

The organisation of conceptual knowledge in the brain: The future's past and some future directions

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We review the development and current status of theories of the organisation and representation of conceptual knowledge in the human brain. The currently known facts from optic aphasia, category-specific semantic deficits, and functional neuroimaging are consistent with a framework in which the first-order constraint on the organisation of conceptual knowledge is domain. Data from functional neuroimaging suggests additionally a framework characterised by both domain- and modality-specific constraints. Work in congenital disorders and in apraxia indicate that the content of conceptual knowledge is not exhausted by modality-specific input/output processes. It is concluded that future empirical and theoretical work on the organisation and representation of conceptual knowledge will profit from a reorientation of the problem from the organisation of distinct processing systems to the content of information represented internal to such systems.

INTRODUCTION

Modern theories of the organisation of conceptual knowledge in the brain can be divided into two groups, depending on their underlying principles. One group of theories, based on the *neural structure principle*, assumes that the organisation of conceptual knowledge is governed by representational constraints imposed by the brain itself. A second group of theories, based on the *correlated structure principle*, assumes that the organisation of conceptual knowledge in the brain is a reflection of the statistical co-occurrence of object properties in the world. Two types of

hypotheses have appealed to the neural structure principle: the Modality-Specific Semantic Hypothesis and the Domain-Specific Hypothesis. Theories based on the correlated structure principle can be distinguished from one another by the types of feature properties (e.g., correlation, distinctiveness) to which they appeal, and how such properties are (assumed to be) distributed in the world.

The modern study of the organisation of conceptual knowledge in the brain began with the work of Warrington, McCarthy, and Shallice in category-specific semantic deficits (Warrington & McCarthy, 1983, 1987;

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Warrington & Shallice, 1984). However, an important precursor is the work on optic aphasia (Lhermitte & Beauvois, 1973), which provided the initial impetus for modality-based theories of conceptual representation. Following the lead of these first reports, the case study approach in cognitive neuropsychology has been central to the development and evaluation of extant hypotheses about the organisation of conceptual knowledge. More recently, researchers have sought convergent evidence in functional neuroimaging. In this article we review the development and current evidential state of extant theories and outline some future theoretical directions.

OPTIC APHASIA

Optic aphasia is a modality-specific naming impairment specific to visually presented objects that cannot be reduced to a general visual agnosia or a general anomia. Lhermitte and Beauvois' (1973) patient was 73% correct at naming objects to visual presentation but 91% correct to tactile naming, 96% correct to definition, and 100% correct at gesturing the correct use associated with visually presented objects (see also, e.g., Campbell & Manning, 1996; Coslett & Saffran, 1989; Hillis & Caramazza, 1995; Riddoch & Humphreys, 1987; for reviews, see Plaut, 2002; Riddoch, 1999). Beauvois (1982) explained this pattern of behaviour by assuming that the conceptual system is organised into visual and verbal semantics: Optic aphasia would result from a disconnection between the two semantic systems. The typical lesion profile of optic aphasics is consistent with this hypothesis: Optic aphasic patients typically present with left occipital lesions extending to the splenium, effectively cutting off the left-hemisphere language centres from visual input.

There were early critiques of the modality-specific semantics proposal (Caramazza, Hillis, Rapp, & Romani, 1990; Riddoch, Humphreys, Coltheart, & Funnell, 1988). It was argued that the phenomenon of optic aphasia did not compel a division between visual and verbal semantics, for two independent reasons. First, the phenomenon of optic aphasia could be explained by assuming that (intact) pre-semantic representations of the visual structure of objects were disconnected from the semantic system but still connected to motor programmes supporting correct object use (Riddoch et al., 1988). A second critique of the Modality-Specific Semantic Hypothesis was that the notion of modality-specificity at the conceptual level had not been sufficiently fleshed out (Caramazza et al., 1990). It was not specified what it was about the information stored in modality-specific semantic subsystems that made them "modality-specific." Is it the format in which information is represented? Is it the content of the information (i.e., what that information is *about*) but not the format in which it is stored? Is it the modality through which the information was acquired?

Caramazza and colleagues (1990) outlined an alternative interpretation of the performance of optic aphasics (the Organized Unitary Content Hypothesis: OUCH), which assumes that certain types of input/output modalities have a privileged relationship with, or privileged access to, certain types of semantic information. To the degree that the notion of privileged access was sufficient to account for the dissociation between naming and gesturing to visually presented objects, there was no need to make the additional assumption of a functional division between visual and verbal modality-specific semantic subsystems.¹

Further proposals were made, including the view that optic aphasia reflected a disconnection

¹ We use the terms "conceptual" and "semantic" interchangeably: i.e., category-specific semantic deficits (see below) could equally be called category-specific conceptual deficits. We will use the term "modality-specific semantic subsystem" to refer to information (or process) that mediates between pre- and post-semantic representations (e.g., between visual structural descriptions and phonological/orthographical lexical representations). We will refer to the latter type of representations as "modality-specific input/output" representations. The distinction between modality-specific input/output representations and modality-specific semantic representations will be examined more closely below.

of left-from right-hemisphere semantics (Coslett & Saffran, 1989, 1992). On this view, right-hemisphere semantics is sufficient to support relatively coarse, visually based semantic processing (e.g., gesturing the use of objects) but cannot communicate with the left-hemisphere language centres. Hillis and Caramazza (1995) argued that if the right hemisphere were disconnected from the left, then the naming errors of optic aphasics should bear no resemblance to the target. However, it is normally observed that the majority of naming errors made by optic aphasics are semantically related to the target. In other words, the nature of the errors made by optic aphasics would compel the assumption that the right hemisphere is not *completely* disconnected from the left hemisphere. However, at this point, the proposal becomes indistinguishable from both the multiple semantics view and the OUCH.

Some data germane but not decisive in regard to this debate were reported by Hillis and Caramazza (1995) in their study of an optic aphasic patient, DHY. This patient presented with the same pattern of performance that was originally used to motivate the assumption of separate (modality- or hemisphere-specific) semantic systems. DHY was impaired for naming to visual presentation but not for naming to definition or in response to tactilely presented stimuli, and showed normal performance in tasks that measured the ability to construct (visual) structural representations of objects. And, as had been reported for other optic aphasics, DHY did not demonstrate any marked semantic impairment on relatively “easy” semantic tasks with visually presented stimuli, such as word–picture matching. However, further testing demonstrated that when visually presented semantic tasks were made more difficult, such that fine-grained discriminations were required between similar concepts, DHY was impaired. The implication of these data is that semantic processing of visually presented stimuli in optic aphasics is not “intact.” This follows both from the dominant type of

naming errors (semantically related to the target, or to a previous response) and the presence of a mild semantic impairment in processing visual stimuli. A plausible interpretation of these results is that DHY’s impairment reflects the failure to normally access a modality independent semantic representation from an intact structural description of visually presented objects.

Recently, Plaut (2002) proposed a reorientation of the debate with an implemented account of optic aphasia in which the semantic system is claimed to exhibit a “graded degree of modality-specificity.” The implemented model’s representation of the semantic system can be schematically captured in terms of a two-dimensional grid, with two input modalities (vision and touch) and two output modalities (oral naming and gesture). (Vision and touch were equidistant from phonology, and vision was equidistant from action and phonology.) The model was trained using a topographic learning bias that favoured short over long connections between a given input modality (i.e., vision or touch) and semantic representations (i.e., patterns of activation over units on the two-dimensional grid). Subsequent to training, the major quantitative patterns of dissociation observed in optic aphasia could be simulated by lesioning the shorter connections between the visual input modality and the semantic system.

The question is: which theoretical account, the Modality-Specific Semantics Hypothesis or OUCH, is supported by the simulations reported by Plaut (2002)? The answer to this question is clear: When the overall levels of activation of semantic units were inspected subsequent to either visual or tactile input “...there was no reliable effect of the horizontal position of the unit [closer to vision or closer to touch], the modality of presentation, or the interaction of these factors ($ps > .29$). Thus, there is no difference in the extent to which the two modalities [vision and touch] generate greater activation over closer semantic units compared to more distant units; the entire² semantic system is

² Note that amodal theories of conceptual representation (e.g., OUCH) are not committed to this (unnecessarily) strong claim that the *entire* semantic system is involved in representing *all* types of information (e.g., see discussion of OUCH below).

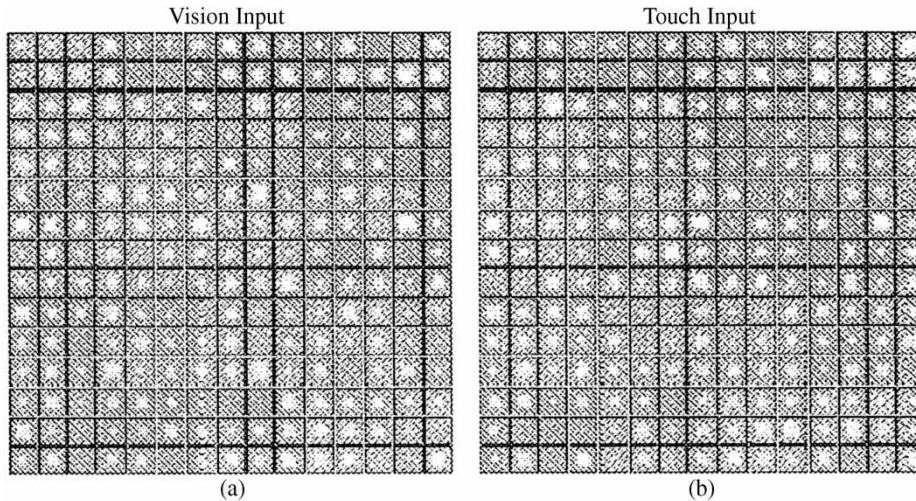


Figure 1. Mean semantic activation for each unit as a function of modality of presentation. (From Figure 4, Plaut, 2002, p. 614; with permission of the author and Psychology Press <http://www.psypress.co.uk/journals.asp>)

involved in representing both visual and tactile input” (p. 615). Since there is no modality specificity (graded or otherwise) in the semantic representations implemented in the model, the reported simulations constitute an existence proof of OUCH. Or stated differently, the topographic learning bias modelled by Plaut (2002) is one way to implement the notion of privileged accessibility, which is the basic assumption made by OUCH in order to account for the performance of optic aphasic patients.

The early critiques of the multiple semantics approach (Caramazza et al., 1990; Riddoch et al., 1988) did not go unanswered (Shallice, 1993) and the answers were further engaged (Hillis, Rapp, & Caramazza, 1995). However, as is evident from this brief overview, the phenomenon of optic aphasia has been a fertile area for developing hypotheses, but has not been nearly as decisive in their evaluation. Much of the empirical and theoretical work in cognitive neuropsychology about the organisation of conceptual knowledge in the brain shifted its focus to the phenomenon of category-specific semantic deficits and to functional neuroimaging studies in normal subjects.

CATEGORY-SPECIFIC SEMANTIC DEFICITS

The phenomenon of category-specific semantic deficits frames what has proven to be a rich question: How could the conceptual system be organised such that various conditions of damage can give rise to conceptual impairments that disproportionately affect specific semantic categories? There is emerging consensus that any viable answer to this question must be able to account for the following three facts (e.g., Caramazza & Shelton, 1998; Cree & McRae, 2003; Moss & Tyler, 2003; Samson & Pillon, 2003; for recent reviews, see Capitani, Laiacona, Mahon, & Caramazza, 2003; Humphreys & Forde, 2001; Tyler & Moss, 2001; see Figure 2 for an example of a patient with a selective deficit to living animate things):

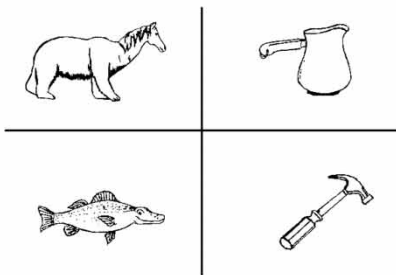
1. The *grain* of the phenomenon: Patients can be disproportionately impaired for either living animate things (animals) compared to living inanimate things (fruits and vegetables) (KR: Hart & Gordon, 1992; EW: Caramazza & Shelton, 1998) or living inanimate things

Picture Naming: EW's naming deficit was restricted to the category "animals" and did not extend to the other living things such as "fruit/vegetables," for which performance was at ceiling. On subsets of the Snodgrass & Vanderwart (1980) picture set matched jointly for familiarity and frequency, and visual complexity and familiarity, EW was disproportionately impaired at naming animals compared to non-animals.

Matched: Familiarity and Frequency		
	Animals	Non-Animals
EW	12/22 (55%)	18/22 (82%)
Controls	11/11 (100%)	10.8 (98%)
Range	11	10-11

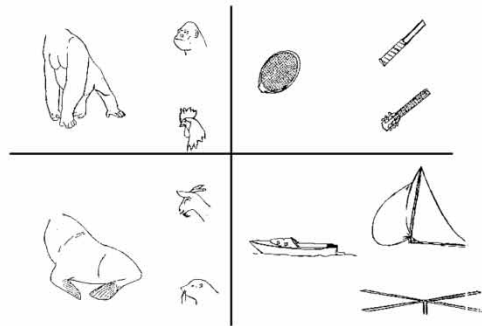
Matched: Visual Complexity and Familiarity		
	Animals	Non-Animals
EW	7/17 (41%)	16/17 (94%)
Controls	16.6/17 (98%)	16/17 (94%)
Range	16-17	16-17

Object Decision: EW was asked to decide (yes or no) whether a depicted object was real (see below for examples of stimuli). Performance on this task is interpreted as reflecting the integrity of the visual/structural description system (i.e., the modality-specific input system that stores representations corresponding to the form or shape of objects, and which is used to access conceptual information). EW performed significantly below the normal range for differentiating real from unreal animals (36/60; 60% correct; control mean: 54/60; 90%) but within the normal range for differentiating real from unreal non-animals (55/60; 92% correct; control mean: 50.5/60; 84% correct). However, EW performed within the normal range on complex visual processing tasks, such as visual matching and face recognition. These data indicate that EW does not have a general deficit for processing visually complex stimuli, and suggest that the patient's impairment for object reality decision for animals is categorically base



Sound Identification: EW was also impaired at naming animals compared to non-animals based on their characteristic sounds (8/32; 25% correct vs. 20/32; 63% correct: $z = 3.06, p < .05$) indicating that the patient's naming impairment is not restricted to visual input.

Parts Decision: EW was asked to decide which of two heads (or parts) went with a headless body (or object missing a part) (see below for examples of stimuli). EW was severely impaired on this task for animals (60% correct; normal mean: 100%) but performed within the normal range for artifacts (97% correct; normal mean: 97%).



Central Attribute Judgments: EW was asked to decide whether a given attribute was true of a given item (see below for examples of stimuli). EW was severely impaired for attributes pertaining to animals (65% correct; control range: 85 – 100%) but within the normal range for non-animals (95% correct; control range: 86-100%). EW was equivalently impaired for both visual/perceptual and functional/associative knowledge of living things (65% correct for both types of knowledge) but within the normal range for both types of knowledge for non-animals (visual/perceptual: 93.5% correct; control range: 86-100%; functional/ associative: 98% correct; normal range: 92-100%).

Examples of Central Attribute Questions

Visual/perceptual	Functional/associative
Does a cow have a mane?	Does a whale fly?
Does a whale have a large tail fin?	Does an eagle lay eggs?
Does a whale have eight legs?	Is a cow a farm animal?

