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Missed Connections:

A connectivity constrained account of the representation and organization of object concepts

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Introduction

One of the most exciting open issues in the cognitive and brain sciences is how conceptual knowledge is represented and organized in the brain. A recent proliferation of methods that allow cognition to be studied in vivo in healthy subjects has accelerated our understanding of how the brain processes conceptual knowledge. Two broad goals can be framed for the empirical study of concepts: a scientific goal and a clinical goal.

The scientific goal is to develop a model of how concepts are organized and represented, at both the cognitive and neural levels. Such a model would specify the format of conceptual information and the processing dynamics that govern how that information is retrieved according to current task demands. For instance, the types of information that are prioritized are different if one looks at a cup with the intention of taking a drink from it, versus with the intention of identifying it as being ‘my cup’, versus checking whether or not it is empty. A model would specify how the same visual input in all such situations is ‘routed’ through sensorimotor and conceptual systems. This would involve specifying what information is necessary for the task, versus relevant but not necessary, versus activated but entirely ancillary, as well as the order in which information is retrieved. Such a model would specify how conceptual knowledge interfaces with other cognitive systems, such as planning and executive function, linguistic processing, as well as how it interfaces with sensorimotor input and output systems. Finally, such a model would also specify not only the structure and processing dynamics of the conceptual system at a cognitive level, but how that system is organized and distributed in the brain.

The clinically-oriented goal can be separated into prognostic, and treatment-oriented components. On the basis of a working model of how concepts are organized and represented, a prognostic clinical goal is, for instance, to develop accurate means for determining expected

outcomes after acute brain injury, or the trajectory of loss of conceptual information in the context of progressive degenerative diseases such as Alzheimer's disease or Semantic dementia. Another clinically-oriented goal is to use a working model of conceptual organization to help guide neurosurgical planning of the location and extent of cortical resections. Finally, we would want to use our understanding of how concepts are organized and represented in the brain to guide rehabilitation of lost function, where rehabilitation can include existing cognitive/behavioral therapy and prospective approaches that may seek to actually repair damaged tissue.

To date, the study of concepts in the brain has generally focused on analyses of the factors that modulate processing local to a particular region of the conceptual system—for instance, the *visual* factors that modulate visual object recognition, or the *motor* factors that modulate object-directed action. This local, bottom-up, approach has been inherited from well-established traditions in neurophysiology and psychophysics, where it has been enormously productive for mapping psychophysical continua in primary sensory systems. Here I argue, however, that the same approach would not yield equally useful insights for understanding the principles that determine the organization and representation of conceptual knowledge. The reason is that unlike the peripheral sensory systems, the patterns of neural responses that reflect conceptual processing are only partially driven by the physical input – they are also driven by how the stimulus is interpreted, and that interpretation does not occur in a single, isolated region. Thus, a critical step for developing a model of conceptual organization and representation is to articulate how multiple sources of information are integrated in real time and how concepts interface with other cognitive and sensorimotor systems. This means that in order to move forward, as a field, connectivity of the conceptual system with language, executive, sensory,

motor and other systems must become the new ‘unit of analysis’. Connectivity is not just wiring; the connections are not passive conduits through which information is passed. The connectivity of the system constrains the order in which information is accessed and can be weighted, and that weighting of information is a central aspect of the computations that form conceptual processing.

The current state of the field, summarized below, is characterized by a somewhat more ‘static’ notion of concepts, and has developed largely by setting issues of connectivity aside. As will be seen, a tremendous amount of progress has been made in recent decades. But, and as I suggest in the following, the depth of our understanding of both old and new theoretical questions will quickly asymptote without a shift in emphasis toward understanding the role played by connectivity. In keeping with the theme of this volume, this chapter is my attempt to shoot an azimuth of where we are headed as a field; I do this by way of outlining a theoretical framework that places connectivity at the center of what needs to be understood.

Overview of the hypothesis space.

A distinction can be drawn between hypotheses about concept organization, and hypotheses about concept representation. Hypotheses about how concepts are organized in the brain are typically concerned with the causes of an observed physical distribution of conceptual information in different regions of cortex, and/or the reasons why the conceptual system is observed to fractionate along the lines that it does under conditions of brain damage. Hypotheses about how concepts are represented are concerned with the representational format of conceptual information. For instance, a representational issue is whether conceptual knowledge is represented in a modality-specific format (visual, motor) or in an abstract format. As might be expected, the distinction between representation and organization is blurred by theories that make claims about, or have implications for both the organization and representation of

concepts. Nevertheless, it is useful to draw a distinction between organization and representation, principally because there exists an asymmetry in the types of confirmatory empirical evidence that have been marshaled in support of theories that focus on representation versus theories that focus on organization.

The literature review below is fast and loose, and heavily curated; it is entirely in the service of motivating a shift in perspective toward studying the connectivity of the conceptual system. It also makes little attempt to be ecumenical, and is guided by a theoretical framework that has been developed over the past 10 years with Alfonso Caramazza (Caramazza & Mahon, 2003; 2006; Mahon & Caramazza, 2003; 2005; 2008; 2009; 2011). An array of excellent reviews from other theoretical perspectives that discuss a broader range of findings can be found in: Barsalou, 1999; Binder & Desai, 2011; Borgo & Shallice, 2003; Chatterjee, 2010; Cree & MacRae, 2003; Gallese & Lakoff, 2005; Glenberg, Sato, & Cattaneo, 2008; Grill-Spector & Malach, 2004; Hart, et al., 2007; Humphreys & Forde, 2001; Johnson-Frey, 2004; Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Kemmerer, forthcoming; Kiefer & Pulvermüller, 2012; Laws, 2005; Lewis, 2006; Martin, 2007; Op de Beeck, Haushofer, & Kanwisher, 2008; Patterson, Nestor, and Rogers, 2007; Pülvermüller, 2005; Sartori & Lombardi, 2004; Simmons & Barsalou, 2003; Thompson-Schill, 2003; Tyler & Moss, 2001; Vinson, Vigliocco, Cappa, & Siri, 2003.

The scope of the argument to follow is restricted to the representation and organization of object concepts. This leaves most of conceptual space unaccounted for, including concepts expressed as nouns but which do not have physical referents (e.g., dream, goal, piety, etc.), as well as concepts that apply to actions, abstract verbs and many other types of concepts, such as numbers, theory of mind, moral concepts, and logical concepts and reasoning (among other domains as well). The restricted scope of the review helps to gain a solid, if limited, footing on

the theoretical issues pertaining to the organization and representation of object concepts. A complete theory would presumably have within its scope all domains of conceptual processing; whether it will be possible to develop such an account is an empirical and methodological challenge that we face as a field.

Associative Evidence and Theories of the Representation of Concepts

A widely discussed theoretical framework about the representation of conceptual knowledge is the ‘Embodied Cognition Hypothesis.’ The central idea of this framework, applied to concepts, is that sensorimotor representations are re-activated or ‘simulated’ in the course of conceptual analysis, and that sensorimotor activation is a necessary and intermediary step in the computation of meaning (see Allport, 1985 for an early formulation of this view). The strong (and arguably most interesting) form of this view is that there is no representational distinction between conceptual information and sensorimotor information: Retrieving concepts consists of simulation or reactivation of sensorimotor information that is/was activated, either when we initially acquired the concept, and/or when we interact with instantiations of that concept. Because this is the central claim of the hypothesis, the theory is committed to the view that conceptual retrieval involves the retrieval of stored sensorimotor information. Because these sensorimotor ‘memories’ are sensory or motor in their format, they are assumed to be ‘token-based’ representations, or representations of actual instances of sensory or motor experiences. Another way to think about such theories is that they are a type of an exemplar-based model of semantic memory, where the exemplars consist of sensorimotor information and are in a sensory or motor format.

