

The Declarative/Procedural Model: A Neurobiological Model of Language Learning, Knowledge, and Use

Michael T. Ullman

Brain and Language Laboratory, Department of Neuroscience, Georgetown University, Washington, DC, USA

Not surprisingly, most research on the neurobiology of language has focused on language itself. Yet even after decades of investigation, we know much less about the neurobiological correlates of language than we do about the neurobiology of many other domains, such as vision, motor function, and memory. This relative lack of progress is likely due not only to the complexity of language and to a lack of animal models, but also to an overly narrow “isolationist” approach to language research. A complementary approach of examining links between language and other domains and their neurobiological substrates could significantly advance our understanding of the neurobiology of language, particularly if the neurobiology of these other domains is well-understood. Such an approach would likely be very powerful in that it could generate novel well-motivated predictions about language based on our independent knowledge of these other domains.

There is, in fact, no clear evidence that the neurobiological bases of language underlie language alone, that is, that they are domain-specific (Ullman, Lum, & Conti-Ramsden, 2014). On the contrary, we should expect language to depend heavily on neurobiological substrates that also subserve(d) other domains. In evolution, mechanisms and structures are constantly being reused for new purposes. For example, fins evolved into limbs, limbs into hands and wings, and scales into feathers (Woltering, Noordermeer, Leleu, & Duboule, 2014). Such co-optation of a given substrate for new functions takes place not only phylogenetically (evolutionarily) but also ontogenetically (developmentally). For example, reading likely depends on brain circuitry that is co-opted for this function during learning and development. A given

structure can even be co-opted for new functions without any further changes in the underlying mechanism (this has been referred to as exaptation) (Gould & Vrba, 1982). For example, certain species of heron spread their wings to provide shade so they can better see their prey.

Therefore, language should depend importantly on previously existing neurobiological systems, whether or not these systems have subsequently become further specialized for language, either phylogenetically or ontogenetically. I will call this the *co-optation hypothesis of language*. Various neurobiological systems may be good candidates for such co-optation, including working memory (Caplan & Waters, 1999; Just & Carpenter, 1992), and dorsal and ventral stream processing (Bornkessel-Schlesewsky & Schlewsky, 2013; Hickok & Poeppel, 2007; Petrides & Pandya, 2009).

Two learning and memory systems in the brain—declarative memory and procedural memory—are also excellent candidates. Most of language must be learned, whether or not there are innately specified aspects of this domain. Moreover, declarative and procedural memory seem to be the two most important learning and memory systems in the mammalian brain, including in humans, in terms of the range of domains, tasks, and functions that they underlie (Eichenbaum, 2012; Mishkin, Malamut, & Bachevalier, 1984; Squire & Wixted, 2011). The declarative/procedural (DP) model simply posits that these systems should therefore play wide-ranging roles in language learning, knowledge, and use. That is, the DP model posits that these two memory systems have been co-opted for language—whether or not they have become further specialized phylogenetically or ontogenetically for this domain.

Importantly, these memory systems have been well-studied both in humans and in nonhuman animals, and are thus quite well-understood at many levels—including their behavioral, computational, neuroanatomical, electrophysiological, cellular, biochemical, and genetic correlates. Many of these levels are far better understood for the two systems than for language. Because the posited co-optation of the memory systems for language leads to the expectation that the systems play similar roles in language as in other domains (although not necessarily identical roles, in part because the systems may have become further specialized for language), our understanding of the memory systems should generate a wide range of specific predictions for language. Crucially, these predictions are generated independently from the study of language itself, and are well-motivated from this independent knowledge. Moreover, many of them are likely to be novel because there would often be no reason to make such predictions based on the more limited study of language alone. Finally, linking language to the memory systems should not only generate new predictions, but may also help to account for already-observed language phenomena for which no good explanation independent of language currently exists.

Here, I first present an overview of the two memory systems, whose neurobiological and other correlates constitute the foundation of our predictions. Next, I present key predictions regarding the roles of these systems in language, with a focus on functional neuroanatomy. Then, I summarize a range of evidence testing these predictions. Converging evidence from multiple methodological approaches provides support for many of the predictions, thus supporting the DP model as well as the co-optation hypothesis more generally, and advancing our understanding of language and its underlying neurobiology. Note that the purpose of this chapter is to present the theory and its predictions; therefore, I focus on the motivating background (the memory systems) and the predictions, and more briefly summarize the evidence.

76.1 THE MEMORY SYSTEMS

Here, I provide an overview of the declarative and procedural memory systems, and discuss interactions between the two systems as well as with other neurocognitive systems. Note that the declarative and procedural memory systems refer here to the entire neurocognitive systems involved in the learning, representation, and use of the relevant knowledge, not just to those portions underlying learning and consolidating new knowledge, which is how some researchers

refer to the systems. For additional information on the memory systems, see Stark and Stark chapter in this book (Chapter 67).

76.1.1 The Declarative Memory System

The declarative memory brain system is quite well-understood (Cabeza & Moscovitch, 2013; Eichenbaum, 2012; Eichenbaum, Sauvage, Fortin, Komorowski, & Lipton, 2012; Henke, 2010; Mishkin et al., 1984; Squire & Wixted, 2011; Stark and Stark chapter in this book; Ullman, 2004). Briefly, the hippocampus and other medial temporal lobe (MTL) structures are critical for learning and consolidating new knowledge that depends on this system, although ultimately the storage of this knowledge depends largely on neocortical regions, particularly in the temporal lobes.

Within the MTL, evidence from human and animal studies suggests that the hippocampus underlies the rapid linking (binding, associating) of different bits of knowledge or experience across multiple domains and modalities, including what may be characterized as knowledge of “what” (e.g., facts, meanings), “where” (e.g., landmarks), and “when” (when an event occurred) (Henke, 2010; Squire & Wixted, 2011). Other MTL structures closely connected with the hippocampus are also important, including the entorhinal, perirhinal, and parahippocampal cortices (Stark and Stark chapter in this book). Perirhinal cortex may underlie the familiarity of newly learned information, whereas the hippocampus subserves its explicit recollection (Brown, Warburton, & Aggleton, 2010; but see Wixted & Squire, 2011). Perirhinal cortex may support memories of single items (at least in the visual modality), whereas the hippocampus underlies more complex relational associations. MTL structures also appear to play a role in detecting and learning novel stimuli, perhaps perirhinal cortex for novel individual items and the hippocampus for novel relational information (Yonelinas, Aly, Wang, & Koen, 2010). Different nonhippocampal MTL regions may preferentially underlie memories in different domains: for example, perirhinal cortex for object recognition and parahippocampal cortex for spatial recognition as well as temporal information (Eichenbaum & Lipton, 2008; Eichenbaum et al., 2012; Squire & Wixted, 2011). Auditory information may particularly rely on parahippocampal cortex (Munoz-Lopez, Mohedano-Moriano, & Insausti, 2010), perhaps due to the temporal nature of this information. In contrast, as mentioned, the hippocampus binds information from a wide variety of domains and modalities, including time (which may explain its importance in episodic memory). More complex high-level concepts (e.g., about Jennifer Aniston) may also be represented in the hippocampus (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). More generally,

the hippocampus and other MTL structures may be not only involved but also required for learning arbitrary bits of information and binding them, as evidenced by the virtual lack of such information acquired by densely amnesic individuals with extensive MTL lesions such as patient H.M. (Henke, 2010; Squire & Wixted, 2011; although some such information may still be learnable; see Stark and Stark chapter in this book). Finally, other structures connected to the MTL also play a role in declarative memory, including the fornix and various diencephalic structures and tracts (especially the mammillary bodies, the mammillothalamic tract, and the medial dorsal and anterior thalamic nuclei) (Squire & Wixted, 2011).

The MTL, including the hippocampus, is not just involved in learning and memory. As we have seen, the MTL plays a role in novelty detection, perirhinal cortex may subserve object recognition, and parahippocampal cortex may underlie spatial recognition and temporal information. It has been suggested that perirhinal cortex plays both memory and perceptual roles that link the declarative memory system with the ventral stream (“what pathway”) in the visual modality (Bussey & Saksida, 2007). In contrast, parahippocampal cortex is closely linked to the dorsal stream (“where”) pathway, particularly in the representation of landmarks (Kravitz, Saleem, Baker, & Mishkin, 2011). Additionally, the hippocampus may underlie other functions not strictly related to long-term memory, including short-term memory and aspects of imagination and prediction (Eichenbaum & Fortin, 2009; Kumaran & Maguire, 2009). Thus, MTL structures may play a number of (very possibly interrelated) roles in learning, memory, and other functions.

As mentioned above regarding the long-term memory functions of this brain system, knowledge that critically depends on the MTL during learning and consolidation eventually relies largely on neocortex. The MTL may rapidly bind neocortical representations together, which, over time and/or experience, eventually develop cortical-cortical links, thereby no longer requiring the MTL (McClelland, McNaughton, & O’Reilly, 1995). However, the MTL continues to play a role in this knowledge. As we have seen, it seems to be involved in object recognition (perirhinal cortex), spatial recognition (parahippocampal cortex), and recognition of higher-level concepts (hippocampus). Moreover, it has been suggested that the MTL continues to underlie long-term memories, particularly for autobiographical (episodic) knowledge (Winocur & Moscovitch, 2011), although this claim has been disputed (Squire & Wixted, 2011).

