. This indicates that it cannot be the case that conceptual knowledge of tools is distributed over sensorimotor representations.

The argument that has been developed against the sensory/motor theory with respect to the category of tools is thus a species of a broader and more general argument that has been articulated against the sensory/functional theory. The fact that the majority of well-studied patients with category-specific deficits have presented with equivalent impairments to both visual/perceptual and functional/associative knowledge of items from the impaired category (Capitani et al., 2003-this issue) demonstrates the inadequacy of the sensory/functional theory to explain the existence of category-specific deficits. In this article we have suggested that the simplest solution is to assume that the broadest constraint on the organisation of conceptual knowledge is object domain. Furthermore, as discussed above, adopting the domain-specific hypothesis does not entail rejecting the assumption that conceptual knowledge is organised in the brain into modality-specific stores. If the domain-specific hypothesis is conjoined with the modality-specific store assumption, the prediction is made that that there will be segregation of information corresponding to different categories of objects within neuroanatomically defined modalities. Functional neuroimaging data consistent with this prediction were reviewed: A number of investigators have observed that living things and nonliving things produced differential and spatially dissociable peaks of activation in inferior and lateral temporal cortex.

The critical issue in regard to these functional neuroimaging data concerns the nature of the information that is activated in a seemingly category-specific pattern. For instance, does the activation in fusiform regions reflect the activation of modality-specific representations (i.e., visual/structural descriptions) or rather *conceptual* knowledge about the visual properties of objects? The same question must be addressed prior to an interpretation of the observation that tool stimuli differentially activated left premotor cortex. Does this finding reflect the activation of conceptual knowledge of tools or rather of modality-specific sensorimotor representations? Either possibility is consistent with a domain-specific interpretation, since this hypothesis assumes that both pre-conceptual and conceptual levels of representation/processing will be organised by domain-specific constraints. Thus, there is currently at best equivocal evidence from neuropsychology (e.g., patient Michelangelo) and functional neuroimaging that *conceptual* knowledge is organised in the brain into modality-specific semantic stores.

However, *if* one assumes that conceptual information is organised by object domain within neuroanatomically defined modalities, then it must also be assumed that conceptual information within a given domain is not functionally dissociable across modalities. But then the following question arises: Why did WC not present with a general conceptual deficit? In other words, if WC had a deficit for *conceptual* knowledge of how objects are used, *and* it is assumed that conceptual knowledge cannot be functionally dissociated across modalities, then this case presents a paradox. A straight-forward solution is to assume that the functional locus of damage in this patient is to the system that stores sensorimotor engrams. In other words, we might draw an analogy between the functional impairment in patient WC and the functional impairment in patients with damage to the visual/structural description system. However, this interpretation of the impairment in patient WC presupposes a positive answer to the question: Must we distinguish between modality-specific input/output representations and conceptual knowledge?

REFERENCES

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron*, *21*, 373–383.

Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. Newman & R. Epstein (Eds.), *Current perspectives in dysphasia.* New York: Churchill Livingstone.

Barbarotto, R., Capitani, E., & Laiacona, M. (1996). Naming deficit in herpes simplex isingencephalitis. *Acta Neurologica Scandinavica*, *93*, 272–280.

Basso, A., Capitani, E., & Laiacona, M. (1988). Progressive language impairment without dementia: A case study with isolated category-specific semantic defect. *Journal of Neurology, Neurosurgery, and Psychiatry*, *51*, 1201–1207

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, *34*, 149–159.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organisation of semantic processing. *Annual Review of Neuroscience*, *25*, 151–88

Buxbaum, L. J., Schwartz, M. F., & Carew, T. G. (1997). The role of semantic memory in object use. *Cognitive Neuropsychology*, *14*, 219–254.

Buxbaum, L. J., Veramonti, T., Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing "what for" but not "how." *Neurocase*, *6*, 83–97.

Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, *20*, 213–261.

Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology*, *7*, 161–189.

Caramazza, A., & Shelton, J. R. (1998). Domain specific knowledge systems in the brain: The animate–inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.

Carey, S. (2000). The origins of concepts. *Journal of Cognition and Development*, *1*, 37–41.

Carey, S., & Markman, E. M. (1999). Cognitive development. In B. Martin & D. E. Rumelhart (Eds), *Cognitive science. Handbook of perception and cognition* (2nd ed., pp. 201–254). San Diego, CA: Academic Press.

Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, *125*, 1839–1849.

Castelli, F., Happé, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, *12*, 314–325.

Chao, L. L., Haxby, J. V., & Martin, A. (1999a). Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, *12*, 478–84

Chao, L. L., Martin, A., & Haxby, J. V. (1999b). Are face-responsive regions selective only for faces? *NeuroReport*, *10*, 2945–50

Chao, L. L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex*, *12*, 545–551.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science*, *248*, 1556–1559

Crutch, S. J., & Warrington, E. K. (2003). The selective impairment of fruit and vegetable knowledge: A multiple processing channels account of fine-grain category specificity. *Cognitive Neuropsychology*, *20*, 355–372.

Cubelli, R., Marchetti, C., Boscolo, G., & Della Sala, S. (2000). Cognition in action: Testing a model of limb apraxia. *Brain and Cognition*, *44*, 144–165.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J. C., & Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature*, *371*, 600–602.

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Moss, H. E., Fadili, M. J., & Tyler, L. K. (2002). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia*, *40*, 54–75.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601

Farah, M. J., Hammond, K. M., Mehta, Z., & Ratcliff, G. (1989). Category-specificity and modality–specificity in semantic memory. *Neuropsychologia*, *27*, 193–200.

Farah, M. J., & Rabinowitz, C. (2003). Genetic and environmental influences on the organisation of semantic memory in the brain: Is "living things" an innate category? *Cognitive Neuropsychology*, *20*, 401–408.

Farah, M. J., & Wallace, M. A. (1992). Semantically bounded anomia: Implication for the neural implementation of naming. *Neuropsychologia*, *30*, 609–621.

Gaillard, M. J., Auzou, P., Miret, M., Ozsancak, C., & Hannequin, D. (1998). Trouble de la dénomination pour les objets manufacturés dans un cas d'encéphalite herpétique. *Révue Neurologique*, *154*, 683–689.

Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2000). Categorization and category-effects in normal object recognition: A PET study. *Neuropsychologia*, *38*, 1693–1703.

Goldenberg, G., & Hagmann, S. (1998). Tool use and mechanical problem solving in apraxia. *Neuropsychologia*, *36*, 581–589.

Gonnerman, L., Andersen, E. S., Devlin, J. T., Kempler, D., & Seidenberg, M. (1997). Double dissociation of semantic categories in Alzheimer's disease. *Brain and Language*, *57*, 254–279.

Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage, 7*, 232–243.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199

Hodges, J. R., Bozeat, S., Lambon Ralph, M., Patterson, K., & Spatt, J. (2000). The role of conceptual knowledge in object use. Evidence from semantic dementia. *Brain*, *123*, 1913–1925.

Hodges, J. R., Spatt, J., & Patterson, K. (1999). "What" and "how": Evidence for the dissociation of object knowledge and mechanical problem-solving skills in the human brain. *Proceedings of the National Academy of Science, USA*, *96*, 9444–9448.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, *3*, 80–84.

Humphreys, G. W., & Forde, E. M. E. (2001). Hierarchies, similarity, and interactivity in object recognition: "Category-specific" neuropsychological deficits. *Behavioral and Brain Sciences*, *24*, 453–509.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Science, USA*, *96*, 9379–9384

Joseph, J. E. (2001). Functional neuroimaging studies of category specificity in object recognition: A critical review and meta-analysis. *Cognitive, Affective and Behavioral Neuroscience*, *1*, 119–136.