An important type of evidence argued to support the Embodied Cognition hypothesis consists of demonstrations that motor processes are automatically engaged when participants

perform conceptual and perceptual tasks that do not require, on a logical analysis of the task, overt activation of the motor system. Such motor activation has been observed in functional neuroimaging, in neurophysiological recordings in non-human primates and humans, EEG, behavior, TMS, and kinematic analyses (for empirical reviews and theoretical discussions, see e.g., Barsalou, Simmons, Barbey, & Wilson, 2003; Boulenger, Roy, Paulignan, Deprez, Jeannerod, & Nazir, 2006; Gallese & Lakoff, 2005; Martin, 2007; Pulvermüller, 2005; Rizzolatti & Craighero, 2004). For instance, Hauk and colleagues (2004) found overlap in the regions of the motor cortex that were activated for both physical actions and for words that describe actions (e.g. “kick”). Foot-related action words like “kick” activated dorsal parts of the motor cortex while hand-related action words like “pick” activated more lateral and ventral parts of the motor cortex, following the known pattern of somatotopy. As another example, Glenberg, Sato and Cattaneo (2008) found that when participants moved hundreds of beans from a container near them to a container farther away, they were slower to judge sentences as sensible that described action events in which objects were moved away from the body. Glenberg and colleagues argued that fatiguing the motor system selectively interfered with the comprehension of sentences whose meaning implied a directionality congruent with the direction of the prior bean movements.

Recent interest in the embodiment of concepts parallels recent interest in motor theories of perception. The original motor theory of speech perception (Liberman, Cooper, Shankweiler & Studdert-Kennedy, 1967; Liberman & Mattingly, 1985) stated that speech recognition was fundamentally a process of recognizing the motor actions (tongue/articulatory movements) of the speaker and not one of recognizing the auditory perceptual information per se. Thus, speech recognition consisted of simulating the motor output programs that would be necessary to

produce the sounds being recognized. The motor theory of speech perception, and more recently, the motor theory of action recognition, have enjoyed a renaissance because of the discovery of so-called mirror neurons: Neurons in premotor and other motor-relevant structures in macaques that fire both when the monkey performs an action and when it observes another individual (man, monkey) performing an action (e.g., di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996). Mirror neurons are thought to provide the empirical substrate for a reformulated motor theory of action perception, and thus provide independent evidence for the notion that processing in one system (perception) is in part constituted by (i.e. involves as a necessary and intermediary step) processing in the motor system (for critical discussion, see Binder & Desai, 2011; Chatterjee, 2010; Dinstein, Thomas, Behrmann, & Heeger, 2008; Hickok, 2009; 2010; Hickok et al., 2008; Hickok, Costanzo, Capasso, & Miceli, 2011; Lingnau, Gesierich, & Caramazza, 2009; Mahon & Caramazza, 2005; 2008; Stassenko, Garcea, & Mahon, in press).

The critical issue is whether demonstrations that the motor system is activated during perceptual or conceptual analysis indicate, as presumed by the Embodied Cognition Hypothesis and the motor theory of action recognition, that motor information plays a constitutive (i.e., necessary) role in perceptual and/or conceptual analysis. The alternative is that activation spreads from perceptual or conceptual levels of processing through to motor processes. There are different ways in which such an alternative could be formulated. For instance, it could be argued, in the context of motor activation during perception, that the dynamics of the sensorimotor systems are such that activation propagates to the motor system only after the stimulus has been recognized as such. Alternatively, it could be argued that activation cascades forward to the motor system from input levels of processing *prior* to completion of processing at those input

levels. The broader point is that a range of alternative accounts can be formulated to explain why the motor system is activated during perception (for discussion, see Mahon & Caramazza, 2008; Stassenko et al., in press).

By analogy, there is evidence that the phonology of words that are never overtly produced, but which are semantically related to actually produced words, is activated in the course of speech production (e.g., Costa, Caramazza, & Sebastián-Gallés, 2000; Peterson & Savoy, 1998). However, it has never been argued that such observations sanction the inference that the activated phonological information constitutes, even in part, the semantics of the unproduced words. Rather, the debate concerned the dynamics of information flow within the speech production system, and whether it was cascaded activation or serial and discrete. While it is admittedly somewhat pedantic to draw out this analogy to the phonological activation of unproduced words, the relationship between evidence and theory exactly mirrors the relationship between observations of motor activation during perceptual or conceptual processing, and the Embodied Cognition Hypothesis. Thus the implication is that the representational inferences that have been argued to support the Embodied Cognition Hypothesis are, at best, premature, and the available evidence is, at best, (only) consistent with the embodied cognition hypothesis.

Patient Evidence and the Embodied Cognition Hypothesis.

Recent work with brain damaged patients had highlighted cases where conceptual and motor abilities are seen to be impaired together – i.e., theoretically interesting associations of impairments. For instance, Pazzaglia, Pizzamiglio, Pes, & Aglioti (2008) observed that patients with buccofacial apraxia (impairments producing sounds related to facial and mouth structures, e.g., whistling or slurping a straw) had greater difficulty recognizing mouth action sounds

compared to hand action sounds, whereas patients with limb apraxia (difficulties performing skilled actions like pounding a hammer) had greater difficulty recognizing limb action sounds compared to mouth action sounds (see Mahon, 2008 for discussion; see also Pazzaglia, Smalia, Corato, & Aglioti, 2008). Buxbaum and colleagues (2005) found an association at the group level in the ability of patients to imitate certain types of actions and their ability to recognize actions (see Negri et al., 2007 for replication, extension and critical discussion). Boulenger and colleagues (2008) combined a masked priming paradigm with a lexical decision task to study semantic priming effects in a non-demented group of Parkinson's patients ($n = 10$) who were either off or on dopaminergic treatment. It is known that Parkinson's patients show relative inactivation of motor cortices when they are off, compared to when they are on, dopaminergic treatment. The authors found that the magnitude of the masked priming was modulated according to whether the patients were on or off their medication, and importantly, this modulation was present only for action word targets and not for concrete nouns. Another recent and rich example is the study by Bonner and Grossman (2012), who found that patients with logopenic variant of primary progressive aphasia, a variant that leads to cortical atrophy first around Hershel's gyrus, were impaired for knowledge about the typical sounds that objects make.

However, there is also dissociative patient evidence indicating that action production can be impaired while action recognition is spared, both in the domain of hand actions (Negri et al., 2007; Rumiati, Zanini, Vorano, & Shallice, 2001; Rapcsak, Ochipa, Anderson, & Poizner, 1995; for reviews, see Mahon & Caramazza, 2005; 2008) and in the domain of speech perception (Hickok et al., 2011; Rogalsky, Love, Driscoll, Anderson, and Hickok, 2011; for reviews, see Hickok, 2009; 2010; Stassenko et al., in press; Toni, de Lange, Noordzij, & Hagoort, 2008). For

instance, patients with apraxia of object use are not necessarily impaired for naming the same objects or retrieving function knowledge about those objects (e.g., Buxbaum, Veramonti, & Schwartz, 2000; Buxbaum & Saffran, 2002; Ochipa, Rothi, & Heilman, 1989; Rapczak et al., 1995; for review see Mahon & Caramazza, 2005).

The existence of *dissociative* evidence is problematic for the claim that motor information forms a necessary component of conceptual or perceptual processing. The dissociative patient evidence is sufficient to reject strong forms of the embodied concept hypothesis and strong forms of the motor theory of action perception (for discussion, see Garcea & Mahon, 2012; Mahon & Caramazza, 2005; 2008; Stassenko et al., in press; Hickok, 2010; Chatterjee, 2010). This conclusion carries with it the burden of explaining **i)** why the motor system is activated during (perceptual and conceptual) tasks that do not, on a logical analysis of what is involved in those tasks, necessitate overt activation of motor information, and **ii)** why the above described associative patient evidence is observed (e.g., Buxbaum et al., 2005; Bonner & Grossman, 2012; Pazzaglia et al., 2008a; 2008b). One possibility is that activation spreads from perceptual and/or conceptual levels of representation to the motor system. In the context of the Embodied Cognition Hypothesis, the question arises as to what function such activation might serve. The associative patient evidence suggests that such activation is not irrelevant or ancillary but that it may play some, as yet unspecified, function. I return to these issues below.

The broader point is that the core issue that must be elucidated concerns how information is exchanged among sensory, motor and conceptual systems. What we are missing, as a field, is a theory of the dynamics of activation spread between perceptual and/or conceptual processes and the motor system. Only in the context of a concrete theory of the dynamics of sensorimotor and conceptual processing can strong inferences about the representational format be derived from

observations that the motor system is automatically activated during perceptual or conceptual tasks.

Dissociative Evidence and Theories of the Organization of Concepts

One of the most intriguing of neuropsychological phenomena are category-specific semantic deficits. Category-specific semantic deficits are impairments to conceptual knowledge that differentially, or selectively, affect information from one semantic category compared to others. Figure 1A shows the picture naming performance from some well-studied patients, and represents the full range of semantic categories that can be differentially or selectively impaired in patients with category-specific semantic deficits. The ‘categories’ of category-specific semantic deficits are: living animate (animals), living inanimate (fruit/vegetables), conspecifics, and tools (for an exhaustive review of the empirical literature through 2001, see Capitani, Laiacona, Mahon, & Caramazza, 2003).

Category-specific semantic deficits have been a particularly fertile ground for the development and evaluation of hypotheses about how conceptual information is organized. The general question that these theories seek to answer is: How is knowledge organized in the normal system such that damage can lead to impairments that respect semantic category distinctions? Current theories can be separated into ‘reductionist’ and ‘non-reductionist’ approaches; ‘reductionist’ theories do not posit semantic category as an organizing principle in the mind/brain, while ‘non-reductionist’ theories do posit semantic category as an organizing principle. Within reductionist theories a further distinction can be made between ‘eliminativist reductionist’ theories and ‘non-eliminativist reductionist’ theories, with eliminativist approaches denying any principles of neural organization whatsoever, and non-eliminativist making clear

positive proposals about neural organization (but not appealing to semantic category or domain as an organizing principle).

Eliminativist Reductionist Theories. It was recognized early on in the study of category-specific semantic deficits that the impairments in some patients could be explained because items from different semantic categories tended to differ along certain variables, such as lexical frequency, concept familiarity, or the visual complexity of the images that were used to establish the presence of impairments. Thus, if items were sampled without attention to those variables, then some categories within the neuropsychological tests might be ‘easier’ than other categories, thus leading to ‘spurious’ category dissociations (see Funnell & Sheridan, 1992; for recent discussion and for extensive normative work see Barbarotto, Laiacina, Macchi, & Capitani, 2002; Cree & MacRae, 2003). More recently, Sartori, Lombardi and colleagues (Mechelli, Sartori, Orlandi, & Price, 2006; Sartori & Lombardi 2004, Sartori, Lombardi, & Mattiuzzi, 2005) developed a measure termed ‘semantic relevance’ which is a nonlinear combination of the frequency with which particular features are produced for an item, and the distinctiveness of that feature across all concepts in the database. In addition, the issue of whether items from some categories are more visually complex than others can be expressed as a cognitive issue and not merely an issue about the stimuli over which patients are tested. It may be argued that the structure of the world, and our representation of that structure, is such that the visual knowledge of one category is more ‘tightly packed’ or ‘crowded’ than other categories. Arguments differ as to which categories have representations that are more densely packed, but proposals agree that a higher density of representations renders them more susceptible to impairment (e.g., Humphreys & Forde, 2001; Laws, 2005).¹

¹ It should be noted, however, that it is not obvious that higher density (i.e. higher within-category similarity) should lead to greater susceptibility to impairment, as for instance, Tyler, Moss and colleagues (Tyler et al., 1998; Tyler &

In summary, a number of dimensions may vary across semantic categories that are represented at both conceptual and non-conceptual levels of processing (e.g., lexical frequency, concept familiarity, visual/structure similarity). The critical test of such accounts, as accounts of the existence of the phenomenon of category-specific deficits, is **i)** whether category dissociations remain when items are carefully matched across categories (for discussion see Capitani et al., 2003), and **ii)** whether double dissociations can be observed over the same materials across patients (e.g., Caramazza & Hillis, 1991). Because both **(i)** and **(ii)** have been answered in the affirmative, we can conclude that category-specific semantic deficits are not spurious, i.e., cannot be reduced to such uncontrolled dimensions. This conclusion rules out the broad class of ‘Eliminativist Reductionist’ Theories (for evidence and arguments, see Caramazza & Mahon, 2003; Mahon & Caramazza, 2009).

Non-Eliminativist Reductionist Theories. The modern study of concepts in the brain was inaugurated by the empirical and theoretical work of Warrington, McCarthy & Shallice (Warrington & McCarthy, 1983, Warrington & McCarthy, 1987; Warrington & Shallice, 1984). In a series of papers, they documented the first well-described cases of category-specific semantic deficits, and also proposed the most influential theory that is still widely discussed today: the Sensory/Functional Theory.

The Sensory/Functional Theory makes two assumptions:

i) The first assumption made by the Sensory/Functional Theory is that the semantic system is organized by modality or type of information. The original distinction that was drawn was between visual/perceptual and functional/associative systems (see Lhermitte & Beauvois, 1973 for earlier work on this assumption). More recently, Crutch & Warrington (2003; see also Cree

Moss, 2001) argued in a somewhat different context that high correlations among shared features confers resistance to damage (but see Devlin, Russell, Davis, Price, Moss, et al, 2002).

& MacRae, 2003; Vinson et al., 2004) proposed that the semantic system may be more finely structured by modality or type of information. For instance, ‘visual/perceptual’ can be further fractionated into color, form, and surface properties (Cree & MacRae, 2003; Crutch & Warrington, 2003).

ii) The second assumption made by the Sensory/Functional Theory is that the ability to recognize items from different semantic categories differentially depends on different modalities or types of information. For instance, the ability to recognize and identify animals, it was argued, differentially depends on visual/perceptual information while the ability to recognize tools and other manmade artifacts differentially depends on functional/associative knowledge. The comprehensive semantic feature norming work of Cree & MacRae (2003; see also Vinson et al., 2004) is largely directed at this second assumption. Those authors asked healthy subjects to produce features of common objects, and the resulting features were taxonomized into nine “knowledge types” that could have plausible neural bases. The authors then used clustering methods to argue that some “knowledge types” were more important/salient for some semantic categories.