Within neocortex, different regions appear to underlie different types of knowledge (Martin, 2007; Squire & Wixted, 2011). For example, knowledge for

living and nonliving things seems to involve different neocortical regions. An important organizational principle appears to be that neocortex proximate to particular sensory cortices underlies knowledge closely linked to those sensory modalities. Thus, knowledge with strong auditory associations depends on superior temporal regions (near primary auditory cortex), whereas knowledge with visual associations involves temporal and other regions downstream from visual cortex. Higher-level knowledge may also be organized neuroanatomically. For example, knowledge of faces involves the “fusiform face area” and knowledge of written words involves the “visual word form area.” More generally, higher-level concepts may rely on more anterior temporal lobe areas (Barense et al., 2012). Information may flow from posterior to anterior regions of the temporal lobe, such that, at least in vision (and possibly in audition, Rauschecker & Scott, 2009), features are represented hierarchically in increasingly complex conjunctions, with low-level features represented more posteriorly and higher-level features represented more anteriorly—perhaps with the most complex conjunctions (e.g., higher-level concepts) in MTL regions, such as in the hippocampus.

Neocortical regions outside of temporal cortex also play roles in declarative memory—not only in the representation of long-term knowledge but also in particular processes associated with declarative memory. A region in inferior frontal neocortex corresponding largely to Brodmann’s areas (BAs) 45 and 47 (within and near classical Broca’s area) seems to underlie the encoding as well as the selection or recall of declarative memories (Ullman, 2004). Portions of the basal ganglia, perhaps with connections to these areas, may play analogous roles (Ullman, 2006). And a posterior parietal region seems to underlie aspects of encoding or retrieval (Uncapher & Wagner, 2009; Wagner, Shannon, Kahn, & Buckner, 2005).

The behavioral correlates of this network of brain structures rooted in the MTL are reasonably well-characterized (Eichenbaum, 2012; Henke, 2010; Squire & Wixted, 2011; Ullman, 2004). The system may be specialized for learning arbitrary bits of information and associating them; it may even be necessary for learning this information. It underlies the learning, representation, and use of knowledge about both facts (semantic memory) and events (episodic memory), such as the fact that Catalan is derived from Latin, or the event of you having a bowl of delicious pho yesterday for lunch. More broadly, the system can learn a wide range of information across sensory modalities and cognitive domains, and may also support various non-long-term memory functions. Unlike other types of long-term memory such as procedural memory or fear conditioning, multiple types of knowledge can be

learned very rapidly in this system with as little as a single exposure to the stimulus, although additional exposures strengthen memories. The acquired knowledge is at least partly, although not completely (Chun, 2000; Henke, 2010; Schendan, Searl, Melrose, & Stern, 2003), explicit—that is, available to conscious awareness. Indeed, this appears to be the only long-term memory system that underlies explicit knowledge; thus, any knowledge that is explicit should have been learned in declarative memory. Once learned, information in declarative memory can be generalized and used flexibly across different contexts.

The molecular bases of declarative memory have also been reasonably well-studied in humans and animals (Green & Dunbar, 2012; Pezawas et al., 2004; Ullman, 2004). Various genes, including those for brain-derived neurotrophic factor (BDNF) and apolipoprotein E (APOE), play roles in declarative memory and hippocampal function, as do the neurotransmitter acetylcholine and the hormone estrogen (higher levels are associated with better declarative memory in humans and rats). BDNF may play a role in consolidation (as may estrogen). Estrogen may modulate declarative memory functionality via BDNF and/or acetylcholine.

Finally, various subject-level factors appear to modulate learning and retention in declarative memory, including not only genetic variability but also age (declarative memory improves during childhood, plateaus in adolescence/early adulthood, and then declines), sex (females seem to have an advantage at declarative memory over males), handedness (left-handedness may be associated with a declarative memory advantage), sleep (memory consolidation seems to improve during sleep), and exercise (which can enhance declarative memory) (Erickson et al., 2011; Marshall & Born, 2007; Ullman, 2005; Ullman et al., under revision; Ullman, Miranda, & Travers, 2008).

76.1.2 The Procedural Memory System

Although procedural memory is still not as well-characterized as declarative memory, its neurobiological and behavioral correlates are becoming clearer (Ashby, Turner, & Horvitz, 2010; Doyon et al., 2009; Ullman, 2004). Procedural memory involves a network of interconnected brain structures rooted in frontal/basal-ganglia circuits, including frontal premotor and related regions, particularly BA 6 and BA 44. (Note that we use the term procedural memory to refer to a particular brain system and its characteristics, rather than implicit memory more generally, which is how some researchers use the term.) The basal ganglia play a critical role in the learning and consolidation of

motor and cognitive skills, whereas neocortical regions may be more important for processing skills after they have been automatized. Within the basal ganglia, the caudate nucleus (and the anterior putamen) may be especially important for skill acquisition.

This circuitry underlies the implicit (nonconscious) learning and processing of a wide range of perceptual-motor and cognitive skills, tasks, and functions (Eichenbaum & Cohen, 2001; Henke, 2010; Ullman, 2004), including navigation, sequences, rules, and categories. It may be specialized for learning to predict (perhaps especially probabilistic outcomes), for example, the next item in a sequence or the output of a rule. Learning in the system requires practice, and thus is slower than learning in declarative memory—though what is eventually learned seems to be processed more rapidly and automatically than knowledge in declarative memory. Although the system is rooted in the basal ganglia, the cerebellum may also play a role; however, exactly how and in what ways it interacts with the basal ganglia remain unclear.

Some aspects of the molecular bases of procedural memory are also beginning to emerge. The neurotransmitter dopamine plays an important role, particularly in learning and consolidation (Ashby et al., 2010). Certain genes involved in procedural memory have been identified, including *FOXP2*, *PPP1R1B* (for the protein DARPP-32), and *DRD2* (Meyer-Lindenberg et al., 2007; Ullman & Pierpont, 2005; Wong, Ettliger, & Zheng, 2013). A recent study found that humanized *Foxp2* in mice (i.e., with human-specific amino acid substitutions) sped up learning, in particular by promoting the transition from declarative to procedural memory (Schreiweis et al., 2014). Finally, other factors may also affect procedural memory, including age. Unlike declarative memory, procedural memory functionality seems to be well-established early in life, after which learning or consolidation in this system may attenuate (Adi-Japha, Badir, Dorfberger, & Karni, 2014; Ullman, 2005). In contrast, sleep and exercise, among other factors, appear to show similar effects in the two memory systems, improving learning in both.

76.1.3 Interactions Between the Memory Systems

The declarative and procedural memory systems interact in a number of ways. First, evidence suggests that the two systems can, to some extent, acquire the same or analogous knowledge or skills (Poldrack & Packard, 2003; Ullman, 2004). According to the *redundancy hypothesis*, they therefore play at least partly redundant roles. Such redundancy can be found for multiple tasks and functions, including navigation,

sequences, rules, and categories. Perhaps not surprisingly, the type and form of knowledge learned in the two systems are often quite different, even while this knowledge underlies the same or similar outcomes. For example, evidence from rodents suggests that navigation can be learned in procedural memory, such that animals learn to turn at a particular point (response strategy), or in declarative memory, by using landmarks (place strategies). Similarly, humans can learn sequences, rules, and categories implicitly in procedural memory or explicitly (and perhaps also implicitly) in declarative memory.

Various factors appear to modulate which of the two systems is used for a given task or function that can be learned or processed by either system. The declarative memory system often acquires knowledge initially, thanks to its fast acquisition abilities, whereas the procedural system gradually learns analogous knowledge that is eventually processed rapidly and automatically. The knowledge in declarative memory seems to remain intact even when procedural memory takes over; for example, lesions of the basal ganglia can lead to a reversion of dependence on knowledge that was initially learned in declarative memory (Packard, 2008). The learning context can also affect which system is relied on more. Explicit instruction (e.g., of sequences), or even just paying attention to the stimuli and underlying rules or patterns, can increase learning in declarative memory. Conversely, a lack of explicit instruction, as well as manipulations that reduce attention to the stimuli (e.g., in dual task paradigms), or a high level of complexity of rules or patterns (thus decreasing the subject's ability to explicitly detect patterns) may all shift learning toward procedural memory.

Many other factors likely also play roles affecting which system is relied on more. Any factor that enhances learning, retention, or retrieval preferentially in one of the memory systems should lead to an increased dependence on that system. Thus, the relative functionality of the two systems can affect which one is relied on more. For example, likely due in part to a female advantage at declarative memory (perhaps thanks to higher estrogen levels), females may rely more on this system, while males correspondingly rely more on procedural memory, for tasks that can be performed by either system (Ullman et al., 2008). And disorders that affect one system can lead to a compensatory role for the other. For example, individuals with Specific Language Impairment (SLI), dyslexia, autism, or obsessive-compulsive disorder, all of which have been associated with abnormalities of procedural memory but relatively intact declarative memory, appear to rely more on this intact system (Ullman & Pullman, 2015). Thus, multiple within- and

between-subject factors may modulate the relative dependence on the two systems.

Second, animal and human studies suggest that declarative and procedural memory also interact *competitively*, resulting in a “seesaw effect” (Ullman, 2004). The dysfunction of one system may lead not only to an increased dependence on the other system for those tasks and functions that can depend on either one, but *also* to the enhanced functioning of that system. Evidence for such a seesaw effect comes from both animal and human studies (Packard, 2008; Poldrack & Packard, 2003; Ullman, 2004). Additionally, estrogen may not only enhance declarative memory but also inhibit procedural memory. Note that the seesaw effect, and compensation due to redundancy, are distinct notions: if only one system is dysfunctional, then the other can compensate whether or not its functionality is enhanced—although, of course, any enhancement from the seesaw effect would bolster any such compensation.

Third, the learning and/or retrieval of knowledge in declarative memory may block (inhibit) the learning and/or retrieval of analogous knowledge in procedural memory (Ullman, 2004). The converse may hold as well. For example, even when a task is learned initially in declarative memory, it can be overridden by procedural memory when it is subsequently learned in that system (Packard, 2008).

The two memory systems are also linked to and interact with *other* neurocognitive brain systems. First, working memory seems to be closely related to (at least) declarative memory. For example, frontal brain structures involved in working memory also underlie declarative memory in both encoding and recall (Ullman, 2004). And deficits of working memory are associated with deficits of declarative memory (Lum, Ullman, & Conti-Ramsden, 2015; Ullman & Pullman, 2015). More generally, we suggest that working memory may constitute input and output mechanisms for at least explicit knowledge in declarative memory. Second, priming depends importantly on knowledge initially learned in the memory systems. For example, the priming of concepts and word forms seems to rely on representations learned in declarative memory, as suggested by the inability of dense amnesics to learn new information of this sort. Finally, as indicated above, there are links between the memory systems and the ventral and dorsal streams (Ullman, 2004). The ventral stream seems to be linked strongly to the declarative memory system. The dorsal stream may also interact with this system, with projections to parahippocampal cortex, which plays a role in representing landmarks. However, the dorsal stream may be particularly tied to procedural memory. While “what” knowledge seems to depend on a combination of the ventral stream

(for processing) and declarative memory (for learning), “how” knowledge may depend on a combination of the dorsal stream (for processing) and procedural memory (for learning). Indeed, learning supported by the basal ganglia may link inputs from parietal structures to motor regions (Ashby et al., 2010; Doyon et al., 2009). This posited interdependence between learning in the declarative and procedural memory systems and respective processing of this knowledge in the ventral and dorsal streams may be referred to as the *memory-processing interdependence hypothesis*.

76.2 PREDICTIONS FOR LANGUAGE

Here, I summarize some key predictions of the DP model—that is, predictions for language that are derived from our understanding of the two memory systems. For each memory system I first present predictions regarding *what* types of language-related knowledge and functions the system should underlie, and then *how* exactly these should be subserved by the system, with a focus on functional neuroanatomy.

Note that the DP model does *not* predict that the memory systems underlie language and other domains in identical ways—both because language is not identical to other domains and because portions of the systems may have become specialized for language (either evolutionarily or developmentally). Rather, because the co-optation hypothesis leads to the expectation that the systems play at least similar if not identical roles across domains, our substantial independent knowledge of the systems’ roles in other domains is an excellent starting point for making predictions about language. Empirical studies will reveal exactly where and how the systems’ roles in language might diverge from those in other domains.

76.2.1 Declarative Memory: Predictions for Language

76.2.1.1 What Should Declarative Memory Underlie in Language?

First, because declarative memory seems to be critical for learning, storing, and accessing arbitrary bits of information, as well as arbitrary associations among them, aspects of language that involve such bits or associations should critically depend on this memory system. Thus, declarative memory should be crucial for all learned idiosyncratic linguistic knowledge at the word or multi-word level (though presumably not for any such knowledge that may be purely innately specified, if such knowledge exists). Simple (i.e., not rule-governed and fully derivable) content words (e.g., *cat*,

devour), including their phonological forms, meanings, (sub)categorization knowledge (e.g., *devour* requires a complement), and mappings between them (e.g., sound-meaning mappings), should be learned in this system. Knowledge about irregular morphological forms, both inflectional and derivational (e.g., *dig-dug*, *solemn-solemnity*), should be stored in declarative memory, as should knowledge about idioms, proverbs, and so on. In principle, such stored knowledge could be represented in a variety of ways, even in parallel for the same forms in the same individuals, such as structured or unstructured, as wholes or as collocations with probabilistic associations between their parts, or even as stored links to rules as suggested by Distributed Morphology (Halle & Marantz, 1993). Storing representations in declarative memory does not preclude the additional involvement of rule-governed aspects of procedural memory, for example, for inflecting forms within larger stored sequences (e.g., *jumps the gun*). Finally, in addition to these types of idiosyncratic language knowledge, which correspond broadly to traditional notions of semantic memory (world knowledge not bound to a particular personal experience), declarative memory should also underlie aspects of episodic knowledge in language—for example, memories regarding whether and in which context one has recently encountered or learned a particular word.

Second, due to its ability to learn a wide range of information, declarative memory should be able to acquire much more than idiosyncratic knowledge. Indeed, there may be few constraints on the types of linguistic knowledge that this system can learn. At the least, all the types of information that it can learn about idiosyncratic aspects of language should also be learnable for nonidiosyncratic, rule-governed aspects. Thus, just like simple and irregular words, one should be able to store fully rule-governed complex forms (e.g., “*walked*,” “*the cat*,” and even longer sequences). More abstract representations could also be stored, such as portions of linguistic hierarchies (e.g., Noun Phrase), as has been posited by linguistic theories such as Tree-Adjoining Grammar (Joshi & Rambow, 2003). More productive aspects of grammar may also be achieved by relying on declarative memory, for example, by generalizing across already-stored representations to new representations (e.g., analogic generalization across similar forms) (Hartshorne & Ullman, 2006) or by “shallow” parsing of sentences (Clahsen & Felser, 2006), which relies on lexical-semantic knowledge (which is learned in declarative memory). Grammatical rules and constraints themselves should also be learnable by declarative memory, either explicitly or implicitly, even though these are generally acquired by procedural memory. Other types of

linguistic knowledge or functions normally learned in procedural memory should also be learnable in declarative memory, such as word segmentation. However, just because such grammatical and other knowledge *can* be learned by declarative memory does not mean it is, or if it is learned, that it is consistently used; rather, this will depend on factors that modulate the relative dependence on declarative and procedural memory and the interactions between them (e.g., blocking).

As we have seen, the brain structures underlying declarative memory, including the MTL, underlie not only learning and long-term memory but also other cognitive processes, including object recognition, spatial recognition, novelty detection, short-term memory, and prediction. Analogous roles for such functions may thus be found in language. Additionally, given the rapidity with which new associations can be learned in this memory system, we might expect it to play an active role in online processes involving integration and binding in language.

76.2.1.2 How Should Declarative Memory Underlie Language?

Based on our independent knowledge of declarative memory, we can make numerous specific neurobiological and other predictions about those aspects of language that should depend on declarative memory. Here, I summarize some of them. First, the functional neuroanatomy of those aspects of language that are learned, stored, and processed by declarative memory should reflect the functional neuroanatomy of this system. Thus, linguistic knowledge learned in this system should depend on the hippocampus and/or other MTL structures, at least during learning and consolidation. The hippocampus itself may be heavily engaged in language-related learning, given the multiple types of information and modalities involved in this domain and the importance of linking and integrating this information. Individual items such as words, however, might rely particularly on perirhinal cortex. Novel linguistic items or relations should involve the MTL, perhaps especially the hippocampus (novel associations) and perirhinal cortex (novel items). These structures should be active mainly during learning, but perhaps also for storage and use. MTL structures may also play roles in language-related short-term memory and prediction. Other structures linked to MTL, such as the fornix and mammillary bodies, may also play learning roles in language.

With time and/or experience, the MTL should play a decreasingly important role for linguistic knowledge learned in declarative memory, with an increasing role for neocortical structures. Linguistic knowledge

should show similar neuroanatomical patterns as non-linguistic knowledge of the same concepts. For example, words, phrases, or sentences referring to living or nonliving things, or with strong visual attributes of particular sorts (e.g., color, form), should involve neocortical regions independently linked to these features. More complex, higher-level linguistic representations may depend on more anterior temporal lobe regions, and perhaps also on MTL structures, particularly the hippocampus. For example, abstract linguistic categories such as Noun or Verb might depend on anterior temporal or even more upstream areas. Inferior frontal cortex, especially BA 45/47, should underlie the encoding of new linguistic information being learned in declarative memory, as well as the recall of that knowledge once it is learned. Posterior parietal cortex may also play a role in the encoding and retrieval of this information.

Linguistic knowledge should be rapidly learnable in declarative memory, even from a single presentation of the information, although repeated exposures should improve learning and retention. Thus, we expect that words can be quickly acquired. Linguistic knowledge in declarative memory could be either explicit (e.g., verbalizable word or rules) or implicit. Conversely, however, if linguistic knowledge is explicit, then it must be stored in declarative memory, because this is the only long-term memory system to underlie explicit knowledge. Once learned in this system, linguistic knowledge can be used flexibly across different contexts.

Finally, molecular and other factors that modulate declarative memory should play analogous roles in language. For example, polymorphisms of BDNF and APOE should modulate declarative memory-dependent aspects of language in a similar manner as for nonlinguistic knowledge, and likewise for estrogen and acetylcholine. For example, higher levels of estrogen may improve language learning in this system. Based on the available evidence, it seems likely that language learning in declarative memory should ameliorate during childhood, plateau in adolescence/early adulthood, and then decline. Thus, word learning should follow this pattern. Females may show advantages at language learning in this system as compared to males. Sleep, exercise, and other factors should improve language learning and retention in declarative memory.

76.2.2 Procedural Memory: Predictions for Language

It is important to emphasize that we know less about this system than about declarative memory; therefore, our predictions are more tentative and less specific.

76.2.2.1 What Should Procedural Memory Underlie in Language?

Procedural memory should underlie the learning and processing of sequences and rules in language, perhaps especially those that are probabilistic rather than deterministic. The system may be particularly important in “learning to predict” in language, such as predicting the next item in a sequence or the output of a linguistic rule. Only rules or sequences that are implicit should be learned by procedural memory (I emphasize that implicit procedural knowledge of a rule or sequence does not preclude either explicit or implicit analogous knowledge in declarative memory). Given that grammar involves largely implicit rules, both probabilistic and deterministic, particularly ones that involve (hierarchical) sequencing, procedural memory should play a major role in this aspect of language. This should hold across linguistic subdomains, including syntax, morphology, and phonology. Exactly what computational roles procedural memory should play in linguistic sequencing and rules cannot be clearly predicted at this point because of our lack of understanding of these issues regarding procedural memory itself. However, also based on our understanding of grammar, it seems likely that procedural memory somehow underlies the learning of rules and the implicit rule-governed composition of both hierarchical and nonhierarchical sequences.

Other aspects of language may also be learned in procedural memory, including categories and other knowledge, especially if the knowledge is implicit and involves probabilistic patterns, sequences, and learning to predict. For example, the implicit learning of word boundaries in a speech stream (Saffran, Aslin, & Newport, 1996) should depend on procedural memory.

76.2.2.2 How Should Procedural Memory Underlie Language?

As with declarative memory, predictions for language follow from what we know about procedural memory from animal and human studies. First, linguistic skills and knowledge that are learned, stored, and processed by procedural memory should reflect this system’s underlying functional neuroanatomy. Thus, these should involve frontal and basal ganglia structures, and perhaps the cerebellum. Learning and consolidation should engage the basal ganglia, especially the caudate nucleus and the anterior putamen. (Note that this learning role of the basal ganglia does not preclude other language roles for this set of subcortical structures, including grammar, because the structures subserve other functions as well, including working memory and attention.) Once automatized,

knowledge and skills should rely especially on neocortical regions, particularly BA 6 and BA 44. Only implicit, not explicit, linguistic knowledge should rely on procedural memory (although of course not all implicit knowledge should depend on this system). Because procedural memory learns only with repeated exposure, this knowledge should be learned and automatized gradually.

Given its role in procedural memory, dopamine should play a role in grammar and other aspects of language, especially in learning and consolidation. Certain genes, such as *FOXP2*, *PPP1R1B*, and *DRD2*, should also be involved. Because procedural memory learns gradually and declarative memory learns rapidly, grammar rules should generally be acquired more slowly than words. Given the developmental trajectory of procedural memory, linguistic learning and consolidation in this system should be better in childhood than adolescence or adulthood, and thus proceduralization of grammar should be slower and more incomplete in later (e.g., second language) learners. Sleep, exercise, and other factors should improve language learning and retention in procedural memory.

76.2.3 Interactions Between the Memory Systems: Predictions for Language

Our understanding of interactions between the two memory systems, and between these and other systems, also leads to various predictions for language.

First, to some extent, we expect the two memory systems to acquire the same or analogous knowledge or skills, that is, to play at least partly redundant roles. According to the redundancy hypothesis, in language as in nonlinguistic domains, such redundancy may be found for any tasks or functions that could be subserved by either system. Given the learning power of declarative memory, and the fact that it can underlie implicit as well as explicit knowledge, it may be able to at least partly support most if not all aspects of language subserved by procedural memory, including grammar and word segmentation.

Various factors should modulate which memory system is relied on more for linguistic knowledge that can be learned by both systems. Such knowledge should often be learned first by declarative memory, but eventually by procedural memory, at which point it should be more automatized. Thus, both first and second language learners should generally depend initially on declarative memory for grammatical functions (e.g., by chunking or explicit rules, with the exact nature of this dependence perhaps differing between first and second language learners), but both should gradually learn grammar in procedural memory.

(For more on the DP model and second language, see Ullman, 2005; Ullman, 2015). After such proceduralization, the declarative knowledge may still remain intact and could become accessible again in certain circumstances, such as subsequent procedural memory dysfunction. Explicit instruction or attention to the input may increase learning in declarative memory, whereas a lack of such instruction or attention, or greater complexity of rules or patterns (e.g., more complex grammatical rules or constraints), may lead to a greater dependence on procedural memory. Estrogen may promote linguistic learning in declarative memory at the expense of procedural memory. Females may rely more on declarative memory than males for aspects of language (e.g., grammar) that can rely on either system, and they may show superior learning of idiosyncratic linguistic knowledge (which must be learned in declarative memory). The developmental trajectories of the two systems suggest that young children should more easily proceduralize their grammar (in first or second language) than adults. And a relative dysfunction of one system should lead to a greater (compensatory) dependence of language on the other.

Second, we might expect a seesaw effect in language. Estrogen might not only promote language learning or use in declarative memory but may also inhibit it in procedural memory. Similarly, a dysfunction of one system might lead not only to language compensation by the other but also to its enhanced functioning.

Third, learning or processing in one system may block or inhibit the other. For example, grammar learning in declarative memory may inhibit grammar learning in procedural memory. And successful retrieval of irregular forms (e.g., *dug*), or chunked rule-governed forms (*walked*), should block the rule-based computation of corresponding forms in procedural memory (*dig* + *-ed*, *walk* + *-ed*). Conversely, a highly automatized rule in procedural memory should tend to override the use of analogous declarative knowledge, especially if this declarative knowledge is not well-learned. Thus, over the course of language learning, grammar should depend increasingly on procedural memory and correspondingly less on declarative memory.

Finally, the two memory systems should interact with other neurocognitive brain systems in the learning and processing of language. First, working memory in language processing should be closely related to declarative memory. For example, some of the same frontal structures should play roles in verbal working memory and in the encoding and recall of language knowledge learned in declarative memory. Second, linguistic knowledge that can be primed (e.g., lexical or grammatical knowledge) should, in most cases, have been learned by one or the other memory system.

Finally, there should be close links between language learning in the two memory systems and language processing in the dorsal and ventral streams. For example, language knowledge processed in the ventral stream should be learned mainly in declarative memory, which in turn should facilitate further processing of this knowledge in the ventral stream, while a similar relation may hold for procedural memory and the dorsal stream.

76.3 EVIDENCE

Parallel to the predictions presented above, for each memory system I summarize first, evidence regarding *what* types of language knowledge and functions depend on it, and second, *how* the system subserves these, with a focus on functional neuroanatomy.

76.3.1 Declarative Memory in Language: Evidence

76.3.1.1 What Does Declarative Memory Underlie in Language?

Evidence from various methodological approaches, including behavioral, neurological, neuroimaging, and electrophysiological studies, has implicated declarative memory in the learning, storage, and retrieval of idiosyncratic aspects of language. First, behavioral evidence indicates that words can be learned very quickly (fast mapping) and are generally acquired earlier than grammatical rules (in both first and second language) (Bloom, 2000; Marcus et al., 1992; Ullman, 2015). More direct behavioral evidence comes from studies of children that reveal correlations, across participants, between vocabulary abilities and learning abilities in declarative memory (but not procedural memory), whereas grammar shows the opposite pattern (Kidd, 2012a; Lum, Conti-Ramsden, Page, & Ullman, 2012). Behavioral studies using other techniques, such as the examination of frequency and imageability effects, have also revealed links between lexical and declarative memory (Babcock, Stowe, Maloof, Brovotto, & Ullman, 2012; Prado & Ullman, 2009). Second, neurological evidence shows that dense amnesia from substantial MTL lesions seems to preclude word learning, as demonstrated in H.M. and other patients (Davis & Gaskell, 2009; Postle & Corkin, 1998). In contrast, H.M. retained idiosyncratic word forms that were common in English prior to his surgery, as expected if the MTL does not remain crucial for knowledge well after it has been learned (Kensinger, Ullman, Locascio, & Corkin, 1999). Third, functional neuroimaging evidence strongly implicates the MTL in word learning

(Breitenstein et al., 2005; Davis & Gaskell, 2009; Raboyeau, Marcotte, Adrover-Roig, & Ansaldo, 2010). Fourth, the presentation of words, including novel words (pseudowords), reliably leads to N400 event-related potentials (ERPs) (Kutas & Federmeier, 2011), which have independently been tied to nonlinguistic idiosyncratic knowledge (e.g., faces and objects) and the MTL (Kutas & Federmeier, 2011; McCarthy, Nobre, Bentin, & Spencer, 1995; Meyer et al., 2005).

Declarative memory has also been tied to nonidiosyncratic aspects of language. First, behavioral evidence suggests that regular morphological forms can be stored (e.g., as chunks), generalized across similar forms, or computed from explicit rules, all indicating a reliance on declarative memory. For example, like irregulars, regular inflected forms can show frequency, imageability, and phonological neighborhood effects (Alegre & Gordon, 1999; Babcock et al., 2012; Dye, Walenski, Prado, Mostofsky, & Ullman, 2013; Hartshorne & Ullman, 2006; Prado & Ullman, 2009; Ullman et al., under revision). However, whereas these effects are found reliably for irregulars, consistent with their obligatory storage in declarative memory, regulars show them inconsistently, and mainly for those conditions where a dependence on declarative memory is expected (e.g., higher frequency forms, females, left-handers, second language learners). Evidence suggests that even more complex rule-governed forms, that is, surface syntactic structures, can also be learned in declarative memory (Hamrick, 2014). And a recent study found that learning an “analogic grammar” (posited to involve generalization over stored forms) correlated with abilities at declarative but not procedural memory, whereas learning a rule-governed concatenative grammar showed the opposite pattern (Wong et al., 2013). However, as would be expected given faster learning by declarative than procedural memory, syntactic processing at early stages of learning a rule-governed artificial language correlated with declarative (and not procedural) memory, whereas the reverse pattern was found at later stages (Morgan-Short, Faretta-Stutenberg, Brill-Schuetz, Carpenter, & Wong, 2014). Second, neurological evidence from SLI, dyslexia, autism, and agrammatic aphasia suggests that individuals with these disorders compensate for grammatical impairments by relying on declarative memory, via chunking, explicit rules, or other means (Ullman & Pullman, 2015). Third, neuroimaging studies of artificial grammar learning have found MTL activation (Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Yang & Li, 2012). And neuroimaging evidence has implicated the MTL in online sentence integration and processing, including of syntax (Duff & Brown-Schmidt, 2012; Meyer et al., 2005). Fourth,

electrophysiological evidence from ERPs has found that (morpho)syntactic processing can elicit N400s, primarily in those conditions where a dependence on declarative memory is expected (e.g., females, second language learners, and individuals with SLI, dyslexia, or agrammatic aphasia) (Ullman, 2015; Ullman et al., 2008; Ullman & Pullman, 2015).

