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Contributions of memory circuits to language: the declarative/procedural model

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Abstract

The structure of the brain and the nature of evolution suggest that, despite its uniqueness, language likely depends on brain systems that also subserve other functions. The declarative/procedural (DP) model claims that the mental lexicon of memorized word-specific knowledge depends on the largely temporal-lobe substrates of declarative memory, which underlies the storage and use of knowledge of facts and events. The mental grammar, which subserves the rule-governed combination of lexical items into complex representations, depends on a distinct neural system. This system, which is composed of a network of specific frontal, basal-ganglia, parietal and cerebellar structures, underlies procedural memory, which supports the learning and execution of motor and cognitive skills, especially those involving sequences. The functions of the two brain systems, together with their anatomical, physiological and biochemical substrates, lead to specific claims and predictions regarding their roles in language. These predictions are compared with those of other neurocognitive models of language. Empirical evidence is presented from neuroimaging studies of normal language processing, and from developmental and adult-onset disorders. It is argued that this evidence supports the DP model. It is additionally proposed that "language" disorders, such as specific language impairment and non-fluent and fluent aphasia, may be profitably viewed as impairments primarily affecting one or the other brain system. Overall, the data suggest a new neurocognitive framework for the study of lexicon and grammar.

Keywords: Language; Lexicon; Grammar; Declarative memory; Procedural memory; Syntax; Morphology; Regular; Irregular; Basal ganglia; Neostriatum; Caudate nucleus; Cerebellum; Broca's area; Dorsal stream; Ventral stream; Working memory; Sequence learning; Specific language impairment; Dyslexia; Attention deficit hyperactivity disorder; Autism; Aphasia; Parkinson's disease; Alzheimer's disease; Huntington's disease; Semantic dementia; Functional magnetic resonance imaging; Positron emission tomography; Event-related potential

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1. Introduction

The study of language has focused largely on language itself. That is, in order to understand the representation, processing, development, neural correlates and other aspects of language, most theories and investigations have directed their attention to language. This is unsurprising, and not only because of the obvious point that directly investigating a domain generally elucidates it. Additionally, the apparent uniqueness of human language has drawn attention away from evidence suggesting the existence of biological and computational substrates that are shared between language on the one hand, and non-language domains in humans and animals on the other.

Brain organization and evolutionary principles both lead to an expectation of commonalities between language and non-language domains. First, a number of brain structures seem to be organized topographically, with sub-regions performing analogous computations on different domains of information, as a function of each sub-region's particular set of inputs and outputs. This type of brain organization has been claimed for the cerebellum, for various sub-cortical structures, including the basal ganglia, and for certain cortical regions, in particular in frontal cortex (Alexander, DeLong, & Strick, 1986; Middleton & Strick, 2000a; Shimamura, 1995). This suggests that analogous computations may underlie a range of cognitive domains, including language. Second, commonalities between language and non-language domains are not surprising from an evolutionary perspective, given the well-established pattern that biological structures tend to evolve from already-existing structures (Maynard Smith, 1975/1993; Mayr, 1963).

So, whether or not there are aspects of the neurocognition of language that are unique to this faculty and to our species, much and perhaps most aspects of language are likely to *not* be unique. Importantly, other cognitive domains are much better understood than language in a number of respects, including their neuroanatomy, physiology, biochemistry, evolution, development, and neural computation. This follows from the fact that most other domains have benefited from the development of animal models which allow for invasive and highly informative techniques that are not permissible to perform on humans.

A reasonable research program would thus be to identify domains that share commonalities with language: their underlying neural and computational systems will be promising candidates for those subserving language. Importantly, if the systems underlying the target domains are well understood, they should yield clear predictions about language, based solely on non-language theories and data. This should provide far greater predictive power about language than research restricted to language, whose theories and predictions are generally if not always derived from evidence solely related to language itself. Since the research tools we have at our disposal to understand language are quite impoverished compared to those available for the investigation of other domains, a research program limited to language necessarily restricts language theories and their predictions. In contrast, theories that are motivated by non-language domains as well as language have a much wider potential predictive range for language, and thus are likely to lead to important advances in our understanding of this faculty. This should be particularly likely for areas of research that have been given greater attention in non-language than language domains, such as functional neuroanatomy, physiology, biochemistry,

neuroendocrinology, and pharmacology. Importantly, the converse holds as well. That is, our understanding of many aspects of the representation, computation, and processing of language has progressed far beyond that of many other cognitive domains. So, the demonstration of neurocognitive links between language and other domains should also improve our understanding of the latter. Note that I am *not* arguing that research programs directed solely at language should be replaced by those examining language in the context of other cognitive domains. Rather I am maintaining that the latter type of research program must crucially complement the former.

It is in this general spirit that my colleagues and I have proposed and explored the declarative/procedural (DP) model of language (Ullman, 2001a,c; Ullman et al., 1997). The basic premise of the DP model is that important aspects of the distinction between the mental lexicon and the mental grammar in language are tied to the distinction between declarative and procedural memory – two memory systems which have been implicated in non-language functions in humans and other animals (Eichenbaum & Cohen, 2001; Mishkin, Malamut, & Bachevalier, 1984; Schacter & Tulving, 1994; Squire & Knowlton, 2000). That is, lexical memory depends largely on the declarative memory system, whereas aspects of grammar depend on the procedural memory system. Importantly, multiple characteristics of these two systems, including their computational, neuroanatomical, physiological and biochemical substrates, have been quite well studied, and thus should lead to important predictions about language.

2. Lexicon and grammar

Language depends upon a memorized "mental lexicon" and a computational "mental grammar" (Chomsky, 1965, 1995; de Saussure, 1959; Pinker, 1994).[1] The mental lexicon is a repository of all idiosyncratic word-specific information. Thus, it includes all words whose phonological forms and meanings cannot be derived from each other (i.e. their sound–meaning pairings are arbitrary), such as the non-compositional ("simple") word *cat*. It also contains other irregular—i.e. not entirely derivable—word-specific information, such as the particular arguments that must accompany a given verb (e.g. *hit* takes a direct object), and any unpredictable forms that a word takes (e.g. *teach* takes the irregular past-tense *taught*). The mental lexicon may comprise other distinctive information as well, smaller or larger than words: bound morphemes (e.g. the *-ed* or *-ness* suffixes, as in *walked* or *happiness*), and representations of complex linguistic structures whose meanings cