Taxonomic and Thematic Semantic Systems

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Object concepts are critical for nearly all aspects of human cognition, from perception tasks like object recognition, to understanding and producing language, to making meaningful actions. Concepts can have 2 very different kinds of relations: similarity relations based on shared features (e.g., dog—bear), which are called "taxonomic" relations, and contiguity relations based on co-occurrence in events or scenarios (e.g., dog—leash), which are called "thematic" relations. Here, we report a systematic review of experimental psychology and cognitive neuroscience evidence of this distinction in the structure of semantic memory. We propose 2 principles that may drive the development of distinct taxonomic and thematic semantic systems: differences between which features determine taxonomic versus thematic relations, and differences in the processing required to extract taxonomic versus thematic relations. This review brings together distinct threads of behavioral, computational, and neuroscience research on semantic memory in support of a functional and neural dissociation, and defines a framework for future studies of semantic memory.

Keywords: semantic memory, thematic semantics, individual differences

Semantic or conceptual knowledge is fundamental to nearly all aspects of human cognition: it is how we know what to do with objects, it allows us to predict how different entities in the world will interact, and it gives meaning to language (McRae & Jones, 2013; Tulving, 1972; Yee, Chrysikou, & Thompson-Schill, 2013). The representation of this knowledge has diverse consequences for many different cognitive processes. For example, theories of object recognition must specify what object knowledge constitutes "recognition." Assumptions about the format of that knowledge have implications for the efficacy of different object recognition algorithms and neural implementations. Similarly, theories of word comprehension must specify the representation of word meaning. This specification will impact how we think about the algorithms that support word comprehension and their neural instantiation. Theories of conceptual development and impairments also require understanding what is developing or impaired. This systematic review covers behavioral, computational, and neural evidence that semantic knowledge is represented in two complementary systems: a taxonomic system organized around object categories, and a thematic system organized around events or scenarios.

As with other dissociations (e.g., McClelland, McNaughton, & O'Reilly, 1995), some of the strongest evidence comes from individuals with deficits that affect one component more than the other. However, this logic can be extended beyond neurological patients to consider individual differences more broadly, and, as this review shows, there is substantial behavioral evidence that individuals do differ, systematically and consistently, in their reliance on taxonomic versus thematic semantic knowledge. Building on this review, we propose two computational principles that may drive the development of distinct taxonomic and thematic semantic systems, and define a framework for future behavioral, computational, and neuroscience studies of semantic memory.

By the middle of the 19th century, philosophers of mind had already made distinctions between different kinds of meaningful relations, most notably between relations based on similarity and those based on contiguity (Bain, 1864). In contemporary cognitive science, semantic similarity is typically based on shared features, and tends to produce a *taxonomic* structure that groups concepts into categories such as fruits, animals, and tools (e.g., McRae, Cree, Seidenberg, & McNorgan, 2005; McRae, de Sa, & Seidenberg, 1997; Rogers et al., 2004). Contiguity or complementarity reflects co-occurrence in scenarios or events, such as birthday parties or baking, and produces a very different, *thematic*, structure (e.g., Estes, Golonka, & Jones, 2011). For instance, dogs and bears are taxonomically similar because they have common features and, hence, belong in the same category (mammals); dogs and leashes do not share features, but they have complementary features related to occurring in the same scenario or event (walking a dog), and these features are critical to their thematic relationship.

Figure 1 shows how objects can simultaneously belong to these two very different semantic structures. There has been substantial progress in understanding the cognitive and neural basis of taxonomic semantics using feature-based representa-

DOG	BONE	LEASH
HORSE	APPLE	SADDLE
MOUSE	CHEESE	TRAP

Figure 1. Cross-categorization of objects: columns are taxonomic categories; rows are thematic categories.

tions (Barsalou, 2008; Cree & McRae, 2003; Rogers & McClelland, 2004; Vigliocco, Vinson, Lewis, & Garrett, 2004). Research on thematic semantics has not proceeded quite as quickly, in part because there has been somewhat less consistency in the definition of thematic relations. Nevertheless, behavioral and neural evidence now strongly support a functional and neural dissociation between taxonomic and thematic knowledge. This review of the existing literature summarizes the behavioral, computational, and neural evidence that taxonomic and thematic semantic relations are functionally distinct, emphasizing evidence that individuals differ in their reliance on taxonomic versus thematic relations. After the review, we propose computational principles that may give rise to this dissociation and define a framework for future studies of semantic memory.

Categories of Categories: Definitions for Different Kinds of Semantic Relations

Before proceeding, it will be helpful to make concrete definitions for, and distinctions among, different kinds of semantic relations. The focus of this review is taxonomic and thematic relations, which also need to be distinguished from ad hoc and single-feature/rule-based categories, and from semantic associations.

Taxonomic semantic structure has been defined simply by using natural categories such as biological taxonomic hierarchies (e.g., Collins & Quillian, 1969), or by asking participants to list semantic features for concepts ("semantic feature generation norms"; e.g., McRae et al., 1997, 2005) and examining the similarity structure that emerges from these features lists. The result of such feature analysis usually reveals a taxonomic structure (e.g., Rogers et al., 2004). Even without explicit representation of taxonomic hierarchies, feature-based representations can capture interesting aspects of hierarchical taxonomic structure (e.g., O'Connor, Cree, & McRae, 2009; Rogers & Patterson, 2007). Semantic representations that are based on the similarity of word contexts (e.g., Landauer & Dumais, 1997; Lund & Burgess, 1996) can also produce a taxonomic semantic structure (Riordan & Jones, 2011), or to conflate taxonomic and thematic relations see (Jackson & Bolger, 2014). To understand this (possibly surprising) outcome, consider the context of words such as "salmon," "tuna," and "sea": "Salmon" and "tuna" both occur in the context of the word "sea," so "salmon" and "tuna" will have similar representations; but "sea" does not tend to occur near the word "sea" (that would be a repetition). Instead, it tends to occur in the context of "salmon" and "tuna," which, according to standard word co-occurrence algorithms, is a *different* context and therefore produces a somewhat different semantic representation.

Thematic relations are based on frequent co-occurrence in events or situations (e.g., Estes et al., 2011). Such relations can include relations that are explicitly tied to specific roles in events or schemas (e.g., Goldwater, Markman, & Stilwell, 2011; M. Jones & Love, 2007; Markman & Stilwell, 2001). Language is typically used to describe events or situations, and event perception influences language production (e.g., Gleitman, January, Nappa, & Trueswell, 2007). As a result, word co-occurrence patterns can also capture thematic relations (for computational attempts, see Andrews & Vigliocco, 2010; Griffiths, Steyvers, & Tenenbaum, 2007; Johns & Jones, 2014; M. N. Jones & Mewhort, 2007). "Topic" models (e.g., Griffiths et al., 2007) attempt to explicitly capture the underlying generative events that produced sentences and may capture thematic relationships, though this has not yet been investigated systematically. However, thematic relations go beyond simple word co-occurrences because word co-occurrences do not always involve a semantic relationship between their constituent parts (e.g., cheese—cottage; Yee, Overton, & Thompson-Schill, 2009).

This review focuses on the distinction between taxonomic and thematic relations in long-term semantic memory. Other kinds of semantic relationships include ad hoc, single-feature, or rule-based categories, and semantic associations. Ad hoc categories are novel categories constructed to achieve a particular goal, such as "things to save from a burning house" (e.g., Barsalou, 2010). Such categories are similar to thematic relations in that they are based on co-occurrence in an event or situation, but because ad hoc categories are (by definition) based on novel events, ad hoc category relations are not part of long-term semantic memory. If such events were reexperienced frequently, they could become part of long-term thematic semantic memory. For example, a firefighter might frequently need to rescue things from a burning house, and could develop a long-term thematic relation between things that need to be saved from a burning house.

Single-feature or *rule-based* categories are groupings that meet a particular criterion, such as "things that are green" or "objects smaller than a toaster." Such categories have sometimes been called "taxonomic" (e.g., Davidoff & Roberson, 2004), though this is somewhat misleading. Single-feature categories are based on shared features, but they are not part of long-term semantic memory. Compared with taxonomic and thematic relations, single-feature categories appear to rely more strongly on cognitive control (Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012) and naming processes (Lupyan, 2009; Lupyan & Mirman, 2013).

Associations have typically been defined in terms of contiguity or co-occurrence of words or objects, making them very similar to thematic relations. However, associations have been operationalized almost exclusively in terms of the word association task, in which a participant reads or hears a word and must produce the first semantically related word that comes to mind (e.g., Nelson, McEvoy, & Dennis, 2000). Two words are considered associated if participants tend to produce one when prompted by the other. The difficulty with this operational definition is that the word association task draws on the totality of participants' semantic knowledge, so it is not a very effective way to distinguish between possible underlying semantic structures (Cann, McRae, & Katz, 2011). For example, associates of *car* include explicitly taxonomic relations such as superordinate and subordinate relations (e.g., *transportation* and *Toyota*) that clearly do not follow the thematic

definition of associations (for more discussion, see McRae & Jones, 2013). In addition, the responses produced in a word association task vary systematically as a function of whether the probe stimulus is a picture or a word (Saffran, Coslett, & Keener, 2003), suggesting that what aspect of semantic memory is tapped by the word association task depends on how the task is implemented. As a result, the substantial literature comparing and contrasting taxonomic and associative relations is only partly relevant to the taxonomic-thematic distinction.

In sum, semantic memory includes taxonomic and thematic relations. Other kinds of semantic relations are either not part of long-term semantic memory or do not distinguish between relation types. The next section provides a systematic review of studies that examined functional and neural dissociations between taxonomic and thematic semantic relations. The final section proposes computational principles that may give rise to this dissociation.

Systematic Review of Dissociation Between Taxonomic and Thematic Semantics

Method

The systematic review procedure is depicted schematically in Figure 2. An initial literature search was conducted in April 2015 and updated in January and July 2016. The search was conducted by entering the following search string into the PsycInfo, PubMed, and Web of Science[1] online databases:

(Semantic OR Concept OR Conceptual) AND

(Taxonomic OR Categor* OR Feature OR Similarity OR Classification) AND

(Thematic OR Scenario OR Schema OR Experience OR (EVENT NOT ERP))

The results of the three searches were then collated into one reference library and duplicates removed, resulting in 5,886 records. Records were screened for general relevance based on their title and abstract independently by the authors and inclusion decisions made by majority vote. This first round of screening excluded 5,719 articles as irrelevant and another 13 were not available in English. The remaining 154 full-text articles were screened and an additional 49 were excluded for one or more of the following reasons:

1. Did not examine a distinction between taxonomic and thematic semantics.

2. Defined taxonomic or thematic semantics in a way that is incompatible with our definition (e.g., using "taxonomic" to mean single-feature).

3. Did not provide any new data (i.e., review articles or corrections).

For any results reported in a dissertation that were subsequently published in a peer-reviewed journal article, we used the peer-reviewed report rather than the dissertation. After screening of the full-text articles, a total of 105 articles were included in the final list. These articles were then organized by general topic: indepen-

dence of taxonomic and thematic contributions to relatedness, differences in time course of taxonomic and thematic activation, individual differences in taxonomic and thematic processing, and neural dissociations of taxonomic and thematic processing. The 105 articles are grouped under their primary topic in Table 1, which also provides the organizational structure for this review.

Independent Contributions to Relatedness

Taxonomic and thematic relations make independent contributions to semantic relatedness (see also Estes et al., 2011). Many studies have shown that the degree of feature-based similarity predicts relatedness effects (e.g., Cree, McRae, & McNorgan, 1999; see also Mirman & Magnuson, 2009), and common roles, relations, or scenarios similarly increase perceived similarity (Goldwater, Bainbridge, & Murphy, 2016; M. Jones & Love, 2007). Children 4 to 7 years old implicitly learn to group perceptually dissimilar objects when the objects call for a common response (Astley & Wasserman, 1996). Finer-grained experiments further indicate that thematic relations increase perceived similarity by enhancing commonality between concepts rather than by decreasing perceived dissimilarity (Golonka & Estes, 2009), which also raises the important methodological point that conceptual relatedness is not just the inverse of unrelatedness. In this section, we review the evidence that taxonomic and thematic relations make independent contributions to relatedness, beginning with computational analyses of the structure of semantic representations, and then discussing the behavioral evidence. The behavioral evidence is organized by general task type: first, semantic relatedness judgments, and then consequences on other tasks such as memory, picture naming, and generalization of labels.

Computational analyses. Computational analyses suggest that semantic memory is composed of (at least) two qualitatively different semantic representations. Analysis of the similarity structures of 13 different measures of semantic relatedness found that they clustered into separate associative, feature-based, and text-based relations (Maki & Buchanan, 2008). Further, feature-based and text-based distributional semantic representations are qualitatively different (Andrews, Vigliocco, & Vinson, 2009), and combining these different representations provides a better fit to behavioral data from several semantic tasks: semantic errors and picture-word interference effects in word production, semantic priming in word recognition, and word association strengths. A model based on graph theory and trained with text co-occurrence statistics was able to achieve fairly high accuracy on distinguishing taxonomic and thematic relationships, having the most difficulty with word pairs that were both taxonomically and thematically related (Jackson & Bolger, 2014).

Relatedness judgments. Taxonomic and thematic relatedness independently increase semantic relatedness ratings (Wisniewski & Bassok, 1999). A study of semantic relatedness judgments by stroke survivors suggested that thematic relations rely on both

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[1] The Web of Science search was also restricted to the following categories: Audiology Speech Language Pathology, Behavioral Sciences, Clinical Neurology, Language Linguistics, Linguistics, Psychology, Psychology Applied, Psychology Biological, Psychology Clinical, Psychology Developmental, Psychology Educational, Psychology Experimental, Psychology Multidisciplinary, Neuroimaging, and Neurosciences.

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Figure 2. Structure of systematic review. The search string (top) was entered into three databases, and the results were collated and screened, producing 105 full-text records that were included in the systematic review, which were organized by general topic (bottom). See Table 1 for list of records included in each topic.

visual and verbal systems, but taxonomic relations are more uniquely tied to visual relations (Vivas, García-García, Vivas, & Perea-Bartolomé, 2014): Participants exhibited a double dissociation between performance for picture versus word stimuli for thematic relations, but not for taxonomic relations.

The importance of taxonomic similarity and thematic relatedness may differ by concept domain: taxonomic similarity appears to be more important for natural objects such as animals, whereas thematic relations appear to be more important for artifacts such as tools (Bonthoux & Kalénine, 2007; Kalénine et al., 2009), possibly because manipulation actions are particularly important for tools and for thematic relations (Kalénine & Buxbaum, 2016; Plucien-nicka, Wamain, Coello, & Kalénine, 2016). One study also suggests that the domain of History tends to elicit stronger thematic responses from both experts and nonexperts (Wyatt & Rabinowitz, 2010).

Crutch and colleagues have argued that concrete concepts rely more strongly on taxonomic relations, but abstract concepts rely more strongly on thematic (associative) relations (Crutch, 2006; Crutch, Ridha, & Warrington, 2006; Crutch & Warrington, 2010; Duñabeitia, Avilés, Afonso, Scheepers, & Carreiras, 2009; Papagno, Martello, & Mattavelli, 2013). However, other research groups have failed to replicate some of the key results supporting this hypothesis (Brozdowski, Gordils, & Magnuson, 2013; Geng & Schnur, 2015; Hamilton & Coslett, 2008; Skipper, 2014), so it remains unclear whether or not the concrete–abstract dimension functions as another dissociation between taxonomic and thematic semantic knowledge.

The ability to combine taxonomic similarity and thematic relatedness may interact with cognitive development. One series of studies tested 5-year-old children and adults in a "triads" match-to-sample task in which participants were presented with an object and had to choose which of two options "goes with it best." Both response options were taxonomically related to the reference object, but one response option was also thematically related, whereas the other varied in perceptual similarity. Adults were more likely to choose the one that was both taxonomically and thematically related than children were, suggesting that the adults were more sensitive to the additional thematic relatedness (Berger & Donnadieu, 2006, 2008). This developmental difference was even stronger when the objects were presented sequentially rather than simultaneously, suggesting that working memory may limit the ability to combine taxonomic and thematic relations (for additional comparison of simultaneous and sequential presentation, see Rey & Berger, 2001).

Similarly, the ability to switch between taxonomic and thematic relations has a developmental progression. Evidence from a three-alternative match-to-sample task suggests that the ability to identify taxonomic and thematic relations on separate trials develops earlier than the ability to switch between those relations within a single trial (Blaye, Bernard-Peyron, Paour, & Bonthoux, 2006; Blaye, Chevalier, & Paour, 2007; Blaye & Jacques, 2009). Conversely, this switching ability and the ability to avoid interference between thematic and taxonomic relations declines with age, with taxonomic relations particularly susceptible to age-related decline

Table 1
Articles in Each Major Topic Area of Systematic Review

Independent contributions to relatedness	Differences in time course of activation	Individual differences		Neural dissociations
Ackerman (1986)	Jones & Golonka (2012)	**Development**	**Education**	Abel et al. (2009)
Andrews et al. (2009)	Kalénine et al. (2009)	Bauer & Mandler (1989)	Assink et al. (2004)	Bedny et al. (2014)
Astley & Wasserman (1996)	Kalénine, Mirman, Middleton, et al. (2012)	Berger & Aguerra (2010)	Ince & Christman (2002)	Canessa et al. (2008)
Baldwin (1992)	Wamain et al. (2015)		Li et al. (2011)	Chen et al. (2014)
Berger & Donnadieu (2006)		Blanchet et al. (2001)	Nation & Snowling (1999)	Davey et al. (2016)
Berger & Donnadieu (2008)		Borghi & Caramelli (2003)	Whitmore et al. (2004)	de Zubicaray et al. (2013)
Blaye & Jacques (2009)		Brooks et al. (2012)		de Zubicaray et al. (2014)
		Cicirelli (1976)		Geng & Schnur (2016)
		Fenson et al. (1989)	**Domain expertise and culture**	Gutchess et al. (2010)
Blaye et al. (2006)		Hashimoto et al. (2007)	Coley (2012)	Henseler et al. (2014)
Blaye et al. (2007)		Imai et al. (2010)	Crutch & Warrington (2011)	Jackson et al. (2015)
Bonthoux & Kalénine (2007)		Kogan (1974)	Medin et al. (1997)	Kalénine & Buxbaum (2016)
Coane et al. (2016)		Murphy (2001)	Medin et al. (2006)	Kalénine et al. (2009)
Estes et al. (2012)		Nguyen (2007)		
		Osborne & Calhoun (1998)	**Typical and neurological variation**	Kriukova et al. (2013)
Geng & Schnur (2015)		Pennequin et al. (2006)	Au et al. (2003)	Kuchinke et al. (2009)
Goldwater et al. (2016)		Perraudin & Mounoud (2009)	Dunham & Dunham (1995)	Lee et al. (2014)
Golonka & Estes (2009)		Pluciennicka, Coello, & Kalénine (2016)	Kalénine & Bonthoux (2006)	Lewis et al. (2015)
Jackson & Bolger (2014)		Scheuner et al. (2004)	Kalénine, Mirman, & Buxbaum (2012)	Maguire et al. (2010)
Jones & Love (2007)		Sell (1992)	Li & Zhang (2009)	Merck et al. (2014)
Khan & Paivio (1988)		Sharps & Gollin (1985)	Lin & Murphy (2001)	Mirman & Graziano (2012a)
Maintenant et al. (2011)		Sharps (1992)	Mirman & Graziano (2012b	Sachs et al. (2011)
Maintenant et al. (2013)		Smiley & Brown (1979)	Semenza et al. (1980)	Sachs, Weis, Krings, et al. (2008)
Maki & Buchanan (2008)		Unger et al. (2016)	Simmons & Estes (2008)	Sachs, Weis, Zellagui, et al. (2008)
Pluciennicka, Wamain, Coello, & Kalénine (2016)		Walsh et al. (1993)	Tyler et al. (1997)	Sass et al. (2009)
Rey & Berger (2001)		Waxman & Namy (1997)	Vivas et al. (2016)	Schwartz et al. (2011)
Rose & Abdel Rahman (2016)			Yi et al. (2011)	Semenza et al. (1992)
Vivas et al. (2014)				Tsagkaridis et al. (2014)
Ware et al. (2013)				Wamain et al. (2015)
Wisniewski & Bassok (1999)				
Wyatt & Rabinowitz (2010)				

(Maintenant, Blaye, & Paour, 2011; Maintenant, Blaye, Pennequin, & Paour, 2013).