Figure 2. An illustrative case of category-specific semantic deficit: Patient EW (Caramazza & Shelton, 1998). Reprinted from *Trends in Cognitive Sciences*, 7, Caramazza & Mahon, "The organization of conceptual knowledge: The evidence from category-specific semantic deficits", pp. 354–361, © 2003, with permission from Elsevier.

- compared to living animate things (e.g., MD: Hart, Berndt, & Caramazza, 1985; JJ: Hillis & Caramazza, 1991; TU: Farah & Wallace, 1992; FAV: Crutch & Warrington, 2003; RS: Samson & Pillon, 2003).
2. The *profile* of the phenomenon: Category-specific semantic deficits are not associated with disproportionate impairments for modalities or types of information (e.g., FM: Laiacona, Barbarotto, & Capitani, 1993; SB: Sheridan & Humphreys, 1993; EA: Barbarotto, Capitani, & Laiacona, 1996; Laiacona, Capitani, & Barbarotto, 1997; EW: Caramazza & Shelton, 1998; CN98: Gaillard, Auzou, Miret, Ozsancak, & Hannequin, 1998; Jennifer: Samson, Pillon, & De Wilde, 1998; PL: Laiacona & Capitani, 2001). Conversely, disproportionate impairments for modalities or types of information are not necessarily associated with category-specific semantic deficits (e.g., AC: Coltheart, Inglis, Cupples, Michie, Bates, & Budd, 1998; IW: Lambon Ralph, Howard, Nightingale, & Ellis, 1998).
 3. The *severity* of overall impairment: The direction of category-specific semantic deficits (i.e., living things worse than nonliving things, or vice versa) is not related to the overall severity of knowledge impairment (Garrard, Patterson, Watson, & Hodges, 1998; Zannino, Perri, Carlesimo, Pasqualettin, & Caltagirone, 2002).

Most of the empirical and theoretical work in category-specific semantic deficits has been driven by an attempt to evaluate a theoretical proposal first advanced by Warrington, Shallice, and McCarthy: the Sensory/Functional Theory. The

Sensory/Functional Theory is an extension of the Modality-Specific Semantic Hypothesis proposed by Beauvois (1982). In addition to assuming that the semantic system is functionally organised by modality or type of information, the Sensory/Functional Theory assumes that the recognition/identification of items from different semantic categories (e.g., living things compared to non-living things) differentially depends on different modality-specific semantic subsystems (i.e., visual/perceptual information compared to functional/associative information) (for data and/or discussion pertaining to this latter assumption, see Caramazza & Shelton, 1998; Cree & McRae, 2003; Farah & McClelland, 1991; Garrard, Lambon Ralph, Hodges, & Patterson, 2001; Mahon & Caramazza, 2006; Tyler & Moss, 2001; Vinson, Vigliocco, Cappa, & Siri, 2003). Category-specific semantic deficits were thus explained by assuming damage to the modality or type of information upon which recognition/identification of items from the impaired category differentially depends.

The original formulation of the Sensory/Functional Theory is inconsistent with facts (1) and (2). The fact that living animate things and living inanimate things doubly dissociate is at variance with the assumption that both categories are processed/represented by the same semantic system. The fact that category-specific semantic deficits are not associated with deficits to a modality or type of knowledge indicates that the phenomenon is not caused by impairments to modalities or types of knowledge. There have been a number of theoretical responses to this state of the field.³

³ Some early discussions of category-specific semantic deficits raised concerns that the phenomenon may be the result of uncontrolled stimulus variables: e.g., visual, complexity, familiarity, frequency (e.g., Funnell & Sheridan, 1992; Gaffan & Heywood, 1993; Stewart, Parkin, & Hunkin, 1992). Subsequent case reports in which the materials were carefully controlled for the relevant variables, as well as the observation of double dissociations over the same materials (e.g., Hillis & Caramazza, 1991) rule out this possibility (for review, see Capitani et al., 2003). More recently, Sartori and Lombardi (2004) have argued that category-specific semantic deficits for living things compared to nonliving things in a naming to definition task may arise due to a failure to “control” for the variable feature relevance, a measure of how predictable a concept is from a single feature. However, category-specific semantic deficits can manifest in a number of tasks besides naming to definition (e.g., picture naming, picture–word matching; picture matching; part–whole matching; category fluency; semantic attribute questions; see Figure 2). (For discussion and analysis of other stimulus variables, see Cree & McRae, 2003; Howard, Best, Bruce, & Gatehouse, 1995; for further discussion of the relevance framework, see Mahon & Caramazza, 2006).

Reformulating the sensory/functional theory

One proposal has been that specific types of visual/perceptual information are differentially important for living animate things or living inanimate things. For instance, it has been proposed that colour information is more important for fruits than animals (e.g., Cree & McRae, 2003; Crutch & Warrington, 2003; Humphreys & Forde, 2001) while biological motion information is more important for living animate things than living inanimate things (e.g., Cree & McRae, 2003). While it is certainly true that biological motion is crucial for animals while colour may be quite important in distinguishing among fruits, it does not follow that damage to mechanisms dedicated to processing these perceptual attributes would necessarily result in differential impairments for the categories of animals and fruits. Thus, for example, there is ample evidence that selective damage of colour knowledge does not result in disproportionate difficulty for the category of living inanimate objects. For instance, Miceli, Fouch, Capasso, Shelton, Tamaiuolo, and Caramazza (2001) reported a patient with a selective deficit for knowledge of object colour, but no associated disproportionate deficit for fruit/vegetables (see also Luzzatti & Davidoff, 1994). Samson and Pillon (2003) reported a patient with a disproportionate impairment for fruit/vegetables who was unimpaired at attributing the correct colour to fruit/vegetable stimuli (see also Crutch & Warrington, 2003). Similarly, motion-impaired patients have been reported who do not present with difficulties in naming pictured animals (Vaina, Makris, Kennedy, & Cowey, 1998), while patients who were not motion impaired have been reported to be selectively impaired for living animate things (e.g., Caramazza & Shelton, 1998).

Humphreys and Forde (2001) proposed a further modification of the Sensory/Functional Theory, in which it was assumed that there is greater perceptual crowding (due to greater perceptual overlap) between the visual structural descriptions of living things than nonliving things. Thus, damage to the visual structural

system will disproportionately affect living things compared to nonliving things (see also Gale, Done, & Frank, 2001; Laws, Gale, Frank, & Davey, 2002; Tranel, Logan, Frank, & Damasio, 1997). As an account of the existence of category-specific semantic impairments for living things, this proposal is inconsistent with observations of patients with conceptual impairments for living things in the absence of damage to the visual structural description system (FM: Laiacona et al., 1993; EA: Barbarotto et al., 1996; Laiacona et al., 1997; SB: Sheridan & Humphreys, 1993; Jennifer: Samson et al., 1998; for discussion, see Mahon & Caramazza, 2001).

The Correlated Structure Principle

A second line of research has sought an account of category-specific semantic deficits based on the Correlated Structure Principle. For instance, the OUCH model (Caramazza et al., 1990) makes two principal assumptions. First, conceptual features corresponding to object properties that often co-occur will be stored close together in semantic space; and second, focal brain damage can give rise to category-specific semantic deficits either because the conceptual knowledge corresponding to objects with similar properties is stored in adjacent neural areas, or because damage to a given property will propagate damage to highly correlated properties. While the original OUCH model is not inconsistent with the currently available data from category-specific semantic deficits, it is too unconstrained to provide a principled answer to the question of *why* the various facts are as they are.

The most developed extension of OUCH is the Conceptual Structure Account of Tyler, Moss, and colleagues (Tyler & Moss, 2001; Tyler, Moss, Durrant-Peatfield, & Levy, 2000; for similar proposals, see Devlin, Gonnerman, Anderson, & Seidenberg, 1998; Garrard et al., 2001; Gonnerman, Andersen, Devlin, Kempler, & Seidenberg, 1997; McRae & Cree, 2002; Vinson et al., 2004). The Conceptual Structure

Account makes three assumptions. (1) Living things have more shared features than nonliving things, or put differently, nonliving things have more distinctive/informative features than living things. (2) For living things, biological function information is highly correlated with shared perceptual properties (e.g., can see/has eyes). For artifacts, function information is highly correlated with distinctive perceptual properties (e.g., used for spearing/has tines). (3) Features that are highly correlated with other features will be more resistant to damage than features that are not highly correlated. This hypothesis thus explains the cause of category-specific semantic deficits by assuming random (or diffuse) damage to a conceptual system that is not organised by modality or object domain.

The Correlated Structure Account (i.e., the conjunction of the above three assumptions) predicts that a disproportionate deficit for living things will be observed when damage is relatively mild, while a disproportionate deficit for nonliving things will only arise when damage is so severe that all that is left in the system are the highly correlated shared perceptual and function features of living things. This prediction is not consistent with the observation of a severe deficit for nonliving things in the context of relatively spared knowledge of animals (Hillis & Caramazza, 1991). Perhaps even more problematic is that the central prediction of the theory is not confirmed by cross-sectional analyses of patients at varying stages of Alzheimer's disease: there is no interaction between the severity of overall impairment and the direction of category-specific semantic deficits (Garrard et al., 1998; Zannino et al., 2002).⁴

The Domain-Specific Hypothesis

The third route that has been pursued is the Domain-Specific Hypothesis (Caramazza & Shelton, 1998). The Domain-Specific Hypothesis

as developed in the context of category-specific semantic deficits must be distinguished from other possible ways in which a domain-specific approach might be articulated. Common to all approaches is the assumption that a given cognitive process is domain specific if the scope of its extension is delimited by the semantic (i.e., content-defined) class membership of the objects that it processes. This assumption by itself, however, leaves unaddressed three (at least logically) orthogonal extant issues.

First is the issue of whether conceptual processing of objects is domain specific because of *innately* determined neural constraints. We assume that domain-specific constraints on the organisation of conceptual knowledge are innately determined. This assumption makes a strong prediction: The categories of category-specific semantic deficits will be restricted to only those categories that, if identified could have had survival or reproductive value. An example of such a category is that of "conspecifics," which we discuss below.

A second issue is whether modality-specific *input* processes are organised by object domain. We assume that object domain is an innately determined parameter of neural organisation at both the conceptual and perceptual level. In other words, the claim here is that stimuli are categorised (e.g., as animate) at a stage of processing prior to the conceptual level. Below we review functional imaging and neuropsychological data consistent with this assumption.

A third issue is whether the content of object concepts is exhausted by information/processes internal to the sensory-motor systems of the brain. We show that the content of object concepts cannot be reduced to sensory-motor processing; to do this we argue that various patterns of neuropsychological impairments *could not exist* if it were the case that conceptual knowledge was exhausted by information internal to modality-specific input/output representations.

⁴ One study (Gonnerman et al., 1997) reported an association between the severity of conceptual impairment and the direction of category-specific deficit, but the reported interaction has subsequently been shown to be an artifact of ranking the patients according to performance on only one object category (see Zannino et al., 2002, for discussion).

Innately determined domain-specific processes

The proposal that innate structure in the central nervous system can lead to domain-specific organisation is by no means new; there is a range of evidence for innate neural structure in non-human species. For instance, Emlen (1967, 1969) investigated the navigational strategies of a migratory species of bird (Indigo Buntings, *Passerina Cyanea*) and found that a crucial factor is the relative position of the stars (see also work in the navigational abilities of desert ants, e.g., Collett, Collett, Bisch, & Wehner, 1998). The claim that a migratory species of bird such as the Indigo Bunting might be born with innately determined “hardware” in order to solve complex navigational processes based on the relative positions of stars would seem to be relatively uncontroversial. But if we are willing to grant innate constraints on the structure of the bird mind, why not on that of the human mind?

Another example from animal studies comes from a series of studies by Mineka and colleagues (e.g., Cook & Mineka, 1989; Mineka, Davidson, Cook, & Keir, 1984). Rhesus monkeys captured in the wild, but not naïve, laboratory-raised Rhesus monkeys, show a strong fear response when presented with a snake (even a plastic model). Mineka and colleagues found that when naïve, laboratory-raised Rhesus monkeys observe a video of another monkey displaying a fear response to a snake, they will subsequently display the same fear response when confronted with a snake. However, naïve, laboratory-raised monkeys do not show a transfer of fear reaction if they view videos of other monkeys displaying fear responses to flowers or to rabbits. The interesting implication of these data is that the transfer of fear response is mediated, and actually constrained, by the Rhesus monkeys’ categorisation of the stimulus.

Knowledge of conspecifics in humans: Does this category behave like a domain? It follows

from the assumption that domain-specific processing of objects is innately constrained that there will be domain-specific processes only for those categories that could have conferred a survival and/or reproductive value. The category of conspecifics is arguably one of the most salient categories of things in the world that satisfies this condition (Shelton, Fouch, & Caramazza, 1998). Paradoxically, data from processing of conspecifics has until now figured only marginally in discussions of the organisation of conceptual knowledge (but see Haslam, Kay, & Hanley, 2002, for review and discussion). Here we use the category “conspecifics” as a test case and ask whether similar profiles of impairment are observed for this category as are observed for living animate and living inanimate things. A further expectation is that knowledge of conspecifics will include a system for attributing intentional content to other minds: that is, Theory of Mind.

Patient APA (Miceli, Capasso, Daniele, Esposito, Magarelli, & Tomaiuolo, 2000) was impaired for knowledge of people (e.g., 10/32 famous face naming) but did not present with significant (or differential) difficulties naming objects/animals (e.g., 74/80) (see also Kay & Hanley, 1999). Furthermore, APA was normal on the Benton Face Recognition Test, indicating that the patient was not impaired in processing the structural characteristics of faces. A contrasting semantic impairment was reported by Kay and Hanley (2002): Patient ML did not have an impairment in recognising faces as familiar or not, was normal for a number of stringent tests requiring identification of famous people, but was impaired (equivalently) for objects and animals. This contrasting pattern reflected in patients APA and ML has recently been reported over the same battery of materials (Thompson, Graham, Williams, Patterson, Kapur, & Hodges, 2004; patients MA and JP).⁵ Thus, the domain of conspecifics can be spared or impaired

⁵ JP was impaired for knowledge of people but relatively spared for knowledge of objects and animals, while MA showed the reverse profile. Both patients were normal on a range of visuospatial tests, including object decision and perception of unfamiliar faces, and neither patient was more impaired for living or nonliving things.

independently of both objects and other living things (e.g., living animate); importantly, an impairment for people is not associated with a general impairment for living things compared to nonliving things. This observation is significant in the context of the proposal discussed above, that the primary deficit in patients with impairments for living animate things is to knowledge of the typical ways in which living animate things move (e.g., Cree & McRae, 2003). If this were the case, then the category “living animate things” should not fractionate into the domains of animals and conspecifics. Thus, there is a tripartite distinction within the category “living things”: animals, fruit/vegetables, and conspecifics.

It is important that at least some impairments for person-specific knowledge are not reducible to a general anomia for proper names or a modality-specific visual input impairment (i.e., prosopagnosia). As noted above, patient APA was not prosopagnosic, and, although impaired in famous face naming, was normal for naming monuments and geographical places (Miceli et al., 2000).⁶ Patient JP’s impairment (Thompson et al., 2004) was observed across several matching and sorting tasks, using pictures as well as spoken and written names, suggesting that the semantic impairment for person knowledge observed in this patient cannot be reduced to a problem with face recognition (see also Ellis, Young, & Critchley, 1989; Verstichel, Cohen, & Crochet, 1996).

