The organization of conceptual knowledge: the evidence from category-specific semantic deficits

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Questions about the organization of conceptual knowledge in the human brain can be addressed by studying patients with category-specific semantic deficits: disproportionate and even selective impairment of conceptual knowledge of one category of objects compared with other categories. Recently, consensus has emerged regarding the basic facts of category-specific semantic deficits: (1) the categories that can be disproportionately impaired or spared are 'animals', 'fruit/vegetables', and 'artifacts'; and (2) category-specific semantic deficits are not associated with disproportionate deficits for a type or modality of knowledge. Together with findings in functional neuroimaging, these data indicate a complex organization of conceptual knowledge characterized by several independent dimensions of organization.

A series of papers by Warrington, Shallice and McCarthy marked the first detailed empirical investigation of patients with category-specific semantic deficits: patients were reported who were disproportionately impaired for conceptual knowledge of objects from one category compared with other categories ([1–3]; see [4] for earlier work)]. Since those initial reports, a large number of studies have confirmed the phenomenon of category-specific semantic deficits and it has become one of the principal sources of evidence for constraining cognitive theories of the organization of conceptual knowledge in the human brain (Box 1). Here we review the facts of category-specific semantic deficits, as well as recent theoretical and empirical work that has focused on constructing and critically evaluating specific hypotheses of the causes of category-specific semantic deficits.

Theoretical accounts of category-specific semantic deficits can be distinguished according to their underlying principle. One class of theories, based on the 'neural-structure principle', assumes that the organization of conceptual knowledge is governed by representational constraints internal to the brain itself. Two types of neural constraints have been invoked: modality specificity and domain specificity. The second class of theories, based on the 'correlated-structure principle', assumes that the organization of conceptual knowledge in the brain is a reflection of the statistical co-occurrence of object properties in the world.

Most of what is currently known about category-specific semantic deficits is a consequence of attempts to flesh-out and critically evaluate the assumption that the first-order constraint on the organization of conceptual knowledge in the brain is modality or type of information; for this reason, we introduce the facts of category-specific semantic deficits in the context of this proposal.

The neural-structure principle

The Sensory/Functional theory

The original formulation of the Sensory/Functional theory by Warrington and collaborators [1–3] made two basic assumptions: (1) the semantic system is organized into modality-specific semantic subsystems (e.g. visual/perceptual, functional/associative); and (2) the ability to recognize/name living things differentially depends on visual/perceptual information, whereas the ability to recognize/name non-living things differentially depends on functional/associative information (for related proposals, see [5–7]).

The Sensory/Functional theory makes three predictions. First, because this theory assumes that the ability to recognize all living things differentially depends on information internal to the same (visual/perceptual) semantic subsystem, the prediction is made that a dissociation will not be observed *within* the category 'living things'. Contrary to this prediction, patients have been reported with disproportionate deficits for 'fruit/vegetables' compared with 'animals' [8–12] as well as the reverse: disproportionate deficits for 'animals' compared with 'fruit/vegetables' [13,14] (Fig. 1). The Sensory/Functional theory might be reconciled with these facts if it were assumed that a specific type of visual/perceptual information is important for recognizing fruit/vegetables: for instance, it has been proposed that color information is crucially important for recognizing items from this category [2,5]. However, this proposal is at variance with the observation of a patient with a deficit for knowledge of object color but no associated disproportionate deficit for fruit/vegetables [15].

Second, the Sensory/Functional theory predicts that patients with category-specific semantic deficits will necessarily present with disproportionate deficits for the

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Box 1. An illustrative case of category-specific semantic deficit: Patient EW

To appreciate the remarkable nature of category-specific semantic deficits, consider the case of patient EW [14]. This patient presented with a disproportionate semantic impairment for the category ‘animals’ compared with other categories. Here we outline the empirical characteristics of EW’s profile of impairment.

Picture naming

On subsets of the Snodgrass and Vanderwart [63] picture set matched jointly for familiarity and frequency, and for visual complexity and familiarity, EW was disproportionately impaired at naming animals compared with naming non-animals (Table I). This indicates that EW’s category-specific deficit for picture naming cannot be attributed to uncontrolled stimulus variables (e.g. [64,65]).

EW’s picture-naming performance was not only quantitatively different for animals and non-animals but was also qualitatively different. For animals, EW either named the picture incorrectly or did not recognize the picture, whereas for non-animals, EW recognized the picture but could not retrieve the name (Fig. Ia).

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 (see Fig. 1, main text).

Sound identification

EW was also impaired at naming animals compared with non-animals based on their characteristic sounds (8/32; 25% correct versus 20/32; 63% correct: $z = 3.06$, $P < 0.05$), indicating that the naming impairment is not restricted to visual input.

Object decision

EW was asked to decide (‘yes’ or ‘no’) whether a depicted object was real (see Fig. Ib 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).

Table I. EW’s picture-naming performance for matched sets of items [63]

	Matched familiarity and frequency		Matched visual complexity and familiarity	
	Animals	Non-animals	Animals	Non-animals
EW	12/22 (55%)	18/22 (82%)	7/17 (41%)	16/17 (94%)
Controls	11/11 (100%)	10.8 (98%)	16.6/17 (98%)	16/17 (94%)
Range	11	10–11	16–17	16–17

Parts decision

EW was asked to decide which of two heads (or parts) went with a headless body (or object missing a part) (see Fig. Ic 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%).

Visual processing

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 impairment for object reality decision for animals is categorically based.

Central-attribute judgments

EW was asked to decide whether a given attribute was true of a given item (see Table II 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 attributes pertaining to 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%) (see Fig. 2, main text). EW’s performance on answering central-attribute questions indicates that her deficit is not restricted to production.

Table II. 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?

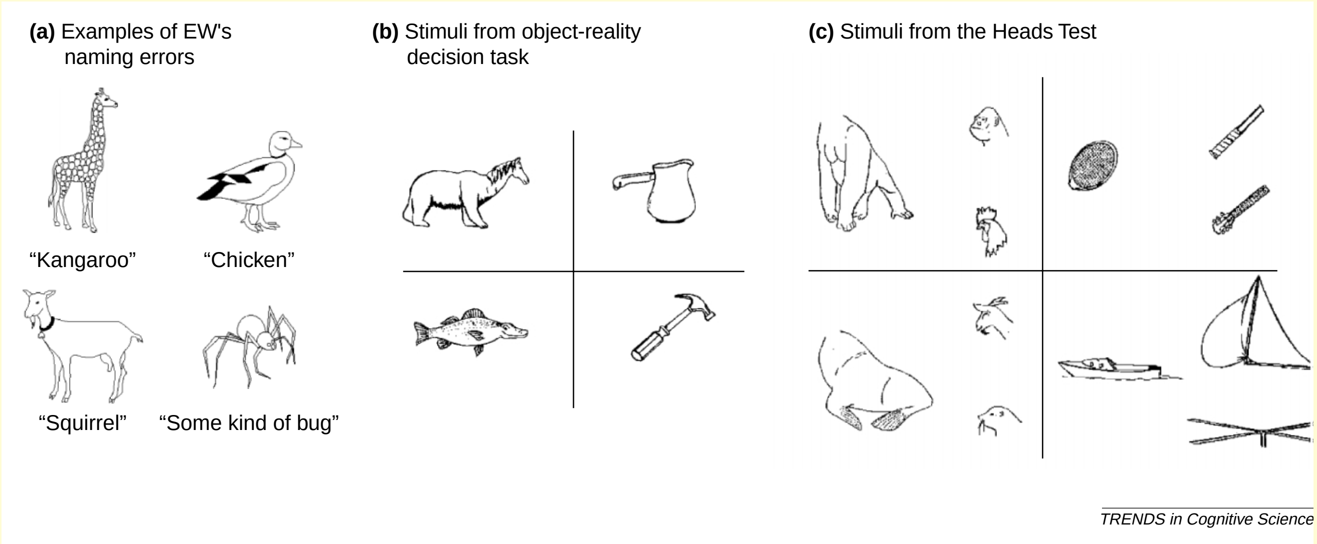

Fig. I. (a) Examples of EW’s naming errors. (b) Examples of stimuli from the object-reality decision task. (c) Examples of stimuli from the ‘Parts Decision Test’ or ‘Heads Test’.