Consequences in other tasks. Taxonomic and thematic relatedness confer equal benefits for list recall (Khan & Paivio, 1988), and recall is facilitated when retrieval cues match the relation

within the studied lists (Ackerman, 1986). For example, for the target word "wrench," a category name cue ("tools") facilitates recall when the word was presented in a taxonomic list (hammer-saw-wrench) more than when it was presented in a thematic list (sink-pipe-wrench), and the reverse holds for an event name cue

("water leak"). These recall benefits are mirrored by independent contributions to producing false recall in the Deese-Roedeger-McDermott false-recall paradigm: Lists composed entirely of thematic relations are sufficient to produce false recall, and lists with both taxonomic similarity and thematic relatedness produced more false recall than lists with only thematic relatedness (Cann et al., 2011; Coane, McBride, Termonen, & Cutting, 2016).

In a picture-word task interference, participants are asked to name a picture while a distractor word is presented either printed over the to-be-named picture or spoken. This task has revealed qualitatively different patterns of effects when the distractor word is thematically versus taxonomically related to the target: For typical adults, a thematically related distractor word tends to facilitate picture naming, whereas a taxonomically related distractor word tends to inhibit picture naming (de Zubicaray, Hansen, & McMahon, 2013). Why taxonomic and thematic relations produce opposite effects in picture-word interference tasks remains a topic of some debate. This debate is further complicated by the observation that both kinds of relations interfere with picture naming when the semantically related items are presented sequentially, which is known as the "cumulative semantic interference effect" (Howard, Nickels, Coltheart, & Cole-Virtue, 2006; Rose & Abdel Rahman, 2016).

Taxonomic and thematic relations may differentially contribute to generalization of labels: Children (3 to 6 years old) extend novel labels based on shape and taxonomic similarity more than on thematic relatedness (Baldwin, 1992). The physical nature of the stimuli may also affect whether taxonomic or thematic relations are more strongly activated: Compared with pictures, physical objects tend to elicit more thematic relations than taxonomic relations in spontaneous mother–child conversation (Ware, Gelman, & Kleinberg, 2013), though perhaps not in a match-to-sample task (Waxman & Namy, 1997). From a more applied perspective, taxonomic and thematic relatedness independently contribute to perceived fit and positive evaluation of brand extensions (Estes, Gibbert, Guest, & Mazursky, 2012).

In sum, taxonomic and thematic relations independently contribute to concept relatedness as demonstrated in relatedness judgment tasks and in other tasks that are sensitive to semantic relatedness, as well as in computational analyses. Combining taxonomic and thematic relations and switching between them requires additional cognitive resources that develop later in childhood than core taxonomic and thematic knowledge, and they decline earlier in typical aging. In addition, taxonomic and thematic relatedness independently influence performance on other tasks, such as memory, picture naming, and generalization of labels. These independent contributions may be driven by differential weighting of particular kinds of information: Visual features are particularly important for taxonomic relatedness, whereas verbal/linguistic and manipulation similarity are particularly important for thematic relatedness. Concept domain is also an important factor: Taxonomic relatedness is more important for living things, whereas thematic relatedness is more important for artifacts.

Differences in Time Course of Activation

Semantic priming studies have shown both feature-based taxonomic priming (e.g., Cree et al., 1999; see also Mirman & Magnuson, 2009) and event-based thematic priming (e.g., Hare, Jones, Thomson, Kelly, & McRae, 2009; see also Kukona, Fang, Aicher, Chen, & Magnuson, 2011; Metusalem et al., 2012; Mirman & Graziano, 2012b). On their own, these results do not require a dissociation between taxonomic and thematic semantic representations; however, these priming effects are differentially sensitive to stimulus-onset asynchrony (SOA), suggesting that they reflect temporally distinct semantic processes (L. L. Jones & Golonka, 2012). Differential time course effects have also been found in an explicit semantic relatedness judgment task, in which participants had to pick which of two candidate objects was related to the target: for natural kinds (such as fruits and animals), taxonomically related candidates were selected faster than thematically related candidates; for artifacts (such as tools and furniture), thematically related candidates were selected faster than taxonomically related candidates (Kalénine & Buxbaum, 2016; Kalénine et al., 2009).

Even more direct evidence of differences in the time course for activation of taxonomic and thematic semantic relations comes from an eye-tracking study (Kalénine, Mirman, Middleton, & Buxbaum, 2012) in which participants' eyes were tracked while they heard a word and had to pick which of four pictures matched that word (known as the "visual world paradigm"; Cooper, 1974; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995). Each display contained a target picture, a thematically or taxonomically[2] related distractor, and two unrelated distractors. As in previous studies (e.g., Huettig & Altmann, 2005; Mirman & Graziano, 2012b; Mirman & Magnuson, 2009; Yee & Sedivy, 2006), participants tended to look at the semantically related distractors more than at unrelated distractors, but the time course of those eye fixations revealed a clear difference between taxonomic and thematic distractors. There was equal overall tendency to look at thematic and taxonomic distractors, but the thematic distractors tended to be fixated earlier than the taxonomic distractors (see Figure 3), suggesting that thematic relations were activated earlier than taxonomic relations. A subsequent event-related potential (ERP) study using similar materials found that thematic priming, but not taxonomic priming, affected early (N1 and P3) ERP components (Wamain, Pluciennicka, & Kalénine, 2015), which is also consistent with earlier activation of thematic relations than taxonomic relations.

The key finding is that the time course of activation differs for thematic and taxonomic relations. In general, thematic relations appear to be activated more quickly than taxonomic relations. This may interact with concept domain such that the temporal advantage for thematic relations is particularly strong for artifacts and manipulable objects, and is reversed for animals, which show an advantage for taxonomic relations.

Individual Differences

One of the oldest and most active lines of research on distinguishing taxonomic and thematic relations is the study of individual differences: evidence that individuals differ in the relative strength of taxonomic and thematic relations. Such individual differences have been linked to cognitive development, education, and domain expertise, and they have been documented as typical variation when overt cognitive differences are not present.

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[2] Kalénine, Mirman, Middleton, et al. (2012) were specifically interested in artifacts that serve similar functions, so they referred to the taxonomic distractors as function distractors.
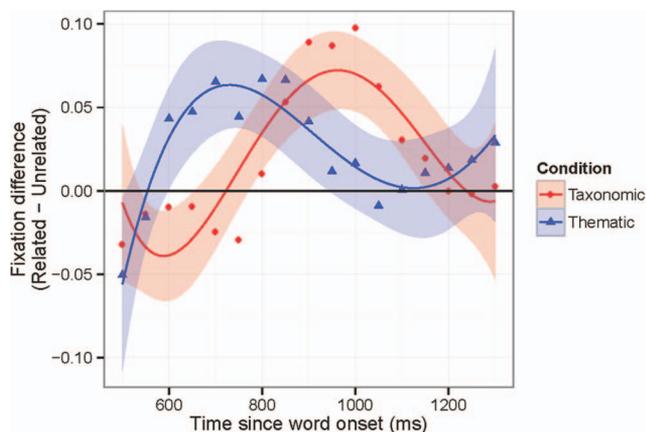
Figure 3. Time course of taxonomic and thematic similarity activation (Kalénine, Mirman, Middleton, et al., 2012). See the online article for the color version of this figure.

Development. Some of the earliest research on the distinction between taxonomic and thematic semantic knowledge focused on a possible developmental shift from thematic to taxonomic thinking in children and a later shift back to thematic thinking in older adults. In a classic study (Smiley & Brown, 1979), participants were presented with three-item triads consisting of a "standard," an item thematically related to the standard, and an item taxonomically related to the standard. Participants were asked to choose which of the two options "goes best with the [standard]." The results revealed a U-shaped pattern, with children 4 to 6 years old preferring the thematic option, 10-year-olds and college students (20 years old) preferring the taxonomic option, and elderly adults (66 to 85 years old) preferring the thematic option. A similar U-shaped developmental trajectory has been found using a free sorting task (Cicirelli, 1976; Kogan, 1974): Taxonomic grouping increased until about 65 years of age, then declined, and the opposite pattern held for thematic grouping. However, this triads task has been widely criticized for sensitivity to task instructions and context (for a review, see Estes et al., 2011), and quite strong thematic relations are required in order to elicit consistent thematic grouping in the free sorting task (Murphy, 2001). Further, these developmental comparisons were cross-sectional rather than longitudinal—the college students were growing up in the 1960s and 1970s, whereas the elderly adults had grown up at the beginning of the 20th century. As a result, this pattern may be reflecting environmental, cultural, or educational differences between the groups, in addition to the hypothesized developmental differences. Two of these potentially confounding factors are supported by concrete evidence. First, education also predicts sorting performance (Cicirelli, 1976); the effects of formal education and experience are discussed in more detail in the next sections. Second, rather than a general preference for taxonomic similarity, young adults may be more sensitive to the particular taxonomic relations in the study (Pennequin, Fontaine, Bonthoux, Scheuner, & Blaye, 2006). That is, the specific materials in the study tested taxonomic relations that were more salient to young adults than to older adults, thus producing a taxonomic-to-thematic shift for older adults that was specific to the study materials rather than semantic cognition more generally.

Several studies have found that children exhibit a developmental shift toward more taxonomic responding in a match-to-sample (e.g., triads) forced-choice semantic relatedness task across different age ranges: 16 to 31 months old (P. J. Bauer & Mandler, 1989), 3 to 4 years old (Blanchet, Dunham, & Dunham, 2001), 4 to 6 years old (Berger & Aguerra, 2010), and 3 to 10 years old (Sell, 1992). However, others have not found this shift, instead demonstrating strong effects of perceptual similarity and a general developmental increase in overall accuracy (Fenson, Vella, & Kennedy, 1989; Hashimoto, McGregor, & Graham, 2007; Imai, Saalbach, & Stern, 2010; Nguyen, 2007; Osborne & Calhoun, 1998). There is also contrasting evidence of a shift toward *stronger* thematic preference from 3 to 4 years of age (Waxman & Namy, 1997), from 4 to 6 years of age (Scheuner, Bonthoux, Cannard, & Blaye, 2004), and from 4 to 9 years of age (Walsh, Richardson, & Faulkner, 1993), and in a comparison of 5-year-old children with adults (Berger & Donnadieu, 2006, 2008).

Word association tasks have revealed a developmental shift, with older children producing relatively more taxonomic or feature responses (e.g., bird—beak) and relatively fewer thematic responses (e.g., doctor—hospital; Borghi & Caramelli, 2003; Sell, 1992). Across both the word association and match-to-sample tasks, this transition may be mediated by slot-filler relations such as *fork–spoon* (Sell, 1992), which integrate both taxonomic similarity and thematic relatedness. This provides some insight into the mechanisms that might drive the developmental shift and illustrates an important methodological concern: Many studies did not isolate slot-filler relations, so interpretation of the results needs to consider how many such relations were included and whether they were considered taxonomic or thematic (which is often not reported).

When typical adults perform a picture-word interference task, a thematically related distractor word tends to facilitate picture naming, but a taxonomically related distractor word tends to inhibit picture naming. Children 7 to 11 years old exhibit the thematic facilitation effect but not the taxonomic inhibition effect (Brooks, Seiger-Gardner, & Sailor, 2014), suggesting that the thematic system matures earlier than the taxonomic system. Compared with adults, 5-year-old children exhibit larger thematic priming (instrument–patient, such as match–candle) effects, but similar-sized taxonomic priming effects (Perraudin & Mounoud, 2009; though for evidence of large taxonomic and thematic priming effects on memory in children, see Sharps & Gollin, 1985; Sharps, 1992).

These studies also highlight the importance of task and cognitive demands, which may differentially impact participants of different ages. A recent study found that a thematic-to-taxonomic developmental shift emerged only after controlling for visual similarity and reducing cognitive load (Unger, Fisher, Nugent, Ventura, & MacLellan, 2016). A related observation is that there may be developmental differences between implicit and explicit measures of semantic cognition. Six-year-old children were able to explicitly identify the taxonomic relations but showed reduced implicit activation of those relations (Pluciennicka, Coello, & Kalénine, 2016).

In sum, there is substantial evidence that developmental changes differentially affect taxonomic and thematic semantic processing, with most (though not all) studies showing increasing reliance on taxonomic similarity as children get older. However, there are also

developmental differences in education, response to task demands, and salience of semantic relations in the materials, which may impact the results as much as—or even more than—development of the semantic system.

Education. Language expertise and ability, and formal education more generally, may influence reliance on taxonomic versus thematic relatedness. Children with poor reading comprehension show slightly larger thematic priming effects in a lexical-decision task than good comprehenders do. This pattern is reversed for taxonomic priming—good comprehenders show a larger taxonomic priming effect than poor comprehenders do (Nation & Snowling, 1999). This pattern appears to be specific to the semantic system because it did not hold in a comparison of children with good versus poor decoding skills (Assink, Van Bergen, Van Teeseling, & Knuijt, 2004). A similar effect has been demonstrated at the within-participant level by comparing words that the participant knows well with words that are on the knowledge "frontier" (Ince & Christman, 2002). Frontier words were operationally defined as familiar words that the participant selected correctly in a two-alternative sentence decision task, but could not define or use correctly in a sentence. These frontier words elicited stronger thematic priming than taxonomic priming, but the opposite pattern (greater taxonomic priming than thematic priming) was found for known words. In a triads task, when choosing between a taxonomic and a thematic option, thematic responses were more common for frontier words than for known words (Whitmore, Shore, & Smith, 2004).

A study of Chinese high school students found that bilingual participants made more thematically related responses than taxonomically related responses in their first language, but equally frequent thematic and taxonomic responses in their second language (Li, Zhang, & Wang, 2011). This study also found that bilingual participants were equally accurate at taxonomic and thematic explicit semantic relatedness judgments when the items were presented as pictures or as words in their first language, but were less accurate at recognizing thematic relations when they were presented as words in their second language. That is, the language expertise difference between first and second language seemed to affect thematic relations more than it affected taxonomic relations (see Figure 4).

More generally, formal education may promote a shift from thematic to taxonomic thinking. Testing participants in remote villages of Uzbekistan in the early 1930s, Luria (1976) documented strong thematic grouping preferences among illiterate participants with no formal education—they rejected taxonomic grouping as "stupid," not "important," or not "right" (pp. 54–55). In contrast, their peers who had even a small amount of formal education tended to group objects according to taxonomic relations. In some cases, the effect of 1 to 2 years of formal education was tremendous (e.g., Luria, 1976, p. 78, Table 7): 21 of 26 participants with no formal education used thematic grouping and only one used taxonomic grouping (the rest used both), whereas 19 of 22 participants with 1 to 2 years of formal education used taxonomic grouping and none used thematic grouping. Similar results were obtained in a large study conducted in rural Yucatan, Mexico, in which participants varied widely in age and education. Across a variety of tasks, higher education was associated with stronger reliance on taxonomic relations (Sharp et al., 1979). Combined effects of age and education on increasing taxonomic sorting have also been found among children 6 to 14 years of age, half of whom were in school and half had never attended school (Scribner, 1974).

In sum, formal education tends to increase strength of taxonomic relations more than of thematic relations. Lexical-semantic expertise is also associated with greater strengthening of taxonomic relations than thematic relations both within individuals
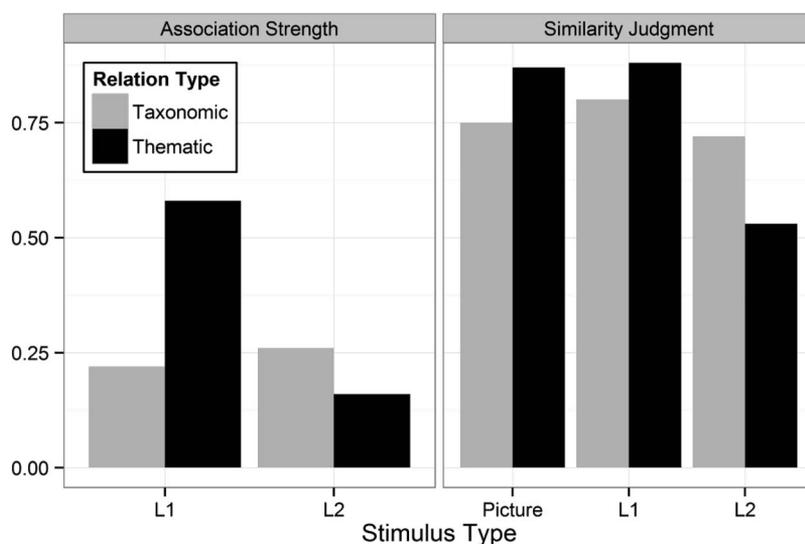
Figure 4. Effect of language experience on taxonomic and thematic relations (from Li et al., 2011). Left panel shows average probabilities of taxonomic versus thematic responses in a word association task; right panel shows accuracy of taxonomic versus thematic similarity judgments. Reduced language experience (L2 compared with L1 or pictures) affects thematic semantic relations more strongly than taxonomic relations. L1 = first language; L2 = second language.

(frontier vs. known words) and between individuals (poor comprehenders vs. good comprehenders). For bilinguals, the weaker language expertise of their second language is associated with weaker thematic relations, but not weaker taxonomic relations. This contrasts with the general finding that education and lexical-semantic expertise tend to increase strength of taxonomic relations, but is consistent with the link between thematic relations and linguistic similarity reviewed in the Independent Contributions to Relatedness section. That is, general education and specific lexical-semantic expertise appear to be particularly important for taxonomic relations, but general language expertise appears to be particularly important for thematic relations.