Is the domain of conspecifics a special domain? The domain of conspecifics is unique in that the object of processing is of the same type as the agent of processing. The ability to attribute intentional states to other people has been termed “Theory of Mind” (Premack & Woodruff, 1978). If the domain of conspecifics constitutes an evolutionarily defined domain, then Theory of Mind abilities is one use to which such

processing might be uniquely applied. What is the evidence that Theory of Mind abilities are functionally isolable from other processes?

Recent neuropsychological work indicates that theory of mind abilities do not depend on intact general executive functioning abilities (Fine, Lumsden, & Blair, 2001; Gregory et al., 2002; Lough, Gregory, & Hodges, 2001; Varley, Siegal, & Want, 2001; for review, see Siegal & Varley, 2002). For instance, Fine and colleagues (2001) reported a patient with either congenital or early amygdala damage, impaired Theory of Mind abilities, but spared executive functioning. The reverse functional dissociation has also been reported: impaired executive functioning but intact Theory of Mind abilities (Varley et al., 2001).

An important area for investigating the functional and neural bases of Theory of Mind comes from the study of individuals with congenitally impaired Theory of Mind abilities (Asperger syndrome and autism; for review, see U. Frith, 2001; Gallagher & Frith, 2002). For instance, Castelli, Frith, Happé, and Frith (2002) compared the activation observed for 10 normal adults and 10 individuals with Asperger syndrome when watching animated geometric shapes moving as “biological stimuli” compared to shapes moving randomly. Replicating previous findings (Castelli, Happé, Frith, & Frith, 2000) normals showed increased activation for the animated condition in the (all primarily right-sided) basal temporal region, superior temporal sulcus, medial prefrontal cortex, and extra-striate cortex (V3). Compared to normals, individuals with Asperger syndrome showed reduced activation in basal and superior temporal regions and in medial prefrontal cortex. The same level of activation was observed in extra-striate cortex.

Other functional neuroimaging work with healthy subjects supports the role of the right ventromedial prefrontal cortex in mental state

⁶ This performance profile can be contrasted with that observed for case GR (Lucchelli, Muggia, & Spinnler, 1997), who presented with an anomia for people’s names, but spared name recognition and face–name matching. The patient could give detailed semantic information about people he could not name, and was in the normal range for visual and verbal naming of other proper name categories (Italian cities, monuments, European cities, rivers, mountains, currencies, commercial brands).

attribution. Mitchell and colleagues (2002) had participants make yes/no judgments on noun/adjective word pairs presented visually (Could the adjective be true of the noun? e.g., Emily-beautiful; orange-seedless). Nouns were taken from the categories clothing, fruit, and proper names of people. It was observed that the person versus object contrast resulted in areas that were less deactivated compared to baseline in (among other areas) dorsal and ventral aspects of medial prefrontal cortex. Consistent findings were obtained in the study by Gallagher, Jack, Roepstorff, and Frith (2002), in which participants played the game "paper, rock, scissors." The crucial contrast was between a condition in which participants thought they were playing against a computer (computer stance) and one in which they thought they were playing against a person (human stance). Actually, in both conditions they were playing against a computer operating randomly. The only area that was more activated in the "human stance" condition vs. the "computer stance" condition was the anterior aspect of the paracingulate cortex (see also McCabe, Houser, Ryan, Smith, & Trouard, 2001).

The relation between biological motion processing, affect, and Theory of Mind has emerged as a central area of study in attempts to understand the functional and neuroanatomical organisation of Theory of Mind abilities (C. D. Frith & Frith, 1999). This brief overview highlights a primarily right-sided network specialised for processing information about conspecifics.

Are modality-specific input processes organised by object domain?

The Domain-Specific Hypothesis assumes that perceptual (i.e., pre-conceptual) stages of object recognition may be functionally organised by domain-specific constraints. With respect to the visual modality, this assumption generates the prediction that patients may present with category-specific visual agnosia (a deficit in recognising visually presented objects despite intact elementary visual processing). Tentative evidence for

this prediction is provided by the observation of patients with equivalent impairments to visual/perceptual and functional/associative knowledge of living things, but a visual agnosia for living things compared to nonliving things (Barbarotto et al., 1996; Barbarotto, Capitani, Spinnler, & Trivelli, 1995; Capitani, Laiacona, & Barbarotto, 1993; Caramazza & Shelton, 1998; Laiacona et al., 1993; Lambon Ralph et al., 1998; but see Capitani et al., 2003, for critical review). Also consistent with such an organisation is the observation that patients can present with impairments for recognizing faces but not visually presented objects (e.g., Newcombe, Mehta, & De Haan, 1994) as well as the reverse: spared face recognition but impaired object recognition (Moscovitch, Winocur, & Behrmann, 1997).

There is a large body of evidence from functional neuroimaging that demonstrates differentiation by semantic domain within modality-specific systems specialised for processing object form (ventral temporal cortex) and object associated motion (lateral temporal cortex). Items from living animate categories (animals, human faces) differentially activate the superior temporal sulcus (right > left) (e.g., Chao, Haxby, & Martin, 1999a; Chao, Martin, & Haxby, 1999b; Haxby, Ungerleider, Clark, Schouten, Hoffman, & Martin, 1999; Hoffman & Haxby, 2000; Kanwisher, McDermott, & Chun, 1997) and the lateral aspect of the fusiform gyrus (e.g., Chao et al., 1999a; Chao, Weisberg, & Martin, 2002; Kanwisher et al., 1997; Kanwisher, Stanley, & Harris, 1999; McCarthy, Puce, Gore, & Allison, 1997), while items corresponding to nonliving things differentially activate the middle temporal gyrus (left > right) (e.g., Chao et al., 1999a; Devlin et al., 2002a; Martin, Wiggs, Ungerleider, & Haxby, 1996) and the medial aspect of the fusiform gyrus (Chao et al. 1999a, 2002; but see Devlin et al., 2002b). For a domain-specific interpretation of these findings, see Kanwisher (2000); for an alternative interpretation see Tarr and Gauthier (2000).

In a recent series of studies, Beauchamp and colleagues (Beauchamp, Lee, Haxby, & Martin, 2002, 2003) demonstrated that, in addition to

the category-specific foci of activation just reviewed, lateral temporal cortex prefers object-associated motion whereas ventral temporal cortex is more sensitive to object-associated form and texture. In their 2002 report, it was found that lateral temporal cortex responded more to moving images than to static images, while ventral temporal regions responded equally to both. In their 2003 report, it was found that ventral temporal cortex preferred videos of moving images to point light displays of the same moving images, while lateral temporal cortex responded either more to point light displays than videos (superior temporal sulcus: humans) or equivalently to videos and point light displays (middle temporal gyrus: tools). Furthermore, within lateral temporal cortex, the superior temporal sulcus preferred human stimuli moving in an articulated manner (e.g., jumping jacks) than an unarticulated manner (e.g., rotating about the centre of mass) (Beauchamp et al., 2002) as well as point light displays of moving humans to point light displays of moving tools (Beauchamp et al., 2003). In contrast, the middle temporal gyrus preferred point light displays of moving tools to point light displays of moving humans (Beauchamp et al., 2003; see also Grossman & Blake, 2002; Grossman et al., 2000; Kourtzi & Kanwisher, 2000; Senior et al., 2000).