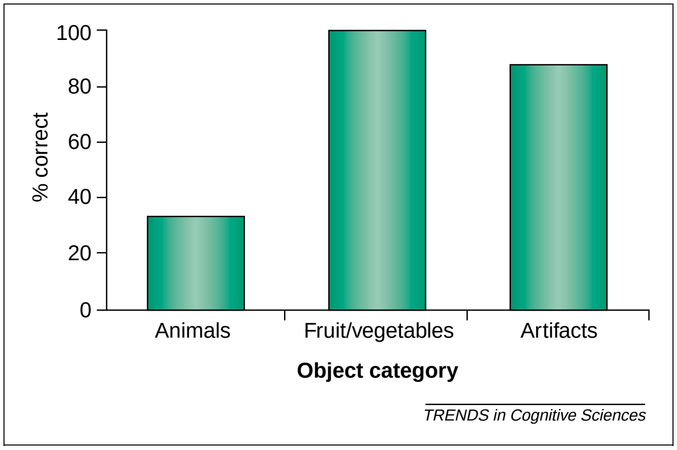

Fig. 1. Patient EW's picture-naming performance by object category. The much poorer performance with 'animals' compared both with other living things ('fruit/vegetables') and with non-living things highlights the grain of category-specific semantic deficits.

modality or type of information upon which successful recognition/naming of items from the impaired category is assumed to differentially depend. Early reports seemed to corroborate this prediction: patients with deficits for living things were also disproportionately impaired for visual/perceptual knowledge compared with functional/associative knowledge [16–18]; however, these data have been criticized on methodological grounds (see [14]). Where such methodological criticisms do not apply, almost all case studies of category-specific semantic deficits reported equivalent impairments to visual/perceptual and functional/associative knowledge. This fact is true both of cases that presented with disproportionate deficits for living things [14,19–22] (Fig. 2) as well as non-living things [23–26] (for review see [27]).

Third, the Sensory/Functional theory predicts that a disproportionate deficit for a type or modality of knowledge must be associated with a disproportionate deficit for the category of objects that differentially depends on that knowledge. Contrary to this prediction, patients have been reported who presented with a greater deficit for visual/perceptual knowledge than for functional/associative knowledge, but with no associated disproportionate deficit for living things compared with non-living things [15,28].

The three basic predictions made by the Sensory/Functional theory are at variance with the facts

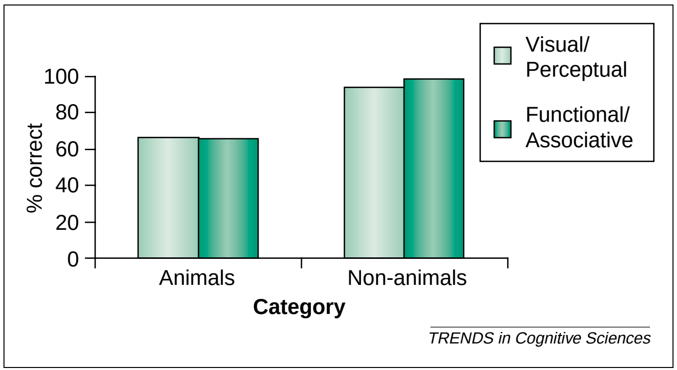

Fig. 2. Patient EW's performance on central-attribute questions. Within the 'animals' deficit, the patient shows equivalent impairments to visual/perceptual and functional/associative knowledge.

of category-specific deficits; this implies that the theory, as formulated, cannot explain the cause of category-specific semantic deficits (for further discussion, see [14,27]).

The Domain-Specific hypothesis

The central assumption of the domain-specific hypothesis [14] is that evolutionary pressures have resulted in specialized (and functionally dissociable) neural circuits dedicated to processing, perceptually and conceptually, different categories of objects. The Domain-Specific hypothesis thus provides independent motivation for specifying what constitutes a conceptual category in the brain because it is restricted to only those categories for which rapid and efficient identification could have had survival and reproductive advantages. Plausible candidate categories are 'animals', 'fruit/vegetables', 'conspecifics', and possibly 'tools'. The basic prediction of the Domain-Specific hypothesis is supported by the observation that the grain of category-specific deficits is as fine as these evolutionarily salient object domains.

The Domain-Specific hypothesis generates several predictions. First, if we assume there are distinct neural systems dedicated to the domains 'animals', 'fruit/vegetables', 'conspecifics', and possibly 'tools', it will not be possible for the function of one such system, if damaged, to be recovered by other systems: in other words, the Domain-Specific hypothesis predicts that there should be poor recovery of impaired performance. Support for this prediction is provided by a recent case study of a 16-year-old patient (at the time of testing) who presented with a disproportionate deficit for living things compared with non-living things; this patient had suffered a bilateral posterior cerebral artery infarction at one day of age [29].

A second prediction made by the Domain-Specific hypothesis is 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. As noted above, it is an established fact that almost all patients with category-specific semantic deficits who have been tested for different types of conceptual knowledge presented with equivalent impairments to visual/perceptual and functional/associative knowledge (see also [29]).

A third prediction made by the Domain-Specific hypothesis follows from the assumption that perceptual (i.e. preconceptual) stages of object recognition might be functionally organized by domain-specific constraints. With respect to the visual modality, this assumption generates the prediction that patients might present with category-specific visual agnosia (a deficit in recognizing visually presented objects despite intact elementary visual processing). Tentative support 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 with non-living things ([14,19,20,30,31]; for review and discussion see [27]).

The correlated-structure principle

The Organized-Unitary-Content hypothesis

Although early discussions of the organization of the conceptual system focused on the assumption that conceptual knowledge is organized into modality-specific subsystems [32], some authors argued against this hypothesis and in favor of a unitary, amodal system of conceptual organization [33–35]. The **O**rganized-**U**nitary-**C**ontent **h**ypothesis (OUCH) [34] is one such proposal. OUCH makes two basic assumptions: (1) conceptual features corresponding to object properties that often co-occur will be stored close together in semantic space; and (2) 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. The original OUCH model is not inconsistent with the currently available data from category-specific semantic deficits but it lacks sufficient specificity to provide a principled account of the facts of category-specific deficits.

The Conceptual-Structure account

In recent years, several researchers have taken up the challenge of fleshing-out an OUCH-type model in enough detail to generate empirically tractable predictions (e.g. [26,36–42]). The most developed extension of OUCH is the Conceptual-Structure account of Tyler, Moss, and colleagues. This hypothesis explains the cause of category-specific semantic deficits by assuming random damage to a conceptual system, which is not organized by modality or object domain. The Conceptual-Structure account makes three assumptions: (1) living things have more shared features than non-living things or, put differently, non-living 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) and 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. Note, with respect to assumption (3), that there is no reason why the opposite prediction could not have been made instead: namely, disrupting access to a given feature will disrupt access to highly correlated features.

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, whereas a disproportionate deficit for non-living things will arise only 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 [26,38,43]. The opposite prediction is made by a similar model, which also assumes that artifacts have more informative/distinctive features than living things. However, this model assumes that, as damage becomes more severe, whole sets of intercorrelated features will be lost, resulting in a disproportionate deficit for living things at severe degrees of damage [39,40].

Investigators working within the Conceptual-Structure framework have emphasized category-specific semantic deficits in patients with progressive degenerative diseases, because the resulting neurological damage tends to be widespread and patchy and is thus assumed to correspond to the assumption of random damage. Several studies of patients with dementia of Alzheimer's type (DAT) have investigated the prediction of an association between the severity of conceptual impairment and the direction of category-specific deficit [40,44,45]. One study reported an association between the severity of conceptual impairment and the direction of category-specific deficit [40] 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 [45] for discussion). In line with this, Garrard and colleagues [44], in a study of 58 DAT patients, observed that both the more and the less severely impaired subgroups of patients were impaired for living things compared with non-living things when the patients were ranked according to their overall naming impairment (collapsing across all categories investigated), as well as when the patients were ranked according to their Mini Mental State Examination score (see Fig. 3 for equivalent findings from Zannino and colleagues [45]).