Domain expertise and culture. General formal education may strengthen taxonomic relations, but more specific training can emphasize either taxonomic or thematic relations. For example, one study examined categorization of trees by three different kinds of tree experts: (a) taxonomists engaged in research, teaching, and other educational activities; (b) landscapers focused on design, aesthetic, and utilitarian aspects of trees; and (c) maintenance workers engaged in planting, pruning, and otherwise maintaining city trees (Medin, Lynch, Coley, & Atran, 1997). Taxonomists produced groupings and justifications for groupings that were very strongly based on scientific taxonomic structures. Maintenance workers produced similar responses, with some additional influence of morphological properties and a utilitarian "weed tree" category (weak-wooded trees that cause maintenance problems). In contrast, landscapers showed the least influence of scientific taxonomy and stronger influences of utilitarian factors such as size and aesthetic value.

Another study tested middle-class North American college students from rural Michigan (knowledgeable novices) and Itzaj adults who grew up in subsistence households in a rainforest region of Guatemala (López, Atran, Coley, Medin, & Smith, 1997). Both groups exhibited very similar patterns of local mammal classification; however, the college students were more influenced by superordinate categories and morphological features, whereas the Itzaj adults were more influenced by ecological properties such as typical habitat and hunting patterns. In sorting and induction tasks using marine creatures, commercial fishermen (experts) were more influenced by thematic constraints such as commercial and ecological factors, whereas university undergraduates (novices) were primarily influenced by taxonomic constraints such as visual features (Shafto & Coley, 2003).

An even more well-controlled comparison compared two groups of nonprofessional fish experts from the same geographic area who engage in similar fishing-related activities: majority-culture and Native American (Menominee) adults from Wisconsin. The two groups had approximately equal expertise with the local fish, but the majority-culture participants tended to exhibit more taxonomic semantic structures for the fish, whereas the Menominee participants tended to exhibit more ecologically based structures (Medin et al., 2006). A large-scale study of 6- to10-year-old children (Coley, 2012) found that engaging in activities related to "exploring nature" was associated with making more ecological inferences (i.e., generalizing a novel property to a dissimilar but ecologically related species). Coley (2012) also found that the (adult) tendency to make ecological inferences for diseases and taxonomic inferences for insides emerges earlier in rural children than in urban children.

In the domain of proper names and brand names, one study of two individuals with aphasia suggested that moderate domain knowledge produced taxonomic organization, whereas detailed domain knowledge produced thematic organization (Crutch & Warrington, 2011). For example, moderate knowledge of film and cinema was sufficient to show sensitivity to a taxonomic grouping of directors (e.g., Roman Polanski, Alfred Hitchcock, Martin Scorsese, Billy Wilder), but detailed knowledge of film was necessary to show sensitivity to a thematic grouping related to a specific film (e.g., *Rear Window*, Alfred Hitchcock, James Stewart, Grace Kelly).

The key point is that culture and experience structure the semantic system. Individuals whose knowledge comes mostly from the classroom, such as majority-culture novices, are relatively more sensitive to visual features and taxonomic relations. In contrast, individuals whose knowledge comes from direct interaction, such as subsistence farmers and children who spend more time exploring nature, are relatively more sensitive to ecological relations. These differences can reflect culture and goals independently of overall domain expertise.

Variation in typical and neurological populations. Individuals demonstrate consistent preferences for either taxonomic or thematic relations even after accounting for effects of age, education, and expertise. In relatedness judgment experiments with varied task instructions and constraints, adult participants (Lin & Murphy, 2001) and children 3 to 4 years old (Kalénine & Bonthoux, 2006) tended to prefer selecting either the thematically or taxonomically related option. These individual preferences are also consistent across similarity and dissimilarity judgment tasks (Simmons & Estes, 2008). This tendency toward preferences far exceeds what would be expected from a random distribution: Across these studies, over 300 North American undergraduates were tested, and about 80% showed a statistically reliable preference for either taxonomic or thematic relations (the nominal expected chance rate would be 5%). The preferences were approximately evenly split between those favoring taxonomic relations and those favoring thematic relations (see also Estes et al., 2011).

One study found that such individual differences also extend across tasks with very different semantic processing demands (Mirman & Graziano, 2012b). Implicit activation of taxonomically and thematically related concepts was measured by fixations on a related distractor compared with an unrelated distractor during a spoken word-to-picture matching task (visual world paradigm; described in the Differences in Time Course of Activation section) in which semantic relations are irrelevant and distracting. Across 30 older adult participants, the relative activation of taxonomic versus thematic relations during spoken word comprehension predicted participants' tendency to choose taxonomic options relative to thematic options in a triads match-to-sample task—an explicit nonverbal semantic relatedness judgment task. No effect of age or education was observed in either of the tasks, so even in the absence of developmental and education effects, individuals exhibit consistent cross-task differences in strength of taxonomic versus thematic relations.

These differences may even be persistent and detectable very early in life. At 36 months of age, choosing the taxonomic option in a triads task was associated with earlier tendencies to produce pointing gestures at 13 months of age and object names and features at 24 months of age (Dunham & Dunham, 1995). In contrast, relational play (bringing together and integrating two objects) at 13 months and relational

speech (e.g., locatives such as "down," "go in there," or "on") at 24 months were associated with choosing the thematic option 1 year later (Dunham & Dunham, 1995).

Two small studies comparing hearing and deaf adolescents found no substantive differences between taxonomically versus thematically grouped pictures in a recall task (Li & Zhang, 2009), or in a triads task (Yi et al., 2011), though deaf students were slower to perform a thematically primed living/nonliving categorization (Yi et al., 2011).

Individual differences can also be produced by neurogenic disorders of language and memory such as stroke and neurodegenerative diseases. In a triads task, individuals with Alzheimer's disease made fewer thematic responses and more shape-based responses than neurologically healthy control participants did (Au, Chan, & Chiu, 2003), suggesting reduced salience of thematic relations. In cases of stroke, one triads study found that individuals with Broca's aphasia made more errors on thematic trials, and individuals with Wernicke's aphasia made more errors in taxonomic trials (Semenza, Denes, Lucchese, & Bisiacchi, 1980). However, a more recent study of 25 participants with poststroke aphasia used triads and free sorting tasks, and observed substantial individual differences, but no consistent relationship between aphasia type and preferences for taxonomic versus thematic relations (Vivas, García García, Perea Bartolomé, Leite D'almeida, & Ladera Fernández, 2016). A study of 17 left-hemisphere stroke patients used the visual world eye-tracking paradigm and found a negative association between sensitivity to thematic versus taxonomic competition (Kalénine, Mirman, & Buxbaum, 2012). That is, individuals who were more sensitive to thematic relatedness were also less sensitive to taxonomic similarity, and vice versa. No dissociation between taxonomic and thematic relations was observed in Williams Syndrome: Taxonomic and thematic relations were found to produce comparable priming effects on word detection in both the neurologically typical control group and the Williams Syndrome group (Tyler et al., 1997).

In sum, individuals exhibit systematic preferences between thematic and taxonomic relations that are consistent across very different tasks, emerge early in childhood, and persist over age, at least over the short age range in which this has been tested longitudinally. Some of these individual differences are related to neurogenic deficits of language and memory, such as stroke or neurodegenerative disease. Both the neurologically intact and compromised populations exhibit a "double dissociation": independent differences in taxonomic and thematic semantics. Double dissociations are traditionally taken as strong evidence of dissociable systems because a single system typically does not allow for one aspect to be systematically favored or impaired without affecting the other. In addition, the neurological behavioral studies suggest that a neural dissociation between taxonomic and thematic semantic processing may exist, but they did not test such a dissociation directly. The next section reviews studies that directly investigated neural dissociations between taxonomic and thematic semantics in both neurologically intact and neurologically compromised individuals.

Neural Dissociations

Neural dissociations provide another rich source of evidence that semantic memory is organized into distinct taxonomic and thematic systems. Although relatively numerous, these studies have yet to converge to a coherent theory of the neural basis of taxonomic and thematic semantics. The anterior temporal lobes (ATLs) are well-established as a "semantic hub," which may support both taxonomic and thematic semantics. An alternative hypothesis is that taxonomic semantics rely particularly strongly on the anterior temporal lobes, whereas thematic semantics rely particularly strongly on the temporoparietal cortex (TPC). This section reviews studies that have investigated the neural basis of taxonomic and thematic semantics and their findings, organized broadly by task paradigm, then discusses the factors that may contribute to the lack of convergence.

A series of studies using the match-to-sample (triads) task found an association between thematic relations and the inferior parietal and posterior temporal regions. The first was a functional MRI (fMRI) study that found greater activation in these regions for thematic compared with taxonomic relations (Kalénine et al., 2009). This finding was further supported by converging evidence from two studies of individuals with left-hemisphere stroke. The first found that temporoparietal lesions specifically impaired sensitivity to thematic relations that involve action, such as wine bottle – corkscrew (Tsagkaridis, Watson, Jax, & Buxbaum, 2014). The second showed a behavioral association between recognition of meaningful gestures (action knowledge) and performance on thematic triads, and that this association was mediated by posterior temporal damage (Kalénine & Buxbaum, 2016). Finally, an fMRI study used conjunction analyses to show that posterior temporal regions were more strongly activated during triads that required global semantic processing and during triads that required tool action judgments (Davey et al., 2016).[3] Together, these studies make a clear case for a relationship between thematic semantics, action representations, and the TPC.