76.3.1.2 How Does Declarative Memory Underlie Language?

Thus, significant language knowledge is learned and even processed in the MTL. But which portions of the MTL are involved and in which circumstances? First, the hippocampus is heavily implicated. Multiple neuroimaging studies of word learning report hippocampal activation (Breitenstein et al., 2005; Davis & Gaskell, 2009), as has a study of chunking in artificial grammar learning (Lieberman et al., 2004). Similarly, the hippocampus has been implicated in the integration of linguistic knowledge (Duff & Brown-Schmidt, 2012; Meyer et al., 2005).

However, other MTL structures also play roles in language. Although lesions restricted to the hippocampus can impair word learning, at least some such patients can still learn words (Davis & Gaskell, 2009; Vargha-Khadem, Gadian, & Mishkin, 2001). It may be that MTL lesions that extend beyond the hippocampus, such as H.M.’s, are required to eliminate word learning altogether. Some evidence suggests that rhinal cortex, in particular perirhinal cortex, may be important for words, perhaps especially for word learning. One study found that remembering the context in which a word was recently presented engaged the hippocampus, whereas the word itself activated perirhinal cortex (Davachi, Mitchell, & Wagner, 2003). In the MTL, N400s have been tied mainly to perirhinal cortex, particularly for novel words (Fernandez, Klaver, Fell, Grunwald, & Elger, 2002). In one study, lexical/semantic violations that typically elicit N400s were tied to rhinal cortex, whereas syntactic violations were linked to the hippocampus, likely due to P600 effects that involve controlled (conscious) syntactic integration (Meyer et al., 2005).

Other structures in the declarative memory system also play roles in language. One study found deficits in word learning after lesions to the mammillary bodies (Martins, Guillery-Girard, Jambaque, Dulac, & Eustache, 2006). Linguistic as well as nonlinguistic stimuli associated with particular concepts engage neocortical regions linked to those concepts (e.g., living things) (Martin, 2007). BA 45/47 is involved in word encoding and recall. For example, word encoding and recall tasks activate this region, and lesions to this area are associated with word recall deficits (Buckner,

Wheeler, & Sheridan, 2001; Wagner et al., 1998). Posterior parietal cortex has been found to correlate with vocabulary size in monolinguals (Lee et al., 2007) and to be larger in bilinguals than in monolinguals (possibly due to the larger total vocabulary of the former) (Mechelli et al., 2004), and it has been implicated in lexical/semantics in both first and second language (Abutalebi et al., 2012; Chee, Hon, Lee, & Soon, 2001) as well as in grammar in second (but not first) language (Wartenburger et al., 2003). For a functional neuroanatomical meta-analysis of first and second language revealing such a pattern, see Tagarelli, Turkeltaub, Grey, and Ullman (in preparation).

There has also been some work on the genetic and molecular bases of linguistic aspects of declarative memory. Quite a few studies have implicated BDNF and APOE, as well as estrogen and acetylcholine, in episodic memory tasks involving words (Ullman, 2007; Ullman et al., 2008). For example, performance at such tasks improves with cholinesterase inhibitors (Freo, Pizzolato, Dam, Ori, & Battistin, 2002). And estrogen has been found to improve retrieval of irregular (but not regular) inflected forms (Estabrooke, Mordecai, Maki, & Ullman, 2002). More research is needed to examine links between language and the genetic and molecular bases of declarative memory.

Finally, evidence suggests that females may be better than males at learning words (Kaushanskaya, Marian, & Yoo, 2011; Ullman et al., 2008), and likewise left-handers as compared with right-handers (Ullman et al., under revision). And, consistent with the developmental trajectory of declarative memory, word learning improves during childhood into adolescence (Bloom, 2000).

76.3.2 Procedural Memory in Language: Evidence

Consistent with our more impoverished understanding of procedural than declarative memory, there is less empirical evidence thus far regarding the role of this system in language.

76.3.2.1 What Does Procedural Memory Underlie in Language?

Evidence from various methodologies suggests links between grammar and procedural memory. First, behavioral evidence has revealed correlations between grammar measures (e.g., syntactic priming and processing) and learning in procedural memory, but not with declarative memory in the same individuals (Kidd, 2012b; Lum et al., 2012). Procedural (but not declarative) memory has also been found to correlate with

learning a rule-governed concatenative grammar (Wong et al., 2013). In another artificial language study, syntactic processing correlated with procedural (and not declarative) memory, but only at later stages of learning (Morgan-Short et al., 2014). In an interference study, syntactic (but not word) processing interfered with procedural memory (Nemeth et al., 2011). And, as mentioned above, regular morphological forms generally do not show signs of reliance on declarative memory; rather they show evidence for composition, consistent with a primary dependence on procedural memory (Walenski, Prado, Ozawa, Steinhauer, & Ullman, under revision).

Second, neurological evidence has tied grammar to procedural memory. (Here, I focus on SLI; for other disorders, including agrammatic aphasia and Parkinson's and Huntington's diseases, see Ullman, 2004, 2013). Children with SLI, who typically have grammatical deficits (of syntax, morphology, and phonology) but less consistent lexical impairments, show reliable procedural memory impairments (Lum, Conti-Ramsden, Morgan, & Ullman, 2014; Ullman & Pierpont, 2005) and consistent brain abnormalities only in frontal cortex and the basal ganglia, as revealed by a recent neuroanatomical meta-analysis (Ullman et al., under review). Moreover, the grammar difficulties in SLI have been directly linked to procedural memory deficits (Hedenius et al., 2011).

Third, neuroimaging evidence has tied artificial grammar learning to the basal ganglia (Lieberman et al., 2004; Petersson, Folia, & Hagoort, 2012; Yang & Li, 2012). Basal ganglia activation is also reliably elicited by grammatical (but not lexical) processing in second language learners, but not in native speakers, as revealed by our recent neuroanatomical meta-analysis of first and second language (Tagarelli et al., in preparation). This is consistent with the prediction that the basal ganglia play a particularly important role in grammar acquisition.

Finally, some research has begun to examine links between procedural memory and nongrammatical implicit aspects of language. For example, a recent fMRI study implicated the basal ganglia in the implicit learning of word boundaries in a speech stream (Karuza et al., 2013).

76.3.2.2 How Does Procedural Memory Underlie Language?

Although evidence is still limited, some specific neurobiological patterns appear to be emerging regarding the role of procedural memory in language. First, within the basal ganglia, the caudate nucleus, and perhaps the caudate head in particular, may play a particularly important role in grammar learning. These structures have been implicated in neuroimaging

studies of artificial grammar learning and of grammar in second (but not first) language (Tagarelli et al., in preparation). And our neuroanatomical meta-analysis of brain abnormalities in SLI revealed that the consistent structural abnormalities in the basal ganglia occur only in the caudate nucleus, with particular involvement of the caudate head (Ullman et al., under review).

Once learned, grammar depends heavily on BA 44, as well as BA 6 (especially the frontal operculum), particularly on the left side. Activation in these regions is strongly associated with syntactic processing in both first and second language (Friederici, 2006; Tagarelli et al., in preparation). And a recent functional neuroimaging meta-analysis of regular and irregular morphology strongly implicates BA 44 in the former but not the latter (Ullman, Campbell, McQuaid, Tagarelli, & Turkeltaub, in preparation).

There has been far less work to date examining links between nongrammatical aspects of language and procedural memory. Nevertheless, as mentioned above, one recent study of the implicit learning of word segmentation reported basal ganglia activation (Karuza et al., 2013)—indeed, mainly in the caudate head and anterior putamen.

Genetic evidence has also tied language to procedural memory. The *FOXP2* gene has been linked to grammar, including syntax, morphology, and phonology, as well as to procedural memory (Ullman & Gopnik, 1999; Ullman & Pierpont, 2005). Moreover, the recent finding that humanized *Foxp2* speeds up learning by promoting the transition from declarative to procedural memory (Schreiweis et al., 2014) suggests that evolutionary changes to procedural memory may be critical for the evolution of language, particularly of grammar. This underscores the utility of the co-optation hypothesis by showing that investigating preexisting systems, and these memory systems in particular, can reveal not only how they work similarly in language as in nonlanguage functions, but also how they might become further specialized for language itself. In other words, the systems constitute *targets* for studying the potential evolutionary changes that may facilitate language (whether or not those changes were due to adaptation for language alone). Finally, *DRD2* (for the dopamine receptor D₂) has also been linked to grammar learning, as well as to basal ganglia activation during the learning of a rule-governed concatenative grammar (Wong et al., 2013).

Some research has also examined the effect on language of subject-level factors that modulate procedural memory. For example, as would be expected if learning and/or consolidating in procedural memory becomes more difficult between early childhood and adulthood, adult second language learners have particular difficulty with grammar (Ullman, 2005).