The Conceptual-Structure account (e.g. [36]) is also committed to the claim that there cannot be patients with disproportionate deficits for non-living things but relatively intact performance for living things. However, this is exactly the pattern presented by patient 'JJ', described by Hillis and Caramazza [12]. In oral picture naming, JJ

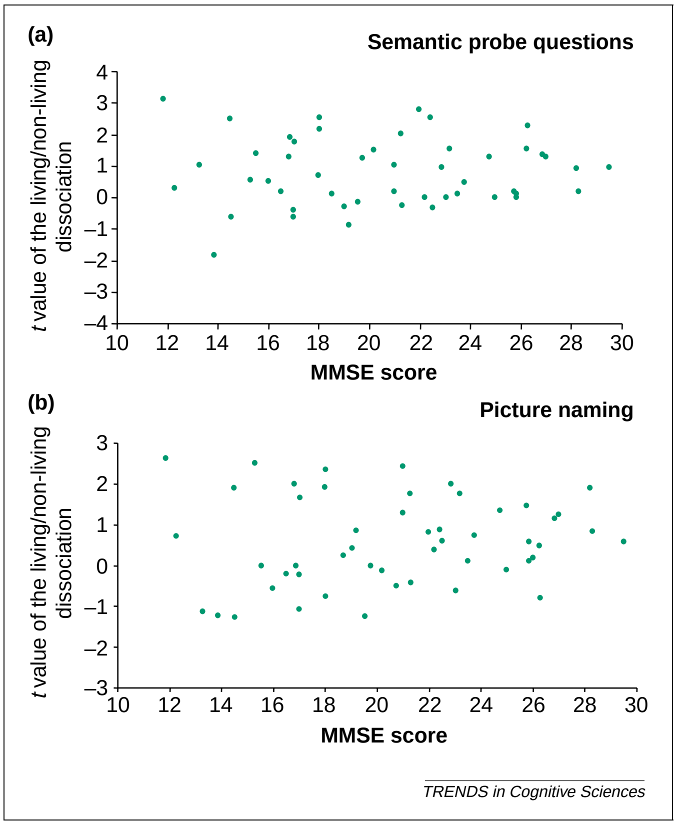

Fig. 3. Plot of t values for individual patients with dementia of Alzheimer's type (DAT) as a function of Mini Mental State Examination (MMSE) score for: (a) the category effect in answering semantic probe questions (see Box 1 for examples of items from this type of test), and (b) the category effect in picture naming. Positive and negative t values correspond to relatively better performance on answering semantic probe questions about (or naming pictures of) artifacts or living things, respectively. The t values higher than 1.9 or lower than -1.9 are significant at a $P = 0.05$ level. Reprinted from Ref. [45], with permission.

performed 91.3% correct for the category animals but only 20.4% correct for nonanimal categories. The Conceptual-Structure account is not able to account for the performance of patient JJ because, according to this model, the only way in which there could be a disproportionate deficit for non-living things is if there was a severe impairment for conceptual knowledge in general. Thus, the central predictions made by the Conceptual-Structure account are at variance with the facts [12,40,44,45].

Interim summary and directions

The three proposals reviewed above (the Sensory/Functional theory, the Domain-Specific hypothesis, and the Conceptual-Structure account) are contrary hypotheses of the causes of category-specific semantic deficits. However, the individual assumptions that comprise each account are not necessarily mutually contrary. For instance, whereas the Sensory/Functional theory can be rejected as a viable hypothesis of the causes of category-specific semantic deficits, it remains an open question as to whether one constraint on the organization of conceptual knowledge in the brain is type or modality of information.

In this context, it is important to note that each of the hypotheses discussed above makes assumptions at a different level in a hierarchy of questions about the organization of conceptual knowledge. At the broadest level is the question of whether conceptual knowledge is organized by domain-specific constraints. We have argued that the facts of category-specific semantic deficits indicate that object domain is one constraint on the organization of conceptual knowledge. The second question is whether conceptual knowledge is represented in modality-specific semantic stores specialized for processing/storing a specific type of information, or in an amodal, unitary system. The third level in this hierarchy of questions concerns the organization of conceptual knowledge within any given object domain (and/or modality-specific semantic store): the principles invoked by OUCH-type models might prove useful for articulating answers to this question.

The data from category-specific semantic deficits do not enable one to discern which assumptions comprising the Sensory/Functional theory and the Conceptual-Structure account are problematic and which might yet prove useful. It thus becomes important to reconsider the individual assumptions comprising these hypotheses in light of a broader range of evidence. In the next section, we illustrate this approach with respect to the second level in the hierarchy of questions just outlined: Is conceptual knowledge organized into modality-specific semantic stores specialized for processing a given type of information (e.g. visual/perceptual)?

Clues from functional neuroimaging

In this section we address two questions: (1) Is there evidence from functional neuroimaging that different areas of the brain are differentially involved in processing/storing information corresponding to different categories of objects? (2) If so, do such data motivate the assumption that one constraint on the physical distribution of conceptual information in the brain is type or modality of information? We note at the outset that the scope of the empirical review to follow is limited to an attempt to address the two questions just framed.

In an elegant series of studies, Martin and colleagues have explored whether the neuroanatomical organization of conceptual knowledge is constrained by object domain and/or modality or type of information. For instance, in one study [46], it was observed that the medial aspect of the fusiform gyri differentially responded to 'tool' stimuli (pictures and words), whereas the lateral aspect of the fusiform gyri differentially responded to 'animal' stimuli. Comparable segregation of activation by object category has been observed in lateral temporal cortex: items corresponding to biological categories differentially activated the superior temporal sulcus (faces [46–50]; animals [46,47]), whereas activation associated with identifying pictures of tools activated more inferior regions centered on the left middle temporal gyrus [46,51] (Fig. 4). Furthermore, it has been observed that the superior temporal sulcus responds differentially to biological motion, whereas the left middle temporal gyrus differentially responds to nonbiological motion (see [52] for data and review).

In response to question (1): there clearly *does* seem to be neural differentiation by semantic category (but see [53] for an alternative interpretation; for recent reviews, see [54–57]). Perhaps most inviting of a domain-specific interpretation of these functional neuroimaging data is a recent study [58] in which subjects viewed the same physical stimuli (e.g. colored triangles) depicting either social or mechanical motion. When these two conditions

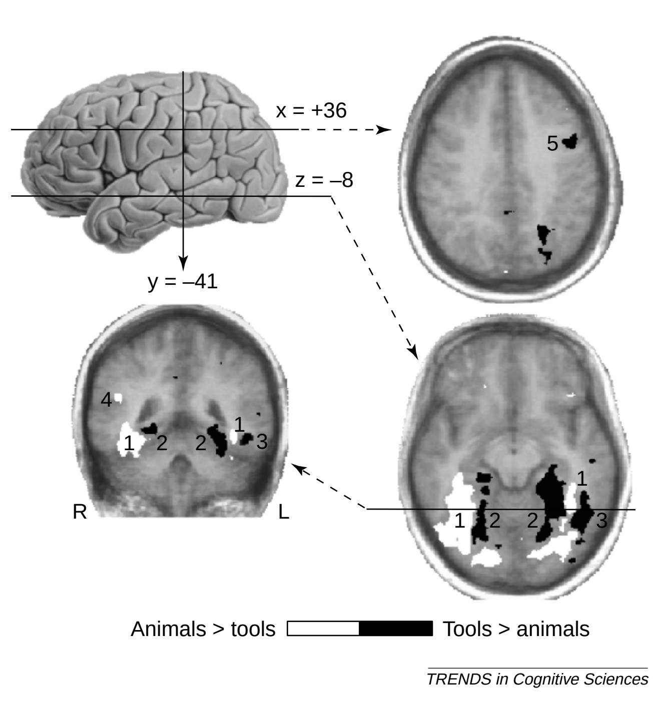

Fig. 4. Segregation of brain activation by object category. Numbers indicate regions showing greater activation for animals (colored white) and tools (colored black). 1 = lateral fusiform gyrus; 2 = medial fusiform gyrus; 3 = left middle temporal gyrus/inferior temporal sulcus; 4 = right superior temporal sulcus; 5 = left ventral premotor (note convention of left and right being reversed in brain images). Reprinted from Ref. [54], with permission.