However, the convergence between those studies is weakened by divergence among three other studies using the triads task, which have found other patterns of results. One fMRI study found that when participants selected a taxonomic relation over a thematic relation, there was greater activation in precuneus, middle frontal gyrus, and thalamus (Sachs, Weis, Krings, Huber, & Kircher, 2008). Another found largely overlapping areas of activation (Jackson, Hoffman, Pobric, & Lambon Ralph, 2015), though in this study, the thematic relations were defined by word co-occurrence statistics that do not tend to isolate thematic relations. (An additional study was primarily concerned with cross-cultural comparisons between U.S. and East Asian participants: Gutchess, Hedden, Ketay, Aron, & Gabrieli, 2010). Finally, an older study of individuals with left-hemisphere stroke found that anterior (frontal lobe) lesions impaired performance on thematic trials and posterior (temporal and parietal lobe) lesions impaired performance on taxonomic trials (Semenza, Bisiacchi, & Romani, 1992).

Other explicit relatedness judgment tasks have revealed similarly mixed patterns of results. One study found stronger frontal and insula activation during script event sequence judgments than during taxonomic judgments (Kuchinke, Meer, & Krueger, 2009).

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[3] Functional and structural connectivity analyses suggested that posterior temporal cortex may also be part of a "semantic control" network that shapes the pattern of semantic retrieval to suit task demands (Davey et al., 2016).

However, the sequence judgments were slower and more error-prone, suggesting that they were also more difficult, so the activation difference may have been caused by a general difficulty difference rather than anything specific to event sequence judgments. Another study found that judgments of object manipulation similarity (i.e., hand shape and motion) elicited greater activation in the inferior parietal and dorsal premotor areas, whereas judgments of object use context (e.g., gardening, cleaning) elicited greater activation in retrosplenial and anterior lateral inferotemporal regions (Canessa et al., 2008). The shared use context items were not objects that are actually used together (e.g., stapler—pencil sharpener; not stapler—papers), so this study may have compared a mixture of thematic and taxonomic similarity judgments against single-feature (manipulation action) similarity judgments. Two studies using word pair relatedness judgment tasks also found conflicting results. A MEG study found that anterior temporal regions responded more strongly during taxonomic relatedness judgments than during thematic relatedness judgments, and that temporoparietal regions responded approximately equally during both kinds of judgments (Lewis, Poeppel, & Murphy, 2015). In contrast, an fMRI study found that, compared with object nouns (e.g., "the alligator"), verbs and event nouns (e.g., "the hurricane") elicited more activation in the left posterior middle temporal gyrus (Bedny, Dravida, & Saxe, 2014).

Picture-word interference studies of the neural correlates of thematic and taxonomic semantics need to be interpreted in the context of the overall behavioral difference: Taxonomic distractors tend to produce interference, but thematic distractors tend to produce facilitation. One fMRI study found that thematic distractors elicit more activation in the left angular gyrus, left posterior middle temporal gyrus, and right supplementary motor area (de Zubicaray et al., 2013). Another study localized that difference to the left lingual and middle occipital gyri, and the reverse contrast (taxonomic more than thematic) to the right inferior frontal and lingual gyri and midbrain (pons) regions (Abel et al., 2009). A noninvasive brain stimulation study (using transcranial direct current stimulation) tested anodal stimulation of the middle temporal gyrus, the inferior frontal gyrus, and sham stimulation. This study found that only middle temporal stimulation eliminated the thematic facilitation effect, and neither stimulation condition affected the taxonomic inhibition effect (Henseler, Mädebach, Kotz, & Jescheniak, 2014).

Interference produced by repeatedly naming a group of taxonomically related pictures (called "blocked cyclic naming") has been associated with greater activation of inferior frontal regions (Schnur et al., 2009) and the hippocampus and middle temporal gyrus (de Zubicaray, Johnson, Howard, & McMahon, 2014). Thematic groupings did not elicit this behavioral effect (de Zubicaray et al., 2014), though they have been found to elicit the closely related cumulative semantic interference effect (Rose & Abdel Rahman, 2016).

A pair of studies used semantically primed lexical decision with the same materials and found that, compared with thematic priming, taxonomic priming was associated with more fMRI signal change in the right precuneus at a short 200-ms SOA (Sachs, Weis, Zellagui, et al., 2008) and the right insula at a long 800-ms SOA (Sachs et al., 2011). Another study from the same research group used cross-modal priming and found that activation of a mid-anterior superior temporal region was associated with thematic relatedness more than with taxonomic relatedness effects (Sass, Sachs, Krach, & Kircher, 2009). A study primarily concerned with syntactic processing found that a comparison of taxonomic noun-noun (spider–scorpion) versus thematic verb-noun (crawl-scorpion) priming showed a few small posterior temporal and anterior superior parietal activation clusters (Lee, Pruce, & Newman, 2014).[4]

An ERP study using primed picture naming found earlier effects of thematic relatedness than of taxonomic similarity (reviewed in the Differences in Time Course of Activation section) and suggested that the thematic relations engaged the TPC to a greater degree (Wamain et al., 2015). This study stands out for using very carefully selected materials that allowed controlling for visual similarity, overall semantic relatedness, and had minimal task demands, thus ruling out alternative (post hoc) explanations. Another ERP study using primed lexical decision found that "productive" relations (e.g., bee—honey) did not elicit a priming effect in reaction time (RT) and showed a reduced late frontal negativity effect relative to taxonomic and other semantic priming conditions (Chen et al., 2014), which the authors interpreted as indicating that processing thematic relations engages additional memory processes. A similar conclusion was drawn in an ERP study testing word-pair memory, which found that taxonomically similar pairs of words elicited a stronger parietal old–new effect than thematically related pairs did (Kriukova, Bridger, & Mecklinger, 2013). An EEG study compared thematic and taxonomic relations in a passive version of the priming task in which words were presented in pairs, but no response was required. Thematic relationships elicited stronger theta (4–7 Hz) power increases over the right frontal areas, and taxonomic relationships elicited stronger alpha (8–12 Hz) power increases over parietal areas for taxonomic (Maguire, Brier, & Ferree, 2010). This pattern was also interpreted to reflect greater engagement of memory processes for thematic semantics, as well as greater involvement of inhibition or attention processes for taxonomic semantics.

One study tested contextual (e.g., camel—desert) and visual (e.g., tiger—stripe) feature priming in eight individuals with semantic dementia (SD) and a group of age- and education-matched neurologically intact control participants (Merck, Jonin, Laisney, Vichard, & Belliard, 2014). Semantic dementia, also known as the semantic variant of primary progressive aphasia, is a progressive neurodegenerative disorder that produces widespread semantic deficits. The degeneration typically begins in the anterior temporal lobes and, as the disease progresses, extends posteriorly through the temporal lobes and dorsally into the posterior inferior frontal lobes (Hodges & Patterson, 2007). Although both taxonomic and thematic relations are affected in SD (e.g., Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000), the most striking deficits are taxonomic (e.g., Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004). In their priming study, Merck et al. (2014) found a significant three-way interaction: the control group showed a larger visual-feature priming effect than the SD group did, and the SD group showed a larger contextual priming effect than the control group did. That is, in addition to their well-documented impair-

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[4] The experiment reported by Lee et al. (2014) appears to be Experiment 4 in Lee's (2009) dissertation, and an analogous posterior middle temporal gyrus (MTG) activation cluster was observed in their Experiment 3.

ment of taxonomic semantics, the SD group exhibited increased reliance on thematic semantics.

A study of a large group ($N = 86$) of individuals with language deficits following left-hemisphere stroke examined semantic errors in picture naming. The tendency to make taxonomic errors (controlling for thematic errors) was associated with damage to the anterior temporal lobe, but the tendency to make thematic errors (controlling for taxonomic errors) was associated with damage to posterior temporal and inferior parietal areas at the junction of the temporal and parietal lobes (Schwartz et al., 2011; see Figure 5). Rogers et al. (2004) showed how damage to an anterior temporal lobe "hub" for integrating feature-based semantic similarity would produce increased taxonomic errors in picture naming. Analogous computational principles may produce thematically related errors in picture naming following damage to a temporoparietal thematic hub.

A smaller study used eye tracking during spoken word-to-picture matching, and compared matched groups of individuals with language deficits following anterior left-hemisphere strokes ($n = 6$) and those with posterior (temporoparietal) left-hemisphere strokes ($n = 7$). The key finding was that individuals with temporoparietal lesions showed reduced activation of thematic relations, but not of taxonomic relations, whereas the anterior lesion group exhibited activation of thematic relations that was statistically indistinguishable from neurologically intact control participants, indicating that the thematic deficit was specific to the temporoparietal lesion group (Mirman & Graziano, 2012a).

These findings inspired a recent preregistered[5] study using an fMRI adaptation paradigm to directly test this hypothesized dissociation (Geng & Schnur, 2016). Participants read pairs of words that were identical, taxonomically similar, thematically related, or unrelated. The results were broadly consistent with the dissociation: taxonomic similarity (but not thematic relatedness) affected activation in the anterior temporal lobes, and thematic relatedness (but not taxonomic similarity) affected activation in the supramarginal gyrus (part of the temporoparietal region identified by Schwartz et al., 2011 and Mirman & Graziano, 2012a).

In sum, converging evidence from about a dozen independent studies makes a strong case for a specific neural dissociation between taxonomic and thematic semantics: ATLs are particularly important for taxonomic semantic processing and the TPC is particularly important for thematic semantic processing (Bedny et al., 2014; Davey et al., 2016; de Zubicaray et al., 2013; Geng & Schnur, 2016; Henseler et al., 2014; Kalénine & Buxbaum, 2016;

Kalénine et al., 2009; Lee et al., 2014; Merck et al., 2014; Mirman & Graziano, 2012a; Schwartz et al., 2011; Tsagkaridis et al., 2014; Wamain et al., 2015). These studies include functional neuroimaging of neurologically typical adults, brain stimulation studies, and studies of individuals with neurogenic deficits of language and semantic memory. However, they are less than half of the 28 studies identified by our systematic review. The other studies did not find the same pattern. In some cases, explicit tests did not show it; in other cases, different regions were found to be associated with taxonomic or thematic semantics, thus implicitly failing to find the ATL–TPC dissociation. Further, one study found the exact opposite pattern: anterior lesions associated with thematic deficit, and posterior lesions associated with taxonomic deficit (Semenza et al., 1992), and there are other studies that have reported ATL involvement in thematic semantics (e.g., Peelen & Caramazza, 2012).