76.3.3 Interactions Between the Memory Systems in Language: Evidence

First, evidence from multiple methodologies suggests that declarative and procedural memory play redundant roles for grammar, but not for lexical/semantics, which seems to require declarative memory. Much of the evidence for such redundancy has been discussed above. In brief, rule-governed compositional forms can be not only learned and computed by procedural memory but also stored and processed by declarative memory, via chunking, analogical generalization in associative memory, composition by explicit rules, and other processes. This dependence on declarative memory seems to be modulated by various factors. It occurs more for higher than lower frequency or imageability items; more for second than for first language learners; more for early versus later stages of learning (at least in second language; it remains unclear whether this predicted pattern is also found in first language); more for females than for males; more for left-handers than for right-handers; and more in disorders associated with a procedural memory system dysfunction but relatively intact declarative memory (e.g., SLI, dyslexia, autism, agrammatic aphasia).

Second, some evidence, though still limited, supports the predicted seesaw effect in language. Thus far, the only evidence we are aware of, which is somewhat indirect, is findings from neurodevelopmental disorders. Children with dyslexia or autism, both of which are linked to grammatical and procedural memory abnormalities (Lum, Ullman, & Conti-Ramsden, 2013; Walenski, Tager-Flusberg, & Ullman, 2006), may also show enhanced lexical or declarative memory abilities (Hedenius, Ullman, Alm, Jennische, & Persson, 2013; Ullman & Pullman, 2015; Walenski, Mostofsky, Gidley-Larson, & Ullman, 2008). Similarly, children with SLI may show not only grammatical and procedural memory deficits but also enhanced declarative memory, in particular at consolidation (Lukacs, Kemeny, Lum, & Ullman, in preparation; Lum, Hedenius, Tomblin, & Ullman, in preparation).

Third, some evidence suggests linguistic inhibition by one or the other system. Perhaps the best studied phenomenon is blocking. For example, the retrieval of a stored irregular form blocks the computation of its corresponding overregularization (e.g., retrieving *dug* blocks *digged*), whereas retrieval difficulties due to lexical/declarative memory deficits yield overregularizations (Ullman, 2004, 2013). Similarly, retrieval of a chunked regular may at least partially block the rule-based computation of the same form (Prado & Ullman, 2009). Inhibition between the systems has also been observed in learning. In a recent study of second language learning, explicit training (which should encourage learning in declarative

memory) delayed the development of automatic syntactic processing that has been associated with procedural memory (Morgan-Short, Finger, Grey, & Ullman, 2012; Morgan-Short, Steinhauer, Sanz, & Ullman, 2012). Conversely, even when an N400 is found for grammar at early stages of second language learning, the later emergence of automatic syntactic processing overrides this lexical/semantic process (Morgan-Short, Finger, et al., 2012; Morgan-Short, Steinhauer, et al., 2012).

Finally, some evidence exists regarding language-related interactions between the two memory systems and other neurocognitive systems. For example, BA 45/47 seems to be involved not only in word encoding and word recall but also in verbal working memory. And words that entered the language after H.M.'s resection do not show priming, whereas amnesic patients do show priming both for previously learned words and for syntax (Ferreira, Bock, Wilson, & Cohen, 2008; Postle & Corkin, 1998).

76.4 SUMMARY AND CONCLUSION

The DP model is premised on three principles of biology and language. First, new biological functions commonly recruit pre-existing biological mechanisms, whether or not those mechanisms then become further specialized—either evolutionarily or developmentally—for the functions. That is, biological mechanisms are often co-opted for new purposes. Second, most of language must be learned, whether or not aspects of this capacity are innately specified. Third, declarative memory and procedural memory are perhaps the two most important learning and memory systems in the brain, in terms of the range of domains and functions that they subserve. Based on these principles, the DP model simply posits that these two memory systems are highly likely to play important roles in language learning, knowledge, and use.

If language depends heavily on the two memory systems, then what we know independently about these memory systems should tend to apply to language as well. That is, the memory systems should play similar roles in language as in nonlanguage functions, and thus our independent knowledge of how these memory systems work should generate predictions for language. Because the memory systems are quite well-understood at many levels, from work with both humans and animal models, the theory can generate a wide range of well-motivated specific predictions, many of which there would be no reason to make based on the more limited study of language. For example, we can make predictions about MTL, or perirhinal cortex, or certain genes, or estrogen, or sex

differences, or age effects in first versus second language, that there might be no *independent* reason to make based on the study of language alone. Thus, this is a very powerful theoretical approach.

As we have seen, converging evidence from multiple methodologies provides support for many of the general as well as specific predictions of the theory. The findings suggest that language does indeed depend on the two memory systems. More generally, the results yield insights that advance our understanding of language and its underlying neurobiology. Importantly, unlike language-specific accounts, the theory can predict and explain aspects of linguistic and neurolinguistic phenomena in the broader context of our understanding of the brain and mind. Thus, the theory has substantial explanatory power.

Finally, many of the predictions I have summarized in this chapter have not yet been tested. In fact, additional predictions have not even been discussed. For example, the theory predicts that behavioral or pharmacological interventions that have been shown to enhance learning or processing in the memory systems are likely to also enhance the learning or processing of language. This prediction may have important educational and translational/clinical outcomes, in particular for second language learning and language disorders. Thus, the theoretical approach presented here promises to continue to be fruitful and to lead to advances in multiple aspects of language and its underlying neurobiology.

Acknowledgments

I thank Goldie Ann McQuaid, Jarrett Lovelett, Kaitlyn Tagarelli, Scott Miles, and Başak Karatas for input on this chapter.

References

- Abutalebi, J., Della Rosa, P. A., Green, D. W., Hernandez, M., Scifo, P., Keim, R., et al. (2012). Bilingualism tunes the anterior cingulate cortex for conflict monitoring. *Cerebral Cortex*, *22*(9), 2076–2086.
- Adi-Japha, E., Badir, R., Dorfberger, S., & Karni, A. (2014). A matter of time: Rapid motor memory stabilization in childhood. *Developmental Science*, *17*(3), 424–433.
- Alegre, M., & Gordon, P. (1999). Frequency effects and the representational status of regular inflections. *Journal of Memory and Language*, *40*(1), 41–61.
- Ashby, F. G., Turner, B. O., & Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity. *Trends in Cognitive Sciences*, *14*(5), 208–215.
- Babcock, L., Stowe, J. C., Maloof, C. J., Brovotto, C., & Ullman, M. T. (2012). The storage and composition of inflected forms in adult-learned second language: A study of the influence of length of residence, age of arrival, sex, and other factors. *Bilingualism: Language and Cognition*, *15*(4), 820–840.
- Barens, M. D., Groen, I. I. A., Lee, A. C. H., Yeung, L. K., Brady, S. M., Gregori, M., et al. (2012). Intact memory for irrelevant information impairs perception in amnesia. *Neuron*, *75*(1), 157–167. Available from: <http://dx.doi.org/10.1016/j.neuron.2012.05.014>.