were compared, activation associated with social motion (e.g. scaring, sharing) was observed in the lateral fusiform gyrus and the superior temporal sulcus, whereas activation associated with mechanical motion (e.g. bowling, conveyor belt) was observed in the medial aspect of the fusiform gyrus and the left middle temporal gyrus. Activation associated with social motion was also found in the amygdala and ventromedial prefrontal cortex [58] (see also [59,60]). 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.

A domain-specific interpretation of these differential effects of object category in inferior and lateral temporal areas is consistent with the possibility that conceptual knowledge is organized by domain-specific constraints within modality-specific semantic stores specialized for processing/storing a specific type of information (in this case, visual/perceptual). Thus, in response to question (2): if we assume that these data reflect the activation of conceptual information corresponding to the visual properties of objects (for discussion see [54]; for an alternative interpretation, see [61], then they would be consistent with the proposal that conceptual knowledge is organized by domain-specific constraints within neuroanatomically defined modality-specific semantic stores. However, these functional neuroimaging data can only be taken as suggestive of an organizational framework of this type, because they could also reflect the activation of modality-specific input representations (in this case, visual/structural descriptions). Either interpretation is consistent with the Domain-Specific hypothesis because this proposal assumes that both conceptual and preconceptual stages of object recognition will be organized by domain-specific constraints (for further discussion, see [14,62]).

Conclusion

We have evaluated three hypotheses of the causes of category-specific semantic deficits. The basic predictions made by the Sensory/Functional theory [1–3], which was until recently the received view, are at variance with the facts of category-specific semantic deficits. The OUCH model [33] is not inconsistent with the facts of category-specific deficits but is too underdeveloped to provide a useful framework for interpreting those facts. When OUCH-type models have been elaborated to the point where they make empirically tractable predictions [36,39] these predictions have not been confirmed. By contrast, the Domain-Specific hypothesis [14] is able to account for the extant facts. This implies that the first-order constraint on the organization of conceptual knowledge is object domain.

The conclusions reached here do not entail the rejection of the individual assumptions that comprise the Sensory/Functional theory and the Conceptual/Structure account. The individual assumptions made by each hypothesis might prove useful for articulating and addressing more fine-grained questions about the functional and neuroanatomical organization of conceptual knowledge. To this end, we have re-evaluated one assumption made by the Sensory/Functional theory with data from functional neuroimaging. It has been observed that spatially dissociable regions in inferior and lateral temporal cortices can be differentially activated by different categories of objects. If it is assumed that inferior and lateral temporal regions correspond (at least in part) to the 'visual semantic' store, then these data might indicate that there are two independent levels of organization of conceptual knowledge in the brain: domain and modality (see Questions for Future Research)).

The combination of neuropsychology and functional neuroimaging is beginning to provide promising grounds for raising theoretically motivated questions concerning the organization of conceptual knowledge in the human brain. At present, however, theories of the organization and representation of conceptual knowledge are to a large extent underdetermined by the data that are often marshaled in support of them.

Questions for Future Research

- Do category-specific semantic deficits for non-living things fractionate into more fine-grained deficits when large numbers of well controlled stimuli are used?
- Are there category-specific deficits *restricted* to modality-specific input (e.g. visual/structural descriptions) or modality-specific output (e.g. lexical phonological or lexical orthographic) representations?
- Do category-specific patterns of activation in inferior temporal areas reflect the activation of modality-specific input representations (i.e. visual/structural descriptions) or conceptual knowledge about the visual properties of objects?

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