Kanwisher, N. (2000). Domain specificity in face perception. *Nature*, *3*, 759–763.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.

Keil, F. C. (1989). *Concepts, kinds, and cognitive development*. Cambridge, MA: MIT Press.

Kraut, M. A., Moo, L. R., Segal, J. B., & Hart, J. Jr. (2002). Neural activation during an explicit categorisation task: Category- or feature-specific effects? *Cognitive Brain Research*, *13*, 213–220.

Laiacona, M., Barbarotto, R., & Capitani, E. (1993). Perceptual and associative knowledge in category specific impairment of semantic memory: A study of two cases. *Cortex*, *29*, 727–740.

Laiacona, M., & Capitani, E. (2001). A case of prevailing deficit for nonliving categories or a case of prevailing sparing of living categories? *Cognitive Neuropsychology*, *18*, 39–70

Laiacona, M., Capitani, E., & Barbarotto, R. (1997). Semantic category dissociations: A longitudinal study of two cases. *Cortex*, *33*, 441–461.

Lambon Ralph, M. A., Howard, D., Nightingale, G., & Ellis, A. W. (1998). Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? Evidence from a category-specific double dissociation. *Neurocase*, *4*, 311–338.

Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review*, *74*, 431–461.

Mahon, B., & Caramazza, A. (2001). The sensory/functional assumption or the data: Which do we keep? *Behavioral and Brain Sciences*, *24*, 488–489.

Mahon, B., & Caramazza, A. (in press). The organization of conceptual knowledge in the brain: Living kinds and artifacts. In E. Margolis & S. Laurence (Eds.), *Creations of the mind: Essays on artefacts and their representation*. Oxford: Oxford University Press.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, *11*, 194–201.

Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category specificity and the brain: The sensory/motor model of semantic representations of objects. In M. S. Gazzaniga (Ed.), *Higher cognitive functions*: *The new cognitive neurosciences* (pp. 1023–1036). Cambridge, MA: The MIT Press.

Martin, A., & Weisberg, J. (2003). Neural foundations for understanding social and mechanical concepts. *Cognitive Neuropsychology*, *20*, 575–587.

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652.

McCarthy, C., Puce, A., Gore, J. C., & Allison, T., (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*, 605–610.

Miceli, G., Fouch, E., Capasso, R., Shelton, J. R., Tomaiuolo, F., & Caramazza, A. (2001). The dissociation of color from form and function knowledge. *Nature Neuroscience*, *4*, 662–667.

Montomura, N., & Yamadori, A. (1994). A case of ideational apraxia with impairment of object use and preservation of object pantomime. *Cortex*, *30*, 167–170.

Moore, C. J., & Price, C. J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, *122*, 943–962

Moss, H. E., & Tyler, L. K. (1997). A category–specific semantic deficit for nonliving things in a case of progressive aphasia. *Brain and Language*, *60*, 55–58.

Moss, H. E., & Tyler, L. K. (2000). A progressive category-specific semantic deficit for non-living things. *Neuropsychologia*, *38*, 60–82.

Mummery, C. J., Patterson, K., Hodges, J. R., & Price, C. J. (1998). Functional neuroanatomy of the semantic system: Divisible by what? *Journal of Cognitive Neuroscience*, *10*, 766–777

Ochipa, C., Rothi, L. J. G., & Heilman, K. M., (1989). Ideational apraxia: A deficit in tool selection and use. *Annals of Neurology*, *25*, 190–193.

Perani, D., Cappa, S. F., Bettinardi, V., Bressi, S., Gorno-Tempini, M., Matarrese, M., & Fazio, F. (1995). Different neural systems for the recognition of animals and man-made tools. *NeuroReport*, *6*, 1637–1641.

Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: A PET study of semantic category effects. *Neuropsychologia*, *37*, 293–306.