The two core assumptions of the Sensory/Functional Theory together explain category-specific semantic deficits as arising from damage to a modality or type of knowledge upon which successful identification of items from the impaired category differentially depends. For this reason, the theory is non-eliminativist (it makes a strong and positive claim about neural organization) but is reductionist with respect to semantic categories (as it posits the relevant underlying organizational principle is modality rather than category).

It is important to note that the Sensory/Functional Theory is not committed to a particular view about the format of conceptual representations—i.e., the Sensory/Functional Theory could,

or could not, be formulated as an Embodied Cognition Hypothesis. In other words, the hypothesis that semantic information can be distinguished by modality or type could be proposed as a claim about the *content* of semantic information and not its format (for discussion, see Caramazza, Hillis, Rapp, & Romani, 1990). This is a point that is often obscured in the literature, where the Sensory/Functional Theory is assumed to be a claim about the format of conceptual knowledge, and thus run together with embodied proposals. However, one can accept a strong representational distinction between concepts and sensorimotor processes (i.e., conceptual information is dissociable from sensory-motor processes), and still argue that modality or type of information is the principle dimension along which concepts are organized. In fact, this was the original proposal by Warrington and her collaborators. Subsequent developments of the theory (e.g., Martin, Ungerleider, & Haxby, 2000) have argued for more nuanced positions, for instance, that object concepts are stored adjacent to the sensory and motor systems that were active when the concept was acquired. However, even the (so-called) Sensory/Motor Theory of Martin and collaborators (see also Martin, 2007) is not committed to the view that the format of conceptual representations is strictly sensorimotor. Still other hypotheses argue for somewhat stronger marriages between the Sensory/Functional Theory and embodied views of concepts (see for instance, Simmons & Barsalou, 2003).

A number of arguments have been raised against the Sensory/Functional Theory. On the one hand, the evidence that has been marshaled in support of the assumption that different categories differentially rely on different types or modalities of knowledge for their recognition has been questioned on methodological grounds (e.g., Caramazza & Shelton, 1998). More recent investigations (e.g., Cree & MacRae, 2003) largely overcame the methodological limitations that attended earlier studies. However, the findings of the more recent and sophisticated normative

studies are not obviously relevant to the key assumption that different types of knowledge are differentially important for distinguishing *within* categories. For instance, Cree and MacRae showed that different types of knowledge are important for distinguishing among different categories, or one category from other categories. In one finding, the authors showed that color is important for distinguishing fruit/vegetables from other categories while biological motion was important for distinguishing animals from other categories. However, patients with category-specific semantic deficits do not have difficulties distinguishing between categories, but rather *within* categories. Thus, it is not obvious that there is in fact evidence for the assumption that different types or modalities of information are differentially important for distinguishing among items *within* categories.

Another argument against the Sensory/Functional Theory, and perhaps the most damaging argument, is that patients with category-specific semantic deficits do not present with differential impairments for the modality or type of knowledge upon which the impaired category (putatively) depends (see Figure 1B). In other words, patients with disproportionate impairments for animals do not have a corresponding disproportionate impairment for visual/perceptual knowledge. Similarly, patients with disproportionate impairments for visual/perceptual knowledge do not necessarily have a disproportionate impairment for animals. Such dissociations between the category-specificity of the deficit and the modality-specificity of the deficit are the norm, rather than the exception (see Capitani et al., 2003).

Non-Reductionist Theories. According to this view, category-specific semantic deficits arise because the damage affects a brain region or network of brain regions that is devoted to a particular semantic domain of knowledge. The ‘domains’ for which there are specialized systems are limited to those domains that could have had an evolutionarily significant history (living

animate, living inanimate, conspecifics, and tools). This hypothesis was initially articulated in the context of category-specific semantic impairments by Caramazza and Shelton (1998; see also e.g., Capitani et al., 2003; Farah & Rabinowitz, 2003; Samson & Pillon, 2003). Subsequent formulations of the domain-specific hypothesis (Caramazza & Mahon, 2003; 2006; Mahon & Caramazza, 2009; 2011) have emphasized that the semantic system is also organized by modality or type of information. In other words, there may be two orthogonal dimensions of organizations, perhaps hierarchically structured: Domain and modality. I return to this issue below.

In summary, the picture that emerges from the last several decades of work on category-specific semantic deficits is as follows: **i)** Category-specific semantic deficits survive stringent control of stimulus variables, and are observed to doubly dissociate across patients tested with the same set of materials. These facts rule out, broadly speaking, theories that posit that the phenomenon arises because a dimension (e.g., visual complexity, relevance) is correlated with a semantic category distinction. **ii)** Category-specific semantic deficits affect all types of knowledge that have been tested, indicating that a deficit to a particular modality or type of knowledge cannot explain the existence of the phenomenon (Figure 1B). In this context, we (e.g., Caramazza & Mahon, 2003; Mahon & Caramazza, 2009) have concluded that semantic domain is an organizing principle of conceptual knowledge of objects, and that the most attractive model (for other reasons, see below) has at least two orthogonal dimensions of organization: Semantic domain and modality or type of information.

Functional MRI evidence for the constraints that shape object knowledge in the brain

Ventral and Dorsal Object Processing Streams.

An important development in cognitive neuroscience that has paralleled the articulation of theories of semantic organization is the discovery of multiple channels of visual processing

(Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). It is now known that cortical visual processing bifurcates into two independent but interconnected streams (for discussion of how best to characterize the two streams, see Pisella, Binkofski, Lasek, Toni & Rossetti, 2006; Schenk, 2006; see also Merigan and Maunsell, 1993). The ventral object processing stream projects from V1 through ventral occipital and temporal cortices, terminating in anterior regions of the temporal lobe, and subserves visual object identification. The dorsal object processing stream projects from V1 through dorsal occipital cortex to posterior parietal cortex, and subserves object-directed action and spatial analysis for the purpose of object-directed grasping. The ‘two-visual systems’ hypothesis was initially formulated on the basis of neuropsychological evidence, in which ventral lesions led to impairments for perception and identification of object attributes but spared action toward the same objects, while dorsal lesions led to action impairments that spared perception (e.g., Goodale, Milner, Jakobsen, & Carey, 1991; Pisella, Gréa, Tilikete, Vighetto, Desmurget, et al., 2000; Ungerleider and Mishkin, 1982). There has since been an enormous amount of imaging work confirming the distinction between ventral and dorsal object processing streams (e.g., Binkofski et al., 1998; Culham et al., 2003; Mahon et al., 2007; Shmuelof & Zohary, 2005).

Category-specificity in the ventral object-processing stream.