A crucial issue concerning these differential patterns of activation in ventral and lateral temporal areas is whether they reflect conceptual or modality-specific input processing (see Whatmough, Chertkow, Murtha, & Hanratty, 2002, for some empirical work on this issue in ventral temporal cortex). At minimum,⁷ these functional neuroimaging data are consistent with the proposal that modality-specific input systems are organised by object domain. Consensus on this interpretation has been, at best, reluctant; a number of researchers have argued that

differential effects of object category (in, e.g., ventral temporal areas) are driven by object-specific features and not object domain (e.g., Bookheimer, 2002; Gerlach, Law, Gade, & Paulson, 2000; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kraut, Moo, Segal, & Hart, 2002; Martin & Chao, 2001; Moore & Price, 1999; Mummery, Patterson, Hodges, & Price, 1998; Perani et al., 1995; Thompson-Schill, 2003; but see, e.g., Kanwisher, 2000). For instance, Martin and colleagues (e.g., Martin & Chao, 2001) have argued that it is not the case that (e.g.) the right superior temporal sulcus processes “biological motion” per se, but rather that it processes “articulated motion.” And it just so happens that biological motion is articulated while mechanical motion is not. The crucial point of difference, then, between this proposal and the Domain-Specific Hypothesis is not necessarily the content of what is processed in a given area, but how a given area comes to process the information that it does. The sensory/motor account of Martin and colleagues is one implementation of OUCH: Objects that share properties are represented close together in the brain. In this regard developmental findings will play an important role in adjudicating between theories (e.g., Farah & Rabinowitz, 2003).⁸

The primary empirical motivation for the Sensory/Motor Theory is the observation that the areas of activation observed for living and non-living things are differential and not selective. Thus, the strongest evidence for a domain-specific interpretation of these findings would come from a demonstration that the same patterns of activation can be observed when object-associated features are removed from the stimuli.

In a recent study by Martin and Weisberg (2003), participants viewed three types of computer-animated displays, all consisting of the

⁷ “At minimum” because all extant theoretical interpretations assume that modality-specific input representations exist, while there is not consensus that concepts are represented independently of modality-specific input/output representations.

⁸ The Domain-Specific Hypothesis must assume that there is some innate content that allows a given domain-specific system to become “locked” to the right category of objects (i.e., a triggering mechanism). The claim is not that individual object concepts are given innately; rather, the claim is more along the lines of the type of content assumed to be localised in the theory of Martin and colleagues.

same geometric shapes, but differing in the type of motion in which the shapes were engaged (for discussion of such stimuli, see Heider & Simmel, 1944; Scholl & Tremoulet, 2000). The geometric shapes could be (1) moving as biological entities (e.g., chasing, playing a game; “biological motion” condition); (2) moving as mechanical entities (e.g., cue balls, bowling balls; “mechanical motion” condition); or (3) moving randomly; “random motion” condition. In lateral temporal cortex, it was observed that the superior temporal sulcus responded more to the “biological motion” condition, while the middle temporal gyrus responded more to the “mechanical motion” condition, indicating that the corresponding neural regions for processing motion were engaged by these stimuli. More striking were the findings in ventral temporal cortex: Lateral regions of ventral temporal cortex responded more to the “biological motion” condition while medial regions responded more to the “mechanical motion” condition. Given that ventral temporal regions are most responsive to object form and texture (e.g., Beauchamp et al., 2003), and given that object form and texture were exactly the same between the “biological” and “mechanical” motion conditions, these data indicate that the activation observed in ventral temporal areas can be driven by higher-order “interpretations” of the semantic domain to which the geometric shapes belong, and not by object-specific features. Perhaps relevant to this inference is the observation that activation associated with the “biological motion” compared to the “mechanical motion” condition was also observed in the right ventromedial prefrontal cortex and the amygdala (for related findings in right superior temporal sulcus using acoustic stimuli, see Kriegstein, Eger, Kleinschmidt, & Giraud, 2003). As discussed above, both of these areas have been implicated in the ability to attribute intentions to (at least) conspecifics.

The activation observed in lateral and ventral temporal areas by Martin and Weisberg (2003)

was not only differential for one type of stimulus (e.g., biological) compared to the other (i.e., mechanical): When an area in ventral temporal cortex responded to one type of stimulus (biological or mechanical motion) it did not respond to the other type of stimulus more than to the random motion baseline.⁹ The observation that different areas of cortex within modality-specific input systems (e.g., form, motion) respond differentially to different semantic categories is contrary to the assumption of modality-specific input systems not internally organised by object domain.

It might be argued that a combination of the Sensory/Functional Theory and a theory based on the Correlated Structure Principle (e.g., OUCH; see also Levy, Hasson, Avidan, Hendler, & Malach, 2001) could accommodate such patterns of activation (e.g., Cree & McRae, 2003; Vinson et al., 2003). However, the observation that such patterns of activation can be demonstrated to not only be “differential” but also “selective” (Martin & Weisberg, 2003) is contrary to an interpretation that assumes that object-specific features are driving the observed effects. The possibility of observing “selective” patterns of category-specific activation is uniquely afforded by the Domain-Specific Hypothesis.

Conceptual content cannot be reduced to modality-specific input/output content

Our discussion of the Domain-Specific Framework has assumed that the content of object concepts is not reducible to information/processes internal to modality-specific input/output systems of the brain. However, and as noted above, this view on the nature of conceptual content is not entailed in any way by the assumption of domain-specific neural circuits for representing/processing conceptual knowledge of some types of objects. Here we distinguish two possible architectures that might be articulated within a Domain-Specific Framework, and we argue for the second.

⁹ This was the case bilaterally in ventral temporal cortex, in the right superior temporal sulcus (social > mechanical), and in the left middle temporal gyrus (mechanical > social).

1. Modality-specific input/output systems are both format and content¹⁰ specific for the modality of information they process, and they are organised by object domain. All conceptual content is grounded in such modality-specific input/output systems. In other words, domain-specific simulation.
2. Modality-specific input/output systems are both format and content specific for the modality of information they process, and they are organised by object domain. There is a level of conceptual content represented independently of modality-specific input/output systems that is organised by object domain.

The issue of whether conceptual information is exhausted by modality-format-specific input/output systems has been a topic of recent research and debate, in large part due to theories developed within the "Simulationist Framework." The central assumption of the strong form of the Simulationist Framework is that in order to go from a physical stimulus to "understanding" one must internally "run" or "simulate" the production processes (i.e., modality-format-specific representations) that would mediate production of an event that is the same as that which is understood (see also the motor theory of speech perception, e.g., Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967, for a similar proposal at the level of recognition).¹¹ Consider the observation of someone drinking a glass of water. The visual input of this event would result in a simulation of the observed motor action. In the

course of simulating the action of drinking a glass of water, a number of conceptual states might be invoked. For instance, one might read off the intentions that could plausibly have formed the basis of the simulation (were the simulation an actual production event). One such state might be, for example, <being thirsty> (for recent reviews, see Blakemore & Decety, 2001; Gallese & Goldman, 1998; see also Adolphs, 2003; Allison, Puce, & McCarthy, 2000). Such intentional states could then be attributed to the observed agent.¹² Another conceptual state that might depend on the simulation of drinking a glass of water would be the concept GLASS (e.g., Allport, 1985; Barsalou, Simmons, Barbey, & Wilson, 2003; Martin, Ungerleider, & Haxby, 2000).

One issue that arises is whether such a framework would provide the means for individuating distinct mental states that are coextensive with the same motor programme (for discussion, see Jacob & Jeannerod, 2005). So for instance, if one observed a person who was about to give a presentation taking a drink of water, the resulting simulation would presumably involve the same motor programme(s); however, it might be inferred that the observed drinker was nervous (instead of thirsty). Or, if one observed the same person taking a drink of water *during* a presentation, again, the motor simulation would be identical, but it might be inferred that that person's throat was parched, but not that they were thirsty or nervous, etc. This would seem to indicate that attributions of mental

¹⁰ Such systems might be modality-context-specific as well; i.e., information is represented in a format congruent with the modality through which the information was acquired, and the only modality in which information can be stored is that through which it was acquired; see Caramazza and colleagues (1990) for discussion. The present point can be made independently of the stronger (i.e., modality-context-specific) assumption.

¹¹ How the notion of "same" is fleshed out is an important aspect of simulation theory. In particular, is the simulation driven by first acknowledging the "type" of event that is occurring, and then a "type" identical simulation is run? If so, the claim would be that modality-format-specific representations are type identified. If not, then the simulation must be in terms of some particular past experience. If the former, then the question becomes how "abstract" is the information internal to modality-format-specific representations assumed to be? If the latter, then the question becomes: How does one learn anything to begin with? See the discussion of developmental data below.

¹² For example: "Inferring intentions from observed actions might depend on the same mechanism that labels the consequences of one's own actions as being produced by one's own intentions" (Blakemore & Decety, 2001, p. 563). Or similarly, Gallese and Goldman (1998) write: "In the present article we will propose that humans' mind-reading abilities rely on the capacity to adopt a simulation routine" (p. 493).

states depend on background knowledge. But how is “background knowledge” embedded in modality-specific input/output systems?

However, the strong form of the Simulationist Framework is not only about the order in which information is processed; it is also about the representation of intentional content (including both object concepts and the representations underlying theory of mind abilities). The Simulationist Framework makes the stronger claim that not only is understanding necessarily *mediated* by production processes; understanding is the running of modality-specific input/output information (e.g., Barsalou et al., 2003; Gallese & Goldman, 1998).

There is a very appealing aspect to the simulation theory, the notion that understanding is a form of action. However, as a hypothesis about the representation of intentional content, the Simulationist Framework depends on at least two things: empirical demonstrations that (1) production programs are run in the course of recognition, and (2) such production programs are sufficient to ground conceptual content. We focus the discussion to follow on studies that have looked at biological motion processing and the representation of object concepts. There are two questions to be addressed: First, does recognition of biological motion involve the processes required to produce such motion? Second, what happens to recognition and access to conceptual knowledge when modality-specific output processes are damaged?

One line of evidence marshalled in support of the Simulationist Framework comes from developmental work indicating that the capacity/proclivity to imitate is “innate.” For instance, babies imitate facial gestures from a very early age and they also will imitate people but not robots (e.g., trying to pick up a dumbbell) (Meltzoff, 1995; Meltzoff & Moore, 1977). But there are also developmental findings cited in support of the Simulationist Framework that would seem to create more problems than they could engender support (see also discussion in Jacob & Jeannerod, 2005). For instance, 8 to 16-week-old infants prefer point-light walking

figures to dynamic noise or the same figure rotated 180 degrees (Fox & McDaniel, 1982) while 3- to 5-month-old infants can discriminate between a point light walker and similar figures with scrambled spatial relationships between the moving dots (Bertenthal, Proffitt, & Kramer, 1987). Given that 3- to 5-month-old babies do not have experience with walking, what are they simulating in order that they can recognise walking?

It is likely that there is much about walking that is innate, and so it might be argued that 3- to 5-month-olds are simulating whatever is given innately in respect of the ability to walk. If this is the direction of argument, then the substrate of simulation is not modality-format-specific information learned through experience, but something more abstract. Alternatively, it might be pointed out that 3- to 5-month-olds have plenty of experience watching people walk, and so they are simulating their past visual (and not motor) experiences. If this is the direction of argument, then why not assume that adults recognise biological movement the way babies do?

Experimental work with adults converges with the developmental findings. For instance, when adult subjects view a specific facial expression, the corresponding muscles in the observer’s face are “activated” (recorded via EMG reactions) (Lundqvist & Dimberg, 1995). A simulationist interpretation of such findings assumes that the capacity to infer emotion from the observation of others’ faces depends on the ability to simulate the observed expressions. What happens to the ability to attribute emotions to faces when the capacity to move one’s face is not present?

Calder, Keane, Cole, Campbell, and Young (2000) report the performance of an individual, LP, who had bilateral paralysis of the face from infancy (Mobius syndrome). LP was normal on an unfamiliar face-matching test (Benton Test), impaired on Warrington’s Recognition Test for unfamiliar faces, and borderline impaired on a test requiring recognition of famous people. On a test of facial affect recognition (apply one of the six basic emotions to a face) LP was not impaired, but was slightly impaired on a more

difficult version (constructed from morphs). The patient was normal in applying one of the six affect labels to typical corresponding sounds (e.g., laughter = happiness). From the performance of patient LP there would seem to be something right about the Simulationist Framework: LP was not unimpaired on all administered tests. However, at the same time, the fact that the patient *could succeed at all* on tasks of emotion attribution based on facial affect indicates that the ability to attribute intentional states is not exhausted by simulation of the observed behaviour.

Another line of evidence that has been marshalled in support of the Simulation Framework is based on apparent motion effects: the (seemingly) perceptual experience of movement induced by static images presented rapidly and alternately in different places. Apparent motion effects induced with geometric shapes follow the shortest possible path. However, when normal subjects observe apparent motion effects that involve parts of the human body, the geometrically longer but biomechanically plausible path is perceived over the geometrically shorter but biomechanically impossible path (e.g., Shiffrar & Freyd, 1993). Furthermore, motor execution areas are activated only during the biomechanically possible conditions (Stevens, Fonlupt, Shiffrar, & Decety, 2000).¹³ An interpretation of these data in terms of the Simulation Framework assumes that recognition of biological motion of conspecifics involves covert production of the same movements.

Servos, Osu, Santi, and Kawato (2002) asked whether the neural areas mediating biological motion perception overlap with areas activated

during motor imagery. The authors compared observation of Johansson point-light displays with a motor imagery task (e.g., scratch back with right arm). There was no overlap observed between biological motion perception and motor imagery, even at a liberal alpha level.

Pavlova, Staudt, Sokolov, Birbaumer, and Krageloh-Mann (2003) asked whether the degree of motor impairment in 13- to 16-year-old children with congenital motor disorders was inversely related to sensitivity to Johansson point-light displays. There was no significant relationship between visual sensitivity to the point-light displays and severity of motor impairments, while there was a relation between degree of motor impairment and the volume of periventricular lesions in parietal-occipital areas. As in the study of Calder and colleagues (2000) a trend is reported by Pavlova and colleagues that is in the direction predicted by the Simulationist Framework. Nevertheless, and as in the study of Calder and colleagues (2000), the data from Pavlova and colleagues indicate that recognition of biological motion does not depend on *ever* having produced such motion in one's life. In other words, there is no past experience to simulate.¹⁴ This implies that modality-specific output representations are not sufficient to ground conceptual knowledge.

Stronger support for this conclusion comes from the study of apraxia and the proposal that the ability to recognise/identify manipulable objects depends on information that is active during the use of such objects: Specifically, that conceptual knowledge of manipulable objects is represented in terms of modality-specific output representations that code the motor movements

¹³ Why were premotor areas activated only during biomechanically *possible* action? In other words, if activation in premotor cortex is the criterion (here) for simulation, then given that there was no such activation for biomechanically impossible actions, wouldn't this suggest that the possible/impossible classification happened somewhere else? In fact, there was some activation in orbito-frontal cortex that was greater for biomechanically implausible motion over plausible motion. But if the decision (or "filter") happens outside the simulator, then the simulator is outside the system it is supposed to replace (see Blakemore & Decety, 2001, for discussion).

¹⁴ It might be argued that the simulation in these cases is more abstract and does not occur over representations corresponding to past experiences. At this point, however, the basic assumption of the Simulationist Framework would have been abandoned, since the claim was that information encoded during past experiences with similar events is "re-activated" in order to understand the present event.

associated with the use of such objects (Barsalou et al., 2003; Gallese & Goldman, 1998). It is important to distinguish the Simulationist Framework from a closely related theory, the Sensory/Motor Theory of Martin and colleagues (2000; see also Allport, 1985). The difference between the Sensory/Motor Theory and the Simulationist Framework is that the Sensory/Motor Theory is not committed to the claim that the same representation underlies production and recognition. Thus, the observation of a dissociation between the ability to use objects and the ability to recognise the correct gestures associated with objects (for reviews, see, e.g., Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Johnson-Frey, 2004; Rothi, Ochipa, & Heilman, 1991) is at variance with the Simulationist Framework, but not the Sensory/Motor Theory.