Plaut, D. C. (2002). Graded modality-specific specialisation in semantics: A computational account of optic aphasia. *Cognitive Neuropsychology*, *19*, 603–639.

Price, C. J., & Friston, K. J. (2002). Functional imaging studies of category specificity. In E. M. E. Forde & G. W. Humphreys (Eds.), *Category-specificity in the brain and mind*. Hove, UK: Psychology Press.

Riddoch, M. J., Humphreys, G. W., Coltheart, M., & Funnell, E., (1988). Semantic systems or system? Neuropsychological evidence re-examined. *Cognitive Neuropsychology*, *5*, 3–25.

Rothi, L. J. G., Ochipa, C., & Heilman, K. M (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology*, *8*, 443–458.

Rumiati, R. I, Zanini, S., Vorano, L., & Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cognitive Neuropsychology*, *18*, 617–642.

Samson, D., & Pillon, A. (2003). A case of impaired knowledge for fruit and vegetables. *Cognitive Neuropsychology*, *20*, 373–400.

Samson, D., Pillon, A., & De Wilde, V. (1998). Impaired knowledge of visual and nonvisual attributes in a patient with a semantic impairment for living entities: A case of a true category-specific deficit. *Neurocase*, *4*, 273–290

Santos, L. R., & Caramazza, A. (2002). The domain-specific hypothesis: A developmental and comparative perspective on category-specific deficits. In E. M. E. Forde & G. W. Humphreys (Eds.), *Category-specificity in the brain and mind* (pp. 1–24). Hove, UK: Psychology Press.

Santos, L. R., Hauser, M. D., & Spelke, E. S. (2002). Domain-specific knowledge in human children and non-human primates: Artifacts and foods. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 205–216). Cambridge, MA: MIT Press.

Sartori, G., Coltheart, M., Miozzo, M., & Job, R. (1994). Category specificity and informational specificity in neuropsychological impairment of semantic memory. In C. A. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV* (pp. 537–550). Cambridge, MA: MIT Press.

Sartori, G., & Job, R. (1988). The oyster with four legs: A neuropsychological study on the interaction between vision and semantic information. *Cognitive Neuropsychology*, *5*, 105–132.

Sartori, G., Job, R., Miozzo, M., Zago, S., & Marchiori, G. (1993a). Category-specific form-knowledge deficit in a patient with herpes simplex virus encephalitis. *Journal of Clinical and Experimental Neuropsychology*, *15*, 280–299.

Sartori, G., Miozzo, M., & Job, R. (1993b). Category-specific naming impairments? Yes. *Quarterly Journal of Experimental Psychology*, *46A*, 489–504.

Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., & David, A. S. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology*, *10*, 16–22.

Sheridan, J., & Humphreys, G. W. (1993). A verbal-semantic category-specific recognition impairment. *Cognitive Neuropsychology*, *10*, 143–184.

Silveri, M. C., & Gainotti, G. (1988). Interaction between vision and language in category-specific semantic impairment. *Cognitive Neuropsychology*, *5*, 677–709.

Sirigu, A., Duhamel, J., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. *Brain*, *114*, 2555–2573.

Thompson-Schill, S. L. (2002). Neuroimaging studies of semantic memory: Inferring "how" from "where." *Neuropsychologia*, *40*, 280–292.

Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, *106*, 859–878.

Warrington, E. K., & McCarthy, R. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain*, *110*, 1273–1296.

Warrington, E. K., & McCarthy, R. A. (1994). Multiple meaning systems in the brain: A case for visual semantics. *Neuropsychologia*, *32*, 1465–1473.

Warrington, E. K., & Shallice, T. (1984). Category-specific semantic impairment. *Brain*, *107*, 829–854.

Whatmough, C., Chertkow, H., Murtha, S., & Hanratty, K. (2002). Dissociable brain regions process object meaning and object structure during picture naming. *Neuropsychologia*, *40*, 174–186.