There is a vibrant literature studying category-specificity in humans using functional Magnetic Resonance Imaging (fMRI). The most widely studied categories, and the categories for which specific regions of the brain exhibit differential Blood Oxygen Level Dependent (BOLD) responses are faces, animals, body parts, tools, places, and words (for reviews, see Bookheimer, 2002; Gerlach, 2007; Grill-Spector & Malach, 2004; Martin, 2007; Op de Beeck et al. 2008; Thompson-Schill, 2003). On the ventral surface of temporal occipital cortex, in the ventral

object-processing stream, there is a consistent topography by semantic category across individuals. For instance, viewing tools leads to differential BOLD contrast in the left medial fusiform gyrus, while viewing animate living things (animals and faces) leads to differential BOLD contrast in the lateral fusiform gyrus (Chao, Haxby, & Martin, 1999; Kanwisher, McDermott, & Chun, 1997; for earlier work, see Allison et al., 1994). The region of the lateral fusiform gyrus that exhibits larger responses to faces compared to a range of other categories (Downing, Chan, Peelen, Dodds, and Kanwisher, 2006) has been dubbed the ‘fusiform face area’ (FFA). The face area tends to be lateralized (or biased) toward the right hemisphere, while often in the homologous region of the left hemisphere, selectivity for printed words is observed (for review see Dehaene, Cohen, Sigman, & Vinckie, 2005; for modeling work and discussion of this asymmetry, see Plaut & Behrmann, 2011). Place stimuli, such as houses or scenes differentially drive BOLD responses in a more anterior and medial location in cortex adjacent to the hippocampus, called the parahippocampal gyrus (and the region has been dubbed the ‘parahippocampal place area’, PPA; Epstein & Kanwisher, 1998; see also Bar & Aminoff, 2003). Finally, there are also articulated category effects in lateral occipital cortex (Weiner, Sayres, Vinberg, & Grill-Spector, 2010), and category-specificity in those lateral occipital regions has been dissociated using TMS (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009).

The organization by semantic category in the ventral object-processing stream described above is largely invariant to the task and stimuli used in the experiment (e.g., linguistic, image, auditory), although the responses are strongly modulated by task and attention (Chao et al., 1999; Kanwisher & Downing, 1998). In other words, what determines the location of category-specific responses is the category (i.e., content) of the stimulus and not its format. Category-specific responses in the ventral stream are also generally invariant to stimulus manipulations such as

orientation, size, and contrast (Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001; see Figure 2 for some examples of category-specificity in the ventral stream). Importantly, what seems to matter for driving category-specific responses in the ventral stream is the interpretation that is applied to a stimulus—i.e., whether it is interpreted as being living animate or inanimate (e.g., Martin and Weisberg, 2003).

There is general agreement that the format of information represented in temporal-occipital regions exhibiting category-specific responses is something like high-level ‘visual’ representations. Damage to the fusiform gyrus, and/or lingual gyrus is known to produce various types of visual agnosia, including color agnosia, and sometimes alexia when the damage is restricted to the left hemisphere (Miceli, Fouch, Capasso, Shelton, Tomaiuolo, & Caramazza, 2001; Stasenko, Garcea, Dombovy, & Mahon, under review), and prosopagnosia when damage involves the right hemisphere. Similarly, damage to lateral occipital cortex can lead to profound visual form agnosia, as in the very well studied patient DF (Goodale et al., 1991).

Category-specificity in the dorsal object-processing stream.

Tools, compared to a range of baseline stimuli, differentially drive BOLD contrast in the left posterior middle temporal gyrus, left parietal cortex, and left premotor cortex (Figure 2). The left middle temporal region that exhibits differential BOLD responses when viewing manipulable objects (e.g., Martin, Wiggs, Ungerleider, and Haxby, 1996; Thompson-Schill, Aguirre, D’Esposito, & Farah, 1999; see Devlin et al. 2002 for a review) plays an important role in processing the semantics of actions (e.g., Kable, Lease-Spellmeyer, & Chatterjee, 2002, Kemmerer, Gonzalez Castillo, Talavage, Patterson, & Wiley, 2008; Martin et al. 1995) as well as mechanical (i.e., unarticulated) motion (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Martin & Weisberg, 2003; Wheatley, Milleville, & Martin, 2007).

Regions of bilateral dorsal occipital cortex, posterior parietal cortex, through to the anterior intraparietal sulcus, are automatically activated when participants observe manipulable objects (e.g., Chao & Martin 2000; Fang & He, 2005). Dorsal occipital and posterior parietal regions are important for determining volumetric and spatial information about objects relevant to pointing, while anterior intraparietal sulcus is thought to be important for object prehension (Binkofski et al., 1998; Culham et al., 2003; Frey, Vinton, Newman-Norlund, & Grafton, 2005). Optic ataxia, an impairment for reaching and/or grasping objects, is classically associated with lesions to posterior and superior parietal structures (e.g., Pisella et al., 2000). Optic ataxia is not necessarily associated with difficulties for manipulating objects according to their function (as optic ataxia patients may be able to manipulate the objects once they are in hand).

Viewing or naming tools also differentially activates the left inferior parietal lobule (e.g., Mahon, Milleville, Negri, Rumati, Caramazza, and Martin, 2007; Rumati, Weiss, Shallice, Ottoboni, Noth, et al., 2004), a region that is important for representing complex object-associated manipulations. This region is also activated when congenitally blind individuals think about tools, indicating that visual experience with objects is not necessary for the specificity to emerge (Mahon, Schwarzbach, and Caramazza, 2010). Damage to the left inferior parietal lobule is classically associated with apraxia of object use (Rothi, Ochipa, & Heilman, 1991; Rushworth, Krams, & Passingham, 1997; Johnson-Frey, 2004; see also discussion above in the context of the Embodied Cognition hypothesis).

Implications of the Imaging Evidence

The power of the functional MRI approach to studying category-specificity is that it provides a window into *all* regions that are involved in processing information about different categories, regardless of whether or not involvement of those regions is necessary. A number of

different accounts have been suggested about the causes of category-specific neural responses in humans. Most of those accounts are directed at understanding the causes of category-specificity in the ventral stream (Grill-Spector & Malach, 2004; Haxby et al., 2001; Martin, 2007; Mahon et al., 2007; Mechelli et al., 2006; Rogers et al., 2005). It is generally agreed that differential BOLD responses for tools in dorsal stream regions are driven by automatic extraction of motor-relevant information (e.g., Martin, 2007; see discussion above in the context of the Embodied Cognition Hypothesis).

Our own view of the causes of category-specificity in the ventral stream is that it emerges because different regions of the ventral stream are innately connected with other regions of the brain that process nonvisual information about the same categories (for discussion of this connectivity-constrained account of category-specificity see Mahon et al. 2007; 2009; Mahon & Caramazza, 2009; 2011). The core aspect of this proposal is that connectivity is what is innate and what drives domain-specificity. In other words, the domain-specificity of a given region is not driven (only) by organizational principles expressed over information local to that region, but by the broader network architecture in which that region is embedded (Mahon & Caramazza, 2011). Thus, for instance, the regions that exhibit specificity for tools (medial fusiform gyrus) do so because that region has (by hypothesis) privileged connectivity with motor-relevant structures that are involved in actually manipulating objects. Thus, the high-level visual representations for tools ‘come to live’ in those regions of the visual system that are already connected up with other regions of the brain that process motor-relevant information about tools. Similarly, the argument would be that faces are represented in regions of high-level visual cortex that have privileged connectivity to regions of the brain that process affective information. By hypothesis, regions of lateral occipital cortex that differentially respond to images of the hands will express privileged

connectivity to somatomotor areas that also represent the hands (Bracci et al, 2012). This kind of a ‘connectivity constrained account’ (Reisenhuber, 2007) can explain why there would be specialization for printed words, a class of stimuli for which there can be no plausible evolutionary history (see Martin, 2006). In other words, the fact that there is specialization for printed words in the same way that there is specialization for categories that could have evolutionarily significant histories (faces, tools, places, etc), suggests that what is innate is not the content of the category, but rather a basic scaffolding of connectivity between high-level visual regions and other parts of the brain. Because those other parts of the brain will have their own biases toward specific functions, innately specified connectivity would be sufficient to drive specialization by semantic category in high level visual regions. In the case of the visual word form area in the ventral object-processing stream, the prediction is made that it will exhibit privileged connectivity to left hemisphere language regions (see also Plaut & Behrmann, 2011; for data from the domain of faces, see Thomas et al., 2009).