The claim that information required to use manipulable objects grounds conceptual knowledge of such objects has been motivated primarily by results from functional neuroimaging. A well-documented finding is that left premotor cortex is differentially activated when subjects perform various tasks over tool stimuli compared to nonmanipulable stimuli (e.g., animals, houses) (e.g., Chao & Martin, 2000; Chao et al., 2002; Gerlach et al., 2000; Gerlach, Law, Gade, & Paulson, 2002; Grabowski, Damasio, & Damasio, 1998; Martin, Wiggs, Ungerleider, & Haxby, 1996; for review, see Grèzes, & Decety, 2001; Martin & Chao, 2001; see Gallese & Goldman, 1998, and Rizzolatti, Fogassi, & Gallese, 2001, for review of work in the monkey model). The area activated in the left premotor cortex is activated when subjects are asked to imagine grasping objects, but not to actually do so (Decety et al., 1994) (see Figure 3).

However, there are also functional neuroimaging data that are inconsistent with an interpretation of such premotor activation as a necessary step in object recognition. Johnson-Frey, Maloof, Newman-Norlund, Farrer, Inati, and Grafton (2003) found greater activation in inferior frontal regions (precentral and inferior frontal gyri, bilaterally) for photographs of a

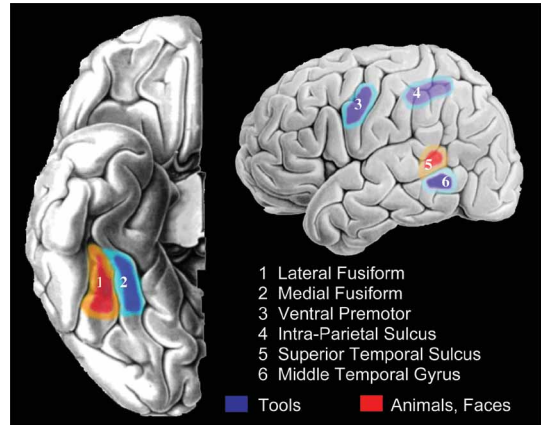


Figure 3. This schematic of activation patterns by semantic category is based on a recent review and discussion of the functional neuroimaging literature by Martin and Chao (2001). Figure provided by Alex Martin.

hand grasping an object compared to photographs of a hand touching the same objects. This activation remained when the objects were nontools (i.e., novel shapes) and when the hand was grasping the object in a way that would not serve the function of the object (see also recent work by Kellenbach, Brett, & Patterson, 2003; Phillips, Noppeney, Humphreys, & Price, 2002).

The decisive issue is what happens to the ability to recognise tools when the ability to use them is impaired. There are now a number of reports of patients with impairments for using objects, but spared recognition/identification (Buxbaum & Saffran, 2002; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003; Buxbaum, Veramonti, & Schwartz, 2000; Cubelli et al., 2000; Hodges, Spatt, & Patterson, 1999; Montomura & Yamadori, 1994; Moreaud, Charnallet, & Pellat, 1998; Ochipa, Rothi, & Heilman, 1989; Rosci, Valentina, Laiacona, & Capitani, 2003; Rumati, Zanini, Vorano, & Shallice, 2001; for review, see Johnson-Frey, in press; for discussion, see Dumont, Ska, & Joannette, 2000; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000; Mahon & Caramazza, 2003). For instance, the patient reported by Ochipa and colleagues (1989) was 17/20 for naming real objects, but

could use only 2 of the 20 objects correctly. The performance of patients such as that reported by Ochipa and colleagues falsifies the claim that conceptual knowledge of manipulable objects is grounded in modality-specific output representations required to use them.

We are compelled to assume an architecture in which modality-specific input/output systems are functionally isolable from conceptual knowledge. One implication of the conclusion that modality-specific input/output representations do not exhaust the content of concepts is that simulations over such representations will also not be sufficient to ground conceptual content. If simulations are not sufficient to ground the conceptual content of object concepts held in the first person, then they are not going to be sufficient to attribute intentional content to other individuals. The argument has not been, nor does it imply, that “simulations” do not exist.

What, then, is the role of simulation in a theory of the organisation and representation of conceptual knowledge? One possibility is that the observed activation of (supposed) modality-specific input/output representations, and which is argued to support the Simulationist Framework, is completely epiphenomenal to conceptual processing. For instance, it could be that biological motion recognition and production (e.g., motor movements associated with language production, facial affect, bodily movements, manipulation of objects) are related to Theory of Mind in a way analogous to how phonological/orthographical processes are related to lexical meaning in language: They are the usual way to get from a physical stimulus to meaning, and from meaning to a physical stimulus, but they do not *ground* meaning or *contain* meaning. This is not to say that the development of Theory of Mind abilities (cf. lexical meaning) does not depend on modality-specific input; rather its acquisition doesn't depend on a *specific* modality, and its subsequent representation, once acquired, is not exhausted by the modality through which it was acquired. On this account, the activation of modality-specific output information (e.g., activation in left premotor cortex while naming

manipulable objects) would be analogous to observations of phonological activation of unproduced words (e.g., Costa, Caramazza, & Sebastián-Galles, 2000; Peterson & Savoy, 1998).

A second possibility is that while simulations over modality-specific input/output representations are not sufficient to ground conceptual content, such “simulations” may contribute in important ways to the “full” meaning of object concepts. In other words, while one's concept of HAMMER is not represented in terms of information required to use hammers, it might be that information required to use hammers nevertheless adds in important ways to our understanding of hammers.

CONCLUSIONS

Beginning with the seminal work of Lhermitte and Beauvois in optic aphasia and Warrington, McCarthy, and Shallice in category-specific semantic deficits, issues of the organisation and representation of conceptual knowledge in the human brain have become central foci of research and discussion in cognitive science. The development of theoretical positions over the last several decades has been greatly influenced by the hypothesis that the semantic system is functionally organised by modality or type of information. There are, at present, many extant models of the organisation and representation of conceptual knowledge in the brain. Different proposals appeal to different principles of organisation, and one way to organise the extant space of hypotheses is to acknowledge where the various proposals fit within a common hierarchy of questions (for discussion, see Caramazza & Mahon, 2003). It has been the structure of this article to outline a framework that can be characterised at three levels of analysis. At the broadest level is the issue of whether conceptual and perceptual processes are organised by object domain. We have argued that the first-order constraint on the organisation of such processes are the domains living animate, living inanimate, conspecifics, and possibly tools. At the second level is the

issue of whether information is organised within domains by modality or type of information. We have argued that there is some evidence for assuming that modality-specific input systems are organised by object domain. It remains an open (and independent) question whether a secondary organisational principle of conceptual knowledge of objects is the modality of content about which the information is concerned. At the most fine-grained level in this hierarchy of questions is the issue of the organisation of information within a given domain-(modality-) specific system. Hypotheses developed on the basis of the correlated structure principle should prove useful for proposing answers to this issue.

Issues of conceptual content can also be examined by looking at the tiers of processing internal to a given “vertical channel.” For instance, internal to the domain “conspicuous” there will be, by hypothesis, distinct systems dedicated to analysis of visual form, visual motion, and conceptual knowledge, as well the attribution of intentional content.

The big questions about the organisation and representation of conceptual knowledge in the brain will have to be approached, simultaneously, from a number of different methodological perspectives. The goal of such work is to seek convergence, both empirically and theoretically, across different perspectives. Such convergence will be attained when extant theories take into account the relative strengths and weaknesses of the various methodological approaches.

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