- Bloom, P. (2000). *How children learn the meanings of words*. Cambridge, MA: The MIT Press.
- Bornkessel-Schlesewsky, I., & Schlewsky, M. (2013). Reconciling time, space and function: A new dorsal-ventral stream model of sentence comprehension. *Brain and Language*, 125(1), 60–76.
- Breitenstein, C., Jansen, A., Deppe, M., Foerster, A.-F., Sommer, J., Wolbers, T., et al. (2005). Hippocampus activity differentiates good from poor learners of a novel lexicon. *NeuroImage*, 25(3), 958–968.
- Brown, M. W., Warburton, E. C., & Aggleton, J. P. (2010). Recognition memory: Material, processes, and substrates. *Hippocampus*, 20(11), 1228–1244.
- Buckner, R. L., Wheeler, M. E., & Sheridan, M. A. (2001). Encoding processes during retrieval tasks. *Journal of Cognitive Neuroscience*, 13(3), 406–415.
- Bussey, T. J., & Saksida, L. M. (2007). Memory, perception, and the ventral visual-perirhinal-hippocampal stream: Thinking outside of the boxes. *Hippocampus*, 17(9), 898–908. Available from: <http://dx.doi.org/10.1002/Hipo.20320>.
- Cabeza, R., & Moscovitch, M. (2013). Memory systems, processing modes, and components: Functional neuroimaging evidence. *Perspectives on Psychological Science*, 8(1), 49–55. Available from: <http://dx.doi.org/10.1177/1745691612469033>.
- Caplan, D., & Waters, G. S. (1999). Verbal working memory and sentence comprehension. *Behavioral and Brain Sciences*, 22(1), 77–126.
- Chee, M. W., Hon, N., Lee, H. L., & Soon, C. S. (2001). Relative language proficiency modulates BOLD signal change when bilinguals perform semantic judgments. *NeuroImage*, 13(6), 1155–1163.
- Chun, M. M. (2000). Contextual cueing of visual attention. *Trends in Cognitive Sciences*, 4(5), 170–178.
- Clahsen, H., & Felser, C. (2006). Grammatical processing in language learners. *Applied Psycholinguistics*, 27(1), 3–42.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, 100(4), 2157–2162.
- Davis, M. H., & Gaskell, M. G. (2009). A complementary systems account of word learning: Neural and behavioural evidence. *Philosophical Transactions of the Royal Society of London*, 364(1536), 3773–3800.
- Doyon, J., Bellec, P., Amsel, R., Penhune, V. B., Monchi, O., Carrier, J., et al. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research*, 199, 61–75.
- Duff, M. C., & Brown-Schmidt, S. (2012). The hippocampus and the flexible use and processing of language. *Frontiers in Human Neuroscience*, 6, 69.
- Dye, C. D., Walenski, M., Prado, E. L., Mostofsky, S. H., & Ullman, M. T. (2013). Children's computation of complex linguistic forms: A study of frequency and imageability effects. *Public Library of Science ONE*, 8, e74683.
- Eichenbaum, H. (2012). *The cognitive neuroscience of memory: An introduction* (2nd ed.). Oxford: Oxford University Press.
- Eichenbaum, H., & Cohen, N. J. (2001). *From conditioning to conscious recollection: Memory systems of the brain*. New York, NY: Oxford University Press.
- Eichenbaum, H., & Fortin, N. J. (2009). The neurobiology of memory based predictions. *Philosophical Transactions of the Royal Society of London*, 364(1521), 1183–1191.
- Eichenbaum, H., & Lipton, P. A. (2008). Towards a functional organization of the medial temporal lobe memory system: Role of the parahippocampal and medial entorhinal cortical areas. *Hippocampus*, 18(12), 1314–1324.
- Eichenbaum, H., Sauvage, M., Fortin, N., Komorowski, R., & Lipton, P. (2012). Towards a functional organization of episodic memory in the medial temporal lobe. *Neuroscience and Biobehavioral Reviews*, 36(7), 1597–1608. Available from: <http://dx.doi.org/10.1016/j.neubiorev.2011.07.006>.
- Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., et al. (2011). Exercise training increases size of hippocampus and improves memory. *Proceedings of the National Academy of Sciences of the United States of America*, 108(7), 3017–3022.
- Estabrooke, I. V., Mordecai, K., Maki, P. M., & Ullman, M. (2002). The effect of sex hormones on language processing. *Brain and Language*, 83, 143–146.
- Fernandez, G., Klaver, P., Fell, J., Grunwald, T., & Elger, C. E. (2002). Human declarative memory formation: Segregating rhinal and hippocampal contributions. *Hippocampus*, 12(4), 514–519. Available from: <http://dx.doi.org/10.1002/Hipo.10050>.
- Ferreira, V. S., Bock, K., Wilson, M. P., & Cohen, N. J. (2008). Memory for syntax despite amnesia. *Psychological Science*, 19(9), 940–946.
- Freo, U., Pizzolato, G., Dam, M., Ori, C., & Battistin, L. (2002). A short review of cognitive and functional neuroimaging studies of cholinergic drugs: Implications for therapeutic potentials. *Journal of Neural Transmission*, 109(5–6), 857–870.
- Friederici, A. D. (2006). Broca's area and the ventral premotor cortex in language: Functional differentiation and specificity. *Cortex*, 42(4), 472–475.
- Gould, S. J., & Vrba, E. S. (1982). Exaptation—A missing term in the science of form. *Paleobiology*, 8(1), 4–15.
- Green, A. E., & Dunbar, K. N. (2012). Mental function as genetic expression: Emerging insights from cognitive neurogenetics. In K. J. Holyoak, & R. G. Morrison (Eds.), *The Oxford handbook of thinking and reasoning* (pp. 90–111). Oxford: Oxford University Press.
- Halle, M., & Marantz, A. (1993). Distributed morphology and the pieces of inflection. In K. Hale, & S. J. Keyser (Eds.), *The view from building 20*. Cambridge, MA: MIT Press.
- Hamrick, P. (2014). Recognition memory for novel syntactic structures. *Canadian Journal of Experimental Psychology*, 68(1), 2–7.
- Hartshorne, J. K., & Ullman, M. T. (2006). Why girls say “holded” more than boys. *Developmental Science*, 9(1), 21–32.
- Hedenius, M., Persson, J., Tremblay, A., Adi-Japha, E., Verissimo, J., Dye, C. D., et al. (2011). Grammar predicts procedural learning and consolidation deficits in children with specific language impairment. *Research in Developmental Disabilities*, 32(6), 2362–2375.
- Hedenius, M., Ullman, M. T., Alm, P., Jennische, M., & Persson, J. (2013). Enhanced recognition memory after incidental encoding in children with developmental dyslexia. *Public Library of Science ONE*, 8(5), e63998.
- Henke, K. (2010). A model for memory systems based on processing modes rather than consciousness. *Nature Reviews Neuroscience*, 11, 523–532.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393–402.
- Joshi, A., & Rambow, O. (2003). A formalism for dependency grammar based on tree adjoining grammar. Meaning Text Theory Conference, Paris.
- Just, M. A., & Carpenter, P. A. (1992). A capacity theory of comprehension: Individual differences in working memory. *Psychological Review*, 99(1), 122–149.
- Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, 127(1), 46–54.
- Kaushanskaya, M., Marian, V., & Yoo, J. (2011). Gender differences in adult word learning. *Acta Psychologica*, 137(1), 24–35.
- Kensinger, E. A., Ullman, M. T., Locascio, J. J., & Corkin, S. (1999). What is the relation between medial temporal lobe structures and

- lexical memory? Evidence from amnesic patient H.M. *Society for Neuroscience Abstracts*, 25, 357.
- Kidd, E. (2012a). Implicit statistical learning is directly associated with the acquisition of syntax. *Developmental Psychology*, 48(1), 171–184.
- Kidd, E. (2012b). Individual differences in syntactic priming in language acquisition. *Applied Psycholinguistics*, 33, 393–418.
- Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, 12(4), 217–230.
- Kumaran, D., & Maguire, E. A. (2009). Novelty signals: A window into hippocampal information processing. *Trends in Cognitive Sciences*, 13(2), 47–54.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, 62, 621–647.
- Lee, H., Devlin, J. T., Shakeshaft, C., Stewart, L. H., Brennan, A., Glensman, J., et al. (2007). Anatomical traces of vocabulary acquisition in the adolescent brain. *The Journal of Neuroscience*, 27(5), 1184–1189.
- Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience*, 16(3), 427–438.
- Lukacs, A., Kemeny, F., Lum, J. A. G., & Ullman, M. T. (in preparation). Effective declarative memory consolidation in children with SLI.
- Lum, J. A. G., Hedenius, M., Tomblin, J. B., & Ullman, M. T. (in preparation). Recognition memory in children with SLI.
- Lum, J. A. G., Conti-Ramsden, G., Morgan, A. T., & Ullman, M. T. (2014). Procedural learning deficits in Specific Language Impairment (SLI): A meta-analysis of serial reaction time task performance. *Cortex*, 51, 1–10. Available from: <http://dx.doi.org/10.1016/j.cortex.2013.10.011>.
- Lum, J. A. G., Conti-Ramsden, G., Page, D., & Ullman, M. T. (2012). Working, declarative and procedural memory in specific language impairment. *Cortex*, 48(9), 1138–1154.
- Lum, J. A. G., Ullman, M. T., & Conti-Ramsden, G. (2013). Procedural learning is impaired in dyslexia: Evidence from a meta-analysis of serial reaction time studies. *Research in Developmental Disabilities*, 34(10), 3460–3476. Available from: <http://dx.doi.org/10.1016/j.ridd.2013.07.017>.
- Lum, J. A. G., Ullman, M. T., & Conti-Ramsden, G. (2015). Verbal declarative memory impairments in specific language impairment are related to working memory deficits. *Brain and Language*, 142, 76–85.
- Marcus, G. F., Pinker, S., Ullman, M. T., Hollander, M., Rosen, T. J., & Xu, F. (1992). Overregularization in language acquisition. *Monographs of the Society for Research in Child Development*, 57(4), 1–165, Serial No. 228.
- Marshall, L., & Born, J. (2007). The contribution of sleep to hippocampus-dependent memory consolidation. *Trends in Cognitive Sciences*, 11(10), 442–450.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, 58, 25–45.
- Martins, S., Guillery-Girard, B., Jambaque, I., Dulac, O., & Eustache, F. (2006). How children suffering severe amnesic syndrome acquire new concepts? *Neuropsychologia*, 44(14), 2792–2805. Available from: <http://dx.doi.org/10.1016/j.neuropsychologia.2006.05.022>.
- McCarthy, G., Nobre, A. C., Bentin, S., & Spencer, D. D. (1995). Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *Journal of Neuroscience*, 15(2), 1080–1089.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102(3), 419–457.
- Mechelli, A., Crinion, J. T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R. S., et al. (2004). Neurolinguistics: Structural plasticity in the bilingual brain. *Nature*, 431(7010), 757.
- Meyer-Lindenberg, A. E. S. R., Lipska, B. K., Verchinski, B. A., Goldberg, T., Callicott, J. H., Weinberger, D., et al. (2007). Genetic evidence implicating DARPP-32 in human frontostriatal structure, function, and cognition. *The Journal of Clinical Investigation*, 117(3), 672–682.
- Meyer, P., Mecklinger, A., Grunwald, T., Fell, J., Elger, C. E., & Friederici, A. D. (2005). Language processing within the human medial temporal lobe. *Hippocampus*, 15, 451–459.
- Mishkin, M., Malamut, B., & Bachevalier, J. (1984). Memories and habits: Two neural systems. In G. Lynch, J. L. McGaugh, & N. M. Weinberger (Eds.), *Neurobiology of learning and memory* (pp. 65–77). New York, NY: The Guilford Press.
- Morgan-Short, K., Faretta-Stutenberg, M., Brill-Schuetz, K. A., Carpenter, H., & Wong, P. C. M. (2014). Declarative and procedural memory as individual differences in second language acquisition. *Bilingualism: Language and Cognition*, 17(1), 56–72.
- Morgan-Short, K., Finger, I., Grey, S., & Ullman, M. T. (2012). Second language processing shows increased native-like neural responses after months of no exposure. *Public Library of Science ONE*, 7(3), e32974.
- Morgan-Short, K., Steinhauer, K., Sanz, C., & Ullman, M. T. (2012). Explicit and implicit second language training differentially affect the achievement of native-like brain activation patterns. *Journal of Cognitive Neuroscience*, 24(4), 933–947.
- Munoz-Lopez, M. M., Mohedano-Moriano, A., & Insausti, R. (2010). Anatomical pathways for auditory memory in primates. *Frontiers in Neuroanatomy*, 4(129).
- Nemeth, D., Janacek, K., Csifcsak, G., Szvoboda, G., Howard, J., James, H., et al. (2011). Interference between sentence processing and probabilistic implicit sequence learning. *Public Library of Science ONE*, 6(3), e17577.
- Packard, M. G. (2008). Neurobiology of procedural learning in animals. In J. H. Byrne (Ed.), *Concise learning and memory: The editor's selection* (pp. 341–356). London: Elsevier Science & Technology Books.
- Petersson, K. M., Folia, V., & Hagoort, P. (2012). What artificial grammar learning reveals about the neurobiology of syntax. *Brain and Language*, 120(2), 83–95.
- Petrides, M., & Pandya, D. N. (2009). Distinct parietal and temporal pathways to the homologues of Broca's area in the monkey. *Public Library of Science Biology*, 7(8), e1000170.
- Pezawas, L., Verchinski, B. A., Mattay, V. S., Callicott, J. H., Kolachana, B. S., Straub, R. E., et al. (2004). The brain-derived neurotrophic factor Val66met polymorphism and variation in human cortical morphology. *Journal of Neuroscience*, 24(45), 10099–10102.
- Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: Converging evidence from animal and human brain studies. *Neuropsychologia*, 41(3), 245–251.
- Postle, B. R., & Corkin, S. (1998). Impaired word-stem completion priming but intact perceptual identification priming with novel words: Evidence from the amnesic patient H.M. *Neuropsychologia*, 15, 421–440.
- Prado, E., & Ullman, M. T. (2009). Can imageability help us draw the line between storage and composition? *Journal of Experimental Psychology: Language, Memory, and Cognition*, 35(4), 849–866.
- Quiroga, R. Q., Reddy, L., Kreiman, G., Koch, C., & Fried, I. (2005). Invariant visual representation by single neurons in the human brain. *Nature*, 435(7045), 1102–1107. Available from: <http://dx.doi.org/10.1038/nature03687>.