Two factors may have contributed to this diversity of findings. The first factor is task properties. When there are behavioral differences between taxonomic and thematic conditions, it becomes difficult to interpret their neural correlates. Perhaps the most obvious example of this is the picture-word interference task, which elicits qualitatively different behavioral effects for taxonomic relations (inhibition) and thematic relations (facilitation). In this case, it is not clear what aspects of the neural differences are caused by differences between taxonomic and thematic semantic relations versus differences between inhibition and facilitation effects. This difficulty also holds for quantitative differences—if one condition has higher error rates and/or RTs, then any differences in neural correlates could be caused by either the difference in semantic relation or the difference in difficulty.

The second factor is differences in how taxonomic and thematic relations are defined and which contrasts are tested. Many of the studies reviewed in this section focus on specific kinds of taxonomic and/or thematic relations: action/manipulation features, object context or location, event sequences, object classes such as animals versus tools, and so forth. Some also use problematic definitions: word co-occurrence statistics and association norms do not effectively isolate thematic relations. The studies also vary in the kinds of contrasts that were tested: some test individual related against unrelated control conditions, others test different relation types against one another, and yet others conduct conjunction analyses. We have chosen to be more inclusive in our review because we believe that it is important to consider the broad scope of research on the possible neural dissociation between taxonomic and thematic semantics, even if some of these studies may ultimately prove to be less informative than others.

An important possible third factor is publication bias. It is possible that there is no consistent neural dissociation between taxonomic and thematic semantic processing, or that the distinction is in the dynamic coordination of different neural processes rather than being localizable to any particular brain region (e.g.,
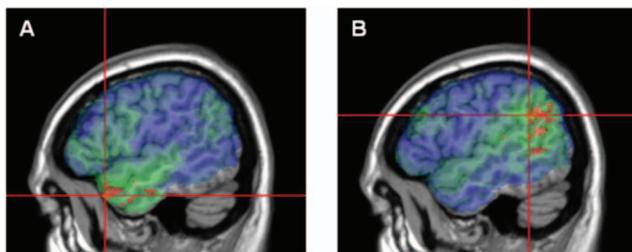
Figure 5. Voxel-based lesion-symptom mapping results of taxonomic errors (left) and thematic errors (right) in picture naming controlling for the other error type (from Schwartz et al., 2011). See the online article for the color version of this figure.

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[5] For this "registered report" format, the study motivation, design, and analysis strategy were peer reviewed in advance of data collection and provisionally accepted so that the study can be published based on the strength of the methods rather than the results. Like registered clinical trials, this approach reduces opportunities for experimenters to adjust analysis strategies after the results are known ("experimenter degrees of freedom") and counteracts publication bias.

Skipper-Kallal, Mirman, & Olson, 2015). If this is true, then the lack of consistency among these results is because they are individual outlier observations that happened to produce a statistically significant result that got published, whereas there are "file drawers" full of studies (or analyses) that found no differences between taxonomic and thematic semantics, but were not published because null results rarely get published. Preregistered reports and incentives for conducting replication studies are promising strategies for addressing these issues.

There is a substantial literature on the neural dissociation of taxonomic and thematic semantic processing, but it has not converged to a single account. Several studies suggest that the ATL is particularly important for taxonomic semantics, and that the TPC is particularly important for thematic semantics, but this should be regarded as a promising hypothesis in need of further testing. Such further testing will need to ensure that the taxonomic and thematic relations are defined in a consistent manner, that task difficulty confounds have been eliminated, and that direct comparisons between taxonomic and thematic relatedness effects are reported.

Summary of Systematic Review

Several lines of evidence indicate a functional and neural dissociation between taxonomic and thematic semantic relations. First, taxonomic and thematic relations make independent contributions to semantic relatedness as demonstrated by computational modeling studies and a wide range of behavioral studies, from relatedness judgments to memory and false memory to brand extension. These different relations also appear to be differentially important across concept domains, have opposite effects in picture-word interference tasks, and require additional cognitive resources for combining or switching between them. Second, differences in the time course of activation of taxonomic and thematic relations have been revealed by eye-tracking and priming studies, further suggesting differences in how such relations are processed.

Third, individual differences provide some of the strongest behavioral evidence for a functional dissociation between taxonomic and thematic semantic systems. Several studies have found a developmental shift from relatively stronger thematic semantics in younger children to taxonomic semantics in adults, and back to thematic semantics in older adults. However, others have not found this pattern, and have pointed out that the developmental trajectory may reflect differences in responses to task demands rather than semantic knowledge, or cross-sectional differences in education and salience of particular semantic relations. Thus, the effect of basic cognitive maturation remains somewhat unclear. However, it is relatively uncontroversial that formal education enhances taxonomic semantics, and that domain expertise and culture can selectively enhance either taxonomic or thematic semantic knowledge.

Even populations that are relatively homogenous with respect to age, education, and culture show individual variability in strength of taxonomic versus thematic relations. These individual differences tend to extend across tasks and persist across development. A stronger form of individual differences is induced by neurogenic impairments of language and memory. Individuals with Alzheimer's disease show greater impairment of thematic semantics than taxonomic semantics, whereas individuals with semantic dementia

(a variant of frontotemporal dementia) show the opposite pattern—greater impairment of taxonomic semantics than thematic semantics. The same sort of double dissociations have been documented among individuals who have suffered strokes: some show greater impairment of taxonomic semantics than thematic semantics, and some show the opposite pattern. Such double dissociations are traditionally considered the strongest evidence of dissociable cognitive systems (a thorough discussion was published in 2003 as a special issue of *Cortex*; see Volume 39, Issue 1).

Finally, the neural correlates of these distinct functional semantic systems have proven more difficult to identify, despite numerous attempts. A substantial set of studies suggests that the ATL is particularly important for taxonomic semantics, and the TPC is particularly important for thematic semantics, but other studies conflict with this claim either directly or indirectly. This lack of convergence is at least partly a result of unequal task demands, such as differences in difficulty of taxonomic and thematic conditions, and inconsistent definitions of taxonomic and thematic relations. In addition, the neural distinction may be based in dynamic differential coordination of common areas rather than the static localization differences that have been the primary subject of prior research. As it currently stands, a plurality of the evidence supports the ATL–TPC "dual hub" hypothesis, but the substantial conflicting evidence leaves this hypothesis in need of further testing.

Organizational Principles

Given this wealth of evidence that taxonomic and thematic semantic systems are dissociable, it is important to ask what factors might produce this dissociation. This section describes two possible principles of cognitive and neural organization (schematically depicted in Figure 6) that could be responsible for this dissociation.

Differences in Critical Features: Topographic Specialization

The first proposed principle is based on which kinds of features contribute most strongly to the different semantic relations. Specifically, taxonomic relations may rely more strongly on shape and color features—relatively static features that determine object categories. In contrast, thematic relations may rely more strongly on location, motion, and functional action features, which are critical
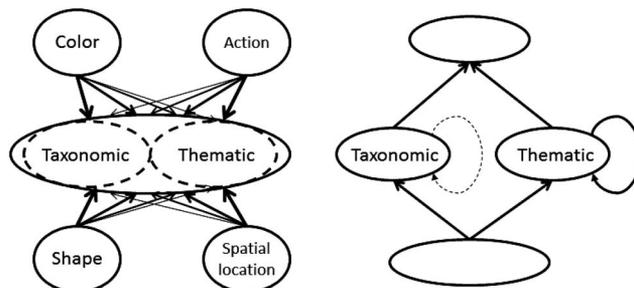
Figure 6. Proposed principles driving the dissociation of taxonomic and thematic processing: topographic specialization (left) and architectural specialization (right).

for determining how objects interact or relate to one another in scenes or events. For example, several studies linked thematic semantics with knowledge of object-use actions (Davey et al., 2016; Kalénine & Buxbaum, 2016; Tsagkaridis et al., 2014). In this view, taxonomic and thematic semantic systems are fundamentally of the same type, but differ in terms of which kinds of features contribute most strongly.

These differences in feature sensitivity could produce differences in neural basis. Because local neural connections are far more numerous than long-distance connections, semantic representations may develop under a bias favoring short connections (Behrmann & Plaut, 2013; Jacobs & Jordan, 1992; Plaut, 2002). Thus, distinct taxonomic and thematic "hubs" could emerge as a result of integration of modality-specific feature representations that are broadly distributed. If different feature types are differentially important for taxonomic versus thematic relations, then a hub that integrates thematically relevant features would become a thematic hub, whereas a hub that integrates taxonomically relevant features would become a taxonomic hub. Both hubs would serve computationally similar functions—integration of sensory-motor features, as in the hub-and-spoke computational models of semantic memory (Rogers et al., 2004)—but they would differ in terms of which specific sensory-motor features are most strongly represented. This proposed difference in connectivity is schematically depicted in the left panel of Figure 6, in which thicker arrows represent stronger connections.