Several lines of evidence have recently been reported that support the view that semantic domain innately constrains the organization of object knowledge, and that connectivity is the substrate for domain-specificity. There are three strands of this evidence.

i. There are deep similarities between monkeys and humans in the ‘semantic space’ of object representations in the ventral stream. An expectation of the view that innate constraints shape category-specificity in the ventral stream is that such specificity, at least for some categories, will also be found in non-human primates. It is well known, using neurophysiological recordings, that preferences for natural object stimuli exist in the inferior temporal (IT) cortex of monkeys (e.g., Kiani et al., 2007; Tanaka et al., 1991), comparable to observations with similar methods in awake human subjects (Kreiman et al., 2000). More recently, functional imaging

with macaques (Tsao et al., 2006) and chimpanzees (Parr et al., 2009) suggests that at least for the category of faces, comparable clusters of face preferring voxels can be found in the temporal cortex in monkeys, as are observed in humans. Such common patterns of neural organization for some classes of items in monkeys and humans could, of course, be entirely driven by dimensions of visual similarity, which are known to modulate responses in the IT cortex (Op de Beeck, Wagemans, & Vogels, 2001). However, even when serious attempts have been made to explain such responses in terms of dimensions of visual similarity, taxonomic structure emerges over and above the contribution of known visual dimensions. For instance, Kriegeskorte and colleagues (2008) used multi-voxel pattern analysis to compare the similarity structure of a large array of different body, face, animal, plant and artifact stimuli in monkey IT cortex and human occipital–temporal cortex. The similarity among the stimuli was measured in terms of the similarity of the patterns of brain responses they elicited, separately on the basis of the neurophysiological data (monkeys; Kiani et al., 2007) and fMRI data (humans). The similarity structure that emerged revealed a tight taxonomic structure common to monkeys and humans (see Figure 3). Importantly, that similarity structure was not present in early visual cortex and could not be reproduced from computational models of low level visual processing (see Kriegeskorte et al., 2008 for details and discussion).

ii. There is an innate component to face recognition. Two recent reports highlight greater neural or functional similarity between monozygotic twin pairs than between dizygotic twin pairs (for discussion see Park et al., 2009; Zhu et al., 2010). The strength of these studies is that experiential contributions are held constant across the two types of twin pairs. In a fMRI study, Polk & colleagues (2007) studied the similarity between twin pairs in the distribution of responses to faces, houses, pseudowords and chairs in the ventral stream. The authors found that

face and place-related responses within face and place selective regions, respectively, were significantly more similar for monozygotic than for dizygotic twins. In another study, Wilmer and colleagues (2010) studied the face recognition and memory abilities in monozygotic and dizygotic twin pairs (using some of the tests developed by Duchaine & Nakayama, 2006). Wilmer and colleagues found that the correlation in performance on the face recognition task for monozygotic twins was more than double that for dizygotic twins. This difference was not present for control tasks of verbal and visual memory, indicating selectivity in the genetic contribution to facial recognition abilities (see also Zhu et al., 2010).

iii. Category-Specific Neural Organization Does not Require Visual Experience. Recent findings indicate that visual experience is not necessary in order for the same, or similar, patterns of category-specificity to be present in the ventral stream. In an early positron emission tomography study, Büchel and colleagues (1998) showed that congenitally blind subjects show activation for words (presented in Braille) in the same region of the ventral stream as sighted individuals (presented visually; see also Reich, Szwed, Cohen, & Amedi, 2011). Pietrini and colleagues (2004) used multi-voxel pattern analysis to show that the pattern of activation over voxels in the ventral stream was more consistent across different exemplars within a category than exemplars across categories. More recently, we have shown that the same medial-to-lateral bias in category preferences on the ventral surface of the occipital–temporal cortex that is present in sighted individuals is present in congenitally blind subjects (Mahon et al., 2009). Specifically, just like in sighted individuals, nonliving things, compared to animals, elicited stronger activation in medial regions of the ventral stream (see Figure 4).

Although these studies on category-specificity in blind individuals represent only a first-pass analysis of the role of visual experience in driving category-specificity in the ventral stream, they

indicate that visual experience is not necessary in order for category-specificity to emerge in the ventral stream. While this is not incompatible with the view that visual experience has an important role to play in shaping the organization of high level visual areas in sighted individuals, it does point to an organizational constraint that cannot be reduced, in its entirety, to visual experience. The hypothesis that we have advanced (Mahon & Caramazza, 2011), and which I believe the functional imaging data from blind individuals support, is that endogenously specified connectivity is the basic organizational constraint, or scaffolding, within which experience-dependent organizational principles operate. Furthermore, and by hypothesis, that endogenously specified connectivity will have a granularity that matches the domains for which neural specificity has been described in the ventral object processing pathway.

Current and New Directions

Based on brief overview of existing theories and evidence summarized above, several conclusions can be extrapolated, which I pull together here. I also try to frame what I believe are the issues that will drive research as the field moves forward, and beyond the issues with which it has been occupied over the last several decades. My approach to these prospective suggestions is to outline forward-leaning conclusions that indicate new questions. The broad and overarching suggestion is that there will be a common answer to the set of questions that are outlined. In short form, that answer is that the only way to gain a deeper understanding of the informational content, the organization of that content, and dynamics of the conceptual system and its interface with other systems, will be through research that unpacks the structure and function of connectivity.

Empirical Generalization I. Category-specific phenomena cannot be dissolved. As described above, there are very rich phenomena of category-specificity in the human brain that

were initially discovered by Warrington and her collaborators in brain-damaged patients in the 80's, and with functional imaging in humans by Martin, Allison, McCarthy, Kanwisher and others in the 90s. Since those initial discoveries, much of the research on category-specificity in the human brain has been concerned with characterizing the boundaries of the phenomena. In the context of patients with category-specific semantic deficits, emphasis has been placed on whether categories vary along continuous dimensions such as familiarity, lexical frequency, structural or visual complexity, distinctiveness of their critical features, relevance (and so on). The common theoretical supposition behind those approaches is that category-specific deficits arise as a result of difficulties with one (or multiple) dimensions that are correlated with a semantic category boundary. In the context of category-specific responses in the ventral object-processing stream, there has been an emphasis on understanding the visual dimensions that putatively drive an organization by category in the ventral stream. The common theoretical assumption is that category-specificity in the ventral stream arises through a type of experience-dependent 'coagulative' process by which dimensions of organization native to the visual system combine in either linear or nonlinear ways to result in a 'lumpy' organization by category.

Because of the common theoretical suppositions that have driven research on category-specificity in the brain, much experimental work has focused on parametrically manipulating a dimension of interest and studying how category-specific phenomena are modulated as a function of that dimension. This approach has been enormously important for describing the boundaries of category-specific phenomena. But perhaps the most important outcome of all of this research is that we still have category-specific phenomena that need explanation. In other words, it could have been the case that a dimension was discovered, that when 'controlled' or parametrically varied, the category effects were 'absorbed' into the dimension. That has not been

the case – we are left with the conclusion that category-specific phenomena are insoluble into the continuous dimensions that have been identified to vary by category. While there is still much ongoing work that will flesh out the details of this conclusion, my prospective suggestions presuppose that this conclusion will endure. This then frames anew an old question:

Question I. What neural and cognitive constraints drive an organization of object knowledge by semantic category in the human brain?

Empirical Generalization II. Important aspects of conceptual processing are not embodied. Research on the putative ‘embodiment’ of concepts and the role of the motor system in supporting perceptual analysis of actions has focused on demonstrations that the motor system is activated across a range of situations that would not seem to necessitate motor activation. There are multiple ways in which motor activation during conceptual and perceptual analysis can be interpreted, ranging from the view that motor activation constitutes a necessary and intermediary step in conceptual/perceptual analysis, to the claim that motor activation is entirely ancillary to, and irrelevant for, conceptual and perceptual analysis. The fact that multiple patient studies have reported associations between motor impairments and conceptual/perceptual impairments would seem to rule out the view that motor activation is entirely irrelevant for conceptual/perceptual analysis. On the other hand, dissociative patient studies demonstrating that motor abilities can be compromised while sparing conceptual and/or perceptual abilities rule out the view that motor activation is necessary or constitutive of conceptual and/or perceptual analysis.

I think that the situation here is analogous to asking whether the function of the engine of a car is ‘embodied’ in the movement of the car – it depends what you mean. If the car is in gear, then there will be a direct mapping of turns of the tires on the road to revolutions of the crank in the engine. But the car can be put in neutral, in which case the engine can turn independently of

the wheels. In fact, it is precisely this property that makes ‘gears’ (i.e., the transmission) such a useful interface between the engine and the tires—gears are what give a car the flexibility to start at a dead stop and go to maximal speed using a single engine. Thus, asking why motor activation attends conceptual processing is like asking why the wheels turn when the engine turns—the answer is because the car is in gear and the engine is connected up with the wheels via the transmission. The answer is the same if you ask why the engine turns if you push a car that is in gear (i.e., jump starting; see e.g., Glenberg et al., 2008).

A counterpoint to this analogy that may be raised is that cars would not be of any use if they did not move—i.e., a car that only sat in neutral would not really ‘be’ a car. So there is a priority placed on being in gear, but at the same time there is not a one-to-one relationship between the output of the motor while in gear and the turning of the tires—the force given off by the engine must be interpreted into a format that can be implemented into turns of the wheels. Likewise, conceptual processing, with no interface with the world, would not be particularly useful. But this objection somewhat misplaces the original question: the theoretical issue at stake concerns the format of conceptual processing, and whether it is dissociable from sensory and motor knowledge. And in that regard, the analogy is robust, in that even though the utility of cars is expressed when the engine is engaged with the wheels, turns of the engine and turns of the wheels are dissociable (cf being in neutral). So while it may make sense at one level to think of the function of an engine as being ‘embodied’ in the movement of the car, that is, at the level of understanding a particular *state* the car can be in—the more basic point is that the function of the engine does not depend, in any constitutive, logical or necessary way, on the wheels.

Imagine that our state of knowledge of the function of cars was what it is with regard to the human brain, and one observed that turns of the engine were related to turns of the tires. One

might then reasonably ask, a la Embodied Cognition, whether the engine and the tires were really one and the same process. This is where I would suggest we are with respect to understanding to the relationship between sensorimotor activation and conceptual processing. But once one discovered the behavior of the car when it was in neutral, then the question would logically shift to asking how the engine was *connected* to the tires. Similarly, I believe that the key issue that we face as a field with respect to issues of embodiment does not have to do with demonstrating *that* cognition can behave in a way that indicates it can be synchronous with, or sensitive to, sensorimotor processing; the key open issue concerns how to understand the structure and dynamics of the interface between concepts and the sensorimotor systems.

Question II. If motor processes are not necessary for conceptual or perceptual processes, then why are they automatically engaged during conceptual and perceptual processing?

A Consilience for Questions I and II.

The suggestion of this chapter is that Questions I and II have a common answer, as yet unspecified in its details, but which in broad strokes consists of a theory of connectivity among sensorimotor and conceptual representations. The strategy within the field has been: divide and then reconnect. In that context, it is generally understood that connectivity does not itself constitute information—the information is ‘represented’ in the local regions that are connected, and the connections are something like passive conduits that pass bundles of information from region to region. The suggestion here is that connectivity is itself a computation that underlies conceptual analysis. This would require that we consider the performance of the entire network of regions as a unit of analysis, and regard the information represented by the function of the whole network as (at least at one level) a ‘unit of analysis’.

According to the task in which participants are engaged, stimuli will be analyzed by the same network in different ways, and information distributed throughout the network will be

combined in different orders, with different weights, and to different ends. As an example, consider how the dorsal and ventral visual pathways interact when you reach out to pick up a hammer in order to simply move it over six inches, versus pick it up with the intention of using it to hammer a nail. When you pick it up to move it, the grasp point on the object need only be calibrated such that the object is picked up efficiently (i.e., at its center of mass) and such that the grasp does not preclude, either because of the arrangement of other objects in the world or for biomechanical constraints, the (planned or intended) final position of the hammer once it is to be put down. However, when you pick up a hammer in order to use it, you *explicitly* do not pick it up at its center of mass, precisely in order to capitalize on the lever-like properties of hammer manipulation that allows the function of the object to be realized. The systems that recognize the object as such, and interface with systems that represent the behavioral intentions, are dissociable from the visuo-motor analysis that actually gets the hand from its starting position to its grip point on the object. Thus, while the same set of regions may be ‘activated’ both when picking up a hammer to move it and picking up a hammer to use it, the role that the different types of knowledge that we have about hammers plays in shaping the overall behavior is very different. What distinguishes the two situations is not therefore the types of information that are accessed (at some point in the action) but the order in which those different types of information are accessed and the weight that the different types of information are given in shaping the overall behavior (for discussion, see Mahon and Wu, in prep). Such dynamic re-ordering and re-weighting of information must be mediated by connectivity, because the different types of information are known to be represented by dissociable brain regions.

Decisions that are made by our cognitive systems about how to act on the world (e.g., what to attend to, how to shape the hand to grasp an object, *that* an object should be grasped) are

not made in isolation: Such decisions are made in concert with information that is computed about the world, including the current state of our body, as well as our behavioral goals and internal states, by widely distributed and dissociable neurocognitive systems. Perception is not just for its own sake; perception always occurs in the context of a behavioral goal, whether that goal is to take a drink of coffee or simply to ‘look’ or ‘inspect’ the mug. The suggestion here is that the structure and dynamics of the conceptual system can be understood as a result of the varied pressures made on the conceptual system in the service of different behavioral goals, or tasks, and the consequent need to integrate qualitatively different types of information. Those pressures can be understood along multiple time scales, including phylogenetic, ontogenetic, and online processing time scales.