- Raboyeau, G., Marcotte, K., Adrover-Roig, D., & Ansaldi, A. I. (2010). Brain activation and lexical learning: The impact of learning phase and word type. *NeuroImage*, *49*(3), 2850–2861.
- Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: Nonhuman primates illuminate human speech processing. *Nature Neuroscience*, *12*, 718–724.
- Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*, 1926–1928.
- Schendan, H., Searl, M., Melrose, R., & Stern, C. (2003). An fMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron*, *37*(6), 1013–1025.
- Schreiwais, C., Bornschein, U., Burguiere, E., Kerimoglu, C., Schreiter, S., Dannemann, M., et al. (2014). Humanized Foxp2 accelerates learning by enhancing transitions from declarative to procedural performance. *Proceedings of the National Academy of Sciences of the United States of America*. Available from: <http://dx.doi.org/10.1073/pnas.1414542111>.
- Squire, L. R., & Zola-Morgan, J. (1991). The cognitive neuroscience of human memory since H.M. *Annual Review of Neuroscience*, *34*, 259–288.
- Tagarelli, K., Turkeltaub, P. E., Grey, S., & Ullman, M. T. (in preparation). The functional neuroanatomy of adult second language: An activation likelihood estimation meta-analysis.
- Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition*, *92*(1–2), 231–270.
- Ullman, M. T. (2005). A cognitive neuroscience perspective on second language acquisition: The declarative/procedural model. In C. Sanz (Ed.), *Mind and context in adult second language acquisition: Methods, theory and practice* (pp. 141–178). Washington, DC: Georgetown University Press.
- Ullman, M. T. (2006). Is Broca's area part of a basal ganglia thalamo-cortical circuit? *Cortex*, *42*(4), 480–485.
- Ullman, M. T. (2007). The biocognition of the mental lexicon. In M. G. Gaskell (Ed.), *The Oxford handbook of psycholinguistics* (pp. 267–286). Oxford, UK: Oxford University Press.
- Ullman, M. T. (2013). The role of declarative and procedural memory in disorders of language. *Linguistic Variation*, *13*(2), 133–154.
- Ullman, M. T. (2015). The declarative/procedural model: A neurobiologically-motivated theory of first and second language. In B. VanPatten & J. Williams (Eds.), *Theories in second language acquisition* (2nd ed., pp. 135–158). New York, London: Routledge.
- Ullman, M. T., Campbell, R., McQuaid, G. A., Tagarelli, K. M., & Turkeltaub, P. E. (in preparation). The functional neuroanatomy of regular and irregular morphology.
- Ullman, M. T., Lovelett, J. T., Gelfand, M. P., Litcofsky, K. A., Pullman, M. Y., Moffa, M., et al. (under revision). The influence of handedness on language: Storage versus composition differences in left- and right-handers.
- Ullman, M. T., & Gopnik, M. (1999). Inflectional morphology in a family with inherited specific language impairment. *Applied Psycholinguistics*, *20*(1), 51–117.
- Ullman, M. T., Lum, J. A. G., & Conti-Ramsden, G. (2014). Domain specificity in language development. In P. Brooks, & V. Kempe (Eds.), *Encyclopedia of language development* (Vol. 1, 1st ed.). Los Angeles, CA: Sage Publications.
- Ullman, M. T., Miranda, R. A., & Travers, M. L. (2008). Sex differences in the neurocognition of language. In J. B. Becker, K. J. Berkley, N. Geary, E. Hampson, J. Herman, & E. Young (Eds.), *Sex on the brain: From genes to behavior* (pp. 291–309). New York, NY: Oxford University Press.
- Ullman, M. T., & Pierpont, E. I. (2005). Specific language impairment is not specific to language: The procedural deficit hypothesis. *Cortex*, *41*(3), 399–433.
- Ullman, M. T., Pullman, M., Lovelett, J. T., McQuaid, G. A., Pierpont, E. I., & Turkeltaub, P. E. (under review). Brain abnormalities in specific language impairment are localized to frontal regions and the caudate nucleus. *Neuroscience and Biobehavioral Reviews*.
- Ullman, M. T., & Pullman, M. Y. (2015). A compensatory role for declarative memory in neurodevelopmental disorders. *Neuroscience and Biobehavioral Reviews*, *51*, 205–222.
- Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory. *Neurobiology of Learning and Memory*, *91*(2), 139–154. Available from: <http://dx.doi.org/10.1016/j.nlm.2008.10.011>.
- Vargha-Khadem, F., Gadian, D. G., & Mishkin, M. (2001). Dissociations in cognitive memory: The syndrome of developmental amnesia. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *356*(1413), 1435–1440.
- Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., et al. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*(5380), 1188–1191.
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*(9), 445–453. Available from: <http://dx.doi.org/10.1016/j.tics.2005.07.001>.
- Walenski, M., Mostofsky, S. H., Gidley-Larson, J. C., & Ullman, M. T. (2008). Brief report: Enhanced picture naming in autism. *Journal of Autism and Developmental Disorders*, *38*(7), 1395–1399.
- Walenski, M., Prado, E. L., Ozawa, K., Steinhauer, K., & Ullman, M. T. (under revision). The compositionality and storage of inflected forms: Evidence from working memory effects. *Cognition*.
- Walenski, M., Tager-Flusberg, H., & Ullman, M. T. (2006). Language in autism. In S. O. Moldin, & J. L. R. Rubenstein (Eds.), *Understanding autism: From basic neuroscience to treatment* (pp. 175–203). Boca Raton, FL: Taylor and Francis Books.
- Wartenburger, I., Heekeren, H. R., Abutalebi, J., Cappa, S. F., Villringer, A., & Perani, D. (2003). Early setting of grammatical processing in the bilingual brain. *Neuron*, *37*, 159–170.
- Winocur, G., & Moscovitch, M. (2011). Memory transformation and systems consolidation. *Journal of the International Neuropsychological Society*, *17*(5), 766–780. Available from: <http://dx.doi.org/10.1017/S1355617711000683>.
- Wixted, J. T., & Squire, L. R. (2011). The medial temporal lobe and the attributes of memory. *Trends in Cognitive Sciences*, *15*(5), 210–217.
- Woltering, J. M., Noordermeer, D., Leleu, M., & Duboule, D. (2014). Conservation and divergence of regulatory strategies at Hox Loci and the origin of tetrapod digits. *Public Library of Science Biology*, *12*(1), e1001773. Available from: <http://dx.doi.org/10.1371/journal.pbio.1001773>.
- Wong, P. C. M., Ettliger, M., & Zheng, J. (2013). Linguistic grammar learning and DRD2-TAQ-1A polymorphism. *Public Library of Science ONE*, *8*(5), e64983.
- Yang, J., & Li, P. (2012). Brain networks of explicit and implicit learning. *Public Library of Science ONE*, *7*(8), e42993.
- Yonelinas, A. P., Aly, M., Wang, W.-C., & Koen, J. D. (2010). Recollection and familiarity: Examining controversial assumptions and new directions. *Hippocampus*, *20*(11), 1178–1194.