The ATL and TPC are good candidates for such topographically constrained hubs: both are known to be involved in semantic cognition and to exhibit multimodal sensitivity (e.g., Binder & Desai, 2011; Gainotti, 2011; Lau, Phillips, & Poeppel, 2008), as well as hub-like connectivity to diverse primary sensory and motor regions (Bonner, Peelle, Cook, & Grossman, 2013; Catani, Howard, Pajevic, & Jones, 2002; Guo et al., 2013; Seghier, 2013; Turken & Dronkers, 2011). However, by virtue of their different locations, they are anatomically closer to different modality-specific regions. The ATL can be thought of as the terminus of the ventral "what" visual pathway (for a recent review of the ventral visual pathway, see Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). It is close to inferior temporal lobe regions representing color and shape, and recent studies suggest that it is involved in integrating shape and color features (Baron, Thompson-Schill, Weber, & Osherson, 2010; Coutanche & Thompson-Schill, 2015).

In contrast, the TPC is part of the dorsal "where"/"how" visual pathway, including regions involved in spatial cognition and action semantics. The parietal cortex has long been associated with spatial cognition (for a review, see, e.g., Husain & Nachev, 2007), including spatial working memory (e.g., Wager & Smith, 2003) and spatial attention (e.g., Yantis & Serences, 2003), and damage to the parietal lobes is the most common cause of disorders of spatial attention, such as neglect (e.g., Buxbaum et al., 2004; Corbetta & Shulman, 2011). This region is also important for integrating spatially distributed objects into a single coherent percept, sometimes called "Gestalt perception" (Huberle & Karnath, 2012; Lestou, Lam, Humphreys, Kourtzi, & Humphreys, 2014). One particularly striking example of this is simultanagnosia, a neurological deficit associated with damage to the parieto-occipito-temporal cortex, and characterized by the inability to visually perceive more than one object at a time despite relatively spared single object perception (a very compact recent review is

provided by R. M. Bauer, 2012, pp. 245–247; for a direct connection with Gestalt perception, see Himmelbach, Erb, Klockgether, Moskau, & Karnath, 2009).

The temporoparietal regions are also strongly associated with action recognition and planning, particularly actions involving skilled use or manipulation of familiar objects (for reviews, see Andersen & Cui, 2009; Buxbaum & Kalénine, 2010; Watson & Chatterjee, 2011). Lesion-symptom mapping studies of individuals with left-hemisphere strokes have revealed an association between TPC lesions and deficits in recognition and production of meaningful gestures and object-use actions (Buxbaum, Shapiro, & Coslett, 2014; Kalénine, Buxbaum, & Coslett, 2010; Tarhan, Watson, & Buxbaum, 2015; for fMRI evidence, see also Watson, Cardillo, Ianni, & Chatterjee, 2013). Particularly relevant to this proposal are explicit associations between deficits in thematic semantics and deficits in action knowledge (Kalénine & Buxbaum, 2016; see also Tsagkaridis et al., 2014). TPC regions are more strongly activated during semantic similarity judgments of action and event concepts compared with object concepts (Bedny et al., 2014; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002). Nouns referring to tools and verbs referring to tool-use actions tend to activate similar brain regions, particularly the posterior superior and middle temporal gyri (e.g., Tyler et al., 2003), and right-hemisphere TPC regions are more strongly activated during comprehension of sentences describing a person's actions than sentences describing a person's traits (Ma, Vandekerckhove, Van Hoeck, & Van Overwalle, 2012).

In sum, the topographic specialization principle emphasizes feature-based integration, and critically assumes that different feature modalities are differentially important for taxonomic versus thematic semantics: color and shape for taxonomic relations; action and location for thematic relations. Testing this proposal will require targeted assessment of this feature-specificity assumption. Because of their hub-like connectivity, multimodal sensitivity, and relative proximity to different modality-specific areas, the ATL and TPC are promising candidates for taxonomic and thematic neural hubs, respectively.

Differences in Computational Function: Architectural Specialization

The second proposed principle is based on the observation that semantic cognition is involved in (at least) two very different kinds of cognitive tasks: identification and prediction (Bassok & Medin, 1997). As in the case of the separation of dorsal and ventral visual processing streams, the need for these different computations may drive cognitive and neural specialization. Computational "mixture-of-experts" models (Jacobs, Jordan, & Barto, 1991) have shown how subtle differences in the starting architecture can lead to functional specialization for "what" and "where" processing. Analogously, neuroarchitectural differences could lead to the emergence of distinct taxonomic and thematic semantic systems. This is schematically represented in the right panel of Figure 6, in which different recurrent connections represent these hypothesized differences.

In existing feature-based computational models of semantic cognition (e.g., Cree et al., 1999; O'Connor et al., 2009; Rogers et al., 2004), recurrent connections extract coherent covariation, such as the covariation among having feathers and wings, being able to

fly, and being a bird. These regularities across features and objects provide a computational basis for category-based generalization and sensitivity to taxonomic typicality. Critically, these are object-based regularities that require abstracting across different events or scenarios. Event-based temporal regularities are orthogonal to such object-based regularities, and can also be extracted by recurrent connections (e.g., Altmann & Mirković, 2009; Elman, 1990). Recurrent connections can also integrate temporal sequences of actions or words into a holistic event or sentence representation (e.g., Botvinick & Plaut, 2004; McClelland, St. John, & Taraban, 1989). However, the computations required for extracting coherent covariation of features across objects and the computations required for learning the temporal structures of events or sentences are very different, and may drive functional specialization.

Again, the ATL and TPC are promising candidates for these distinct functions. The ATL is strongly associated with integration of features for semantic cognition (e.g., Coutanche & Thompson-Schill, 2015; Rogers et al., 2004). Object naming is the quintessential object identification task, and there is mounting evidence that the left ATL is particularly important for object naming compared with other semantic tasks (Bi et al., 2011; Mesulam et al., 2013; Mirman, Zhang, Wang, Coslett, & Schwartz, 2015; Schwartz et al., 2009; Walker et al., 2011).

In contrast, TPC is particularly sensitive to, and critical for, representing temporal and/or contextual relations. In functional neuroimaging studies, TPC has been found to respond more strongly when the amount of thematic context increases (Ross & Olson, 2010, Experiment 2; Xu, Kemeny, Park, Frattali, & Braun, 2005), and to be involved in integrating noun–verb combinations to form minimal event representations (Boylan, Trueswell, & Thompson-Schill, 2015). It is also associated with using semantic or sentence contexts to facilitate speech perception in noise (Golestani, Hervais-Adelman, Obleser, & Scott, 2013; Obleser & Kotz, 2010; Obleser, Wise, Dresner, & Scott, 2007). Together, these results suggest that TPC is involved in integrating sequential linguistic input to form a holistic representation of the event or narrative, and using that event representation to influence interpretation of ambiguous inputs.

Comprehension of reversible sentences such as "The man serves the woman" critically depends on encoding and maintenance of sequential information. Lesion-symptom mapping studies have found that comprehension of reversible sentences is impaired following TPC lesions in both chronic and acute stroke (Race, Ochfeld, Leigh, & Hillis, 2012; Thothathiri, Kimberg, & Schwartz, 2012), and a recent TMS study found that stimulation of the intraparietal sulcus also affected performance in this task (Finocchiaro, Capasso, Cattaneo, Zuanazzi, & Miceli, 2015). Inferior parietal regions are also known to be important for episodic memory (Berryhill, 2012; Rugg & Vilberg, 2013), possibly acting as a convergence zone for binding episodic features (Shimamura, 2011), similar to the hub-and-spoke and convergence zone frameworks for binding semantic features.

In sum, the architectural specialization principle frames the distinction between taxonomic and thematic semantics in terms of the distinction between identification and prediction, both of which are critical cognitive processes that require very different kinds of computational architectures to execute. At least one such dissociation is very well-known: "what" and "where"/"how" are two very different kinds of representations that need to be computed by the

visual system, which has developed distinct subsystems for computing them. It is possible that the semantic system similarly decomposes the identification and prediction tasks into distinct subsystems, which become the taxonomic and thematic semantic systems. Identification is fundamentally an object-based process, but prediction is an event-based process that is based on a broader range of knowledge (sensory-motor, as well as causal, social, etc.). A full evaluation of this principle will require consideration of the possibility that thematic relations between object concepts are a reflection of a broader representation of event knowledge.

Summary and Concluding Remarks

This review began by defining taxonomic and thematic semantic relations and systematically reviewing a diverse set of behavioral, computational, and neural evidence that they are functionally dissociable. The evidence includes independent contributions to relatedness, different time courses of activation, a wide range of individual differences in strength of taxonomic versus thematic semantic knowledge, and differences in neural correlates of taxonomic and thematic semantic cognition. These dissociations do not require a strictly modular architecture—distinct taxonomic and thematic semantic subsystems can be (and likely are) deeply interactive, and performance in many tasks will reflect engagement of both subsystems.

In an effort to connect this dissociation to more general principles of cognitive and neural organization and computation, we have identified two principles that may drive this dissociation. The "topographic specialization" principle proposes that distinct taxonomic and thematic semantic subsystems emerge because they rely more strongly on different subsets of object features. Taxonomic relations may rely more strongly on shape, color, and other ventral stream features, whereas thematic relations make rely more strongly on spatial location, motion, object use, and other dorsal stream features. The "architectural specialization" principle proposes that the competing needs of identifying entities in our environment, and of making predictions about those entities, leads to task decomposition in which (possibly subtle) architectural differences lead to the emergence of quite different computational structures.

Several functional neuroimaging and lesion studies suggest that taxonomic semantic processing relies particularly strongly on the ATLs, whereas thematic semantic processing relies particularly strongly on TPC. Other cognitive processes associated with these regions are also consistent with the topographic and architectural specialization principles that could be responsible for the ATL and TPC becoming hubs for taxonomic and thematic semantic processing, respectively. These proposals are motivated by established computational and neural considerations, but, at this point, they are plausible speculations rather than comprehensive accounts. That is, the purpose of these proposals is to provide clear directions for future computational, behavioral, and neuroscience research on semantic memory, in general, and thematic semantics, in particular.

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