The structure of neurocognitive information models is typically constrained by an analysis of what information is necessary in order to complete a given task. However, more than what is ‘strictly necessary’ in order to perform a task, conceptual processing is also sensitive to information that is available, but which may not be (strictly speaking) necessary in order to perform the task. This notion of the ‘availability’ of multiple types of information that could bear on a given cognitive decision is what we have referred to as ‘cognitive promiscuity’ (for discussion see Mahon & Caramazza, 2008). Cognitive promiscuity, implemented through the dynamics of information exchange among sensory, motor, and conceptual representations, is the foothold for understanding why the motor system is activated during conceptual and perceptual analysis. Cognitive promiscuity is also responsible, by hypothesis, for the need to integrate high-level visual analysis with motor-relevant computations about manipulable objects, or computations about the affective quality of facial expressions with visual information about faces, or phonology with representations of printed words; thus, cognitive promiscuity is the

umbrella property that motivates why connectivity between regions of the ventral stream and other regions of the brain would drive specialization by semantic category in the ventral stream. Understanding the constraints that shape the organization of the conceptual system then becomes a project of unpacking the dynamics of cognitive promiscuity.

One answer for a distributed question. It is a well-established fact that conceptual information is widely distributed in the brain, in the sense that different aspects or ‘parts’ of a concept are represented in dissociable brain systems. For instance, for the concept ‘hammer’, knowledge about its typical visual appearance and structure, knowledge about the sounds created when hammering, knowledge about the function of hammers, and knowledge about how to actually use hammers, are all represented in dissociable brain systems. To date, the general approach in the field has been to dissect out the components of concepts, sometimes referred to as the features of the concept, and describe the principles (cognitive and neural) that affect the representation and organization of each individual part. But that would be like treating leg pain with only an understanding of the function and physiology of the leg, and no understanding of how compression of spinal nerve fibers might (remotely) cause leg pain. Rather, the suggestion here is that in order to understand the constraints that shape specificity over one type of information (e.g., visual) in one part of the brain for a given category of items, it is critical to understand how that visual information about that class of items is integrated with nonvisual information about the same category, and which is represented by other brain regions.

While functional imaging or anatomical studies of white matter tractography might seem to be the most obvious means for understanding connectivity in humans, they are by no means the only approach. In particular, there are many rich empirical phenomena that have been taken as motivation for hypotheses about the format of conceptual representations (i.e., that they are

embodied) but which may better be understood as phenomena that result from the connectivity of the system. For instance, as noted above, making repetitive arm movements, such as moving beans from a close to a far container can lead to slower responses for judging the grammaticality of sentences that describe actions away from the body (Glenberg et al., 2008). This has been taken to mean that the understanding of the sentence, 'You passed the salt to your friend', involves as a constitutive part, motor simulation. An alternative explanation is that understanding that sentence occurs without intervening access to motor information, but that the state of the motor system is not irrelevant for understanding the sentence. In other words, the decision mechanism that oversees the grammaticality judgment may be sensitive to information that is not part of the grammaticality judgment, but being available cannot be ignored, and it therefore affects response time. Thus, rather than asking whether the format of lexical semantic representations is motoric, it may be more productive to ask about the nature of the decision mechanism involved in making judgments about sentences, and the types of information to which that decision mechanism is sensitive.

Another class of data that could be brought to bear on understanding the cognitive promiscuity of the conceptual system are the patterns of association and dissociation of function observed in brain damaged patients. Findings from brain damaged patients are generally emphasized in the measure to which different types of information dissociate from one another. Such dissociations are critical for drawing inferences about the functional independence of different types of knowledge. However, of particular importance for informing a theory of connectivity may be associations of impairments. Price, Friston, and colleagues (Friston & Price, 2011; Price & Friston, 2002; Price, Warburton, Moore, Frackowiak, & Friston, 2001) have explored what they refer to as 'dynamic diaschisis'. Dynamic diaschisis is the idea that damage

to one region of the brain can alter, and potentially impair, the function of anatomically remote but functionally interconnected regions. For instance, consider the fact that all types of knowledge (visual perceptual and functional/associative) are impaired for the damaged categories in patients with category-specific deficits (Figure 1B). Such patterns of associated impairments are ambiguous between the brain damage actually destroying tissue that is critical for representing the different types of knowledge (either the same region or neighboring regions), and the damage propagating at a functional level through ‘dynamic diaschesis’.

Concepts, as they are deployed in the service of behavior, are more than the sum of their parts. As functionally unified representations they allow the flexible recombination of information on the basis of inferences that go beyond the dissociable pieces of information that form the concept. Connectivity, as the basis for the functional integrity of concepts, lies at the heart of how concepts are both ‘distributed’ and ‘functionally unified’. Thus, my argument here has been that characterizing connectivity at a cognitive and neural level is not just an incremental step that will finally allow us to understand how the different parts of the system are ‘wired’ together and how information is ‘communicated’ among regions. Connectivity is an information-bearing property of the system that must be understood on its own terms. Furthermore, I would suggest that connectivity is the key to unlocking the reason why there is neural specificity for different categories in the first place, and why the motor system is engaged in many tasks that ‘should not’ require motor activation.

Figure Captions

Figure 1. Patients with category-specific semantic deficits may be differentially, or even selectively impaired for knowledge of animals, plants, conspecifics, or artifacts. The knowledge impairment cannot be explained in terms of a differential impairment to a sensory or motor-based modality of information. While discussion and debate continues as to whether non-categorical dimensions of organization may lead to category-specific brain organization, there is consensus that the phenomenon itself is ‘categorical’. **Panel A.** Picture naming performance of patients studied with materials that were carefully balanced so as to equate various continuous dimensions across categories (e.g., frequency, familiarity, visual complexity). The four major patterns of category-specific semantic deficits are represented. **Panel B.** Semantic attribute question performance for six representative patients with differential impairments for living animate. As shown across the patients, impairments for a category are associated with impairments for all types of knowledge about items from that category. Figure reproduced from Mahon & Caramazza (2011), with permission.

Figure 2. Category-specific patterns of BOLD response in the healthy brain. This figure shows in red, a network of regions that are differentially activated for animals, and in blue, a network of regions that are differentially activated for tools (Data from Chao et al 2002; figure reproduced from Martin and Chao, 2001, with permission).

Figure 3. Dendrograms showing similarity of response patterns across visual stimuli in monkey IT and human ventral temporal cortex. Kriegeskorte and colleagues (2008) analyzed neurophysiological data from monkey IT cortex and human fMRI data when participants (monkeys, humans) were viewing numerous stimuli from many different categories. The similarity of the neural responses across the stimuli were analyzed separately for monkeys and humans. The figures, reproduced from Kriegeskorte and colleagues (2008, Figure 4 therein) use hierarchical clustering to describe the similarity space of the stimuli. The fascinating aspect of these data is that they show, with entirely independent analysis pipelines, that high level visual cortex in monkeys and humans represents largely the same similarity space for visual stimuli. Figure reproduced with permission, from Kriegeskorte and colleagues (2008).

Figure 4. Congenitally blind and sighted participants were presented with auditorily spoken words of living things (animals) and nonliving things (tools, nonmanipulable objects) and were asked to make size judgments about the referents of the words. The sighted participants were also shown pictures corresponding to the same stimuli in a separate scan. For sighted participants viewing pictures, the known finding was replicated that nonliving things such as tools and large nonmanipulable objects lead to differential neural responses in medial aspects of ventral temporal-occipital cortex. This pattern of differential BOLD responses for nonliving things in medial aspects of ventral temporal-occipital cortex was also observed in congenitally blind participants and sighted participants performing the size judgment task over auditory stimuli. These data indicate that the medial-to-lateral bias in the distribution of category-specific responses does not depend on visual experience. For details of the study, see Mahon and colleagues (2009). Figure reproduced from Mahon and colleagues (2009) with permission.

Author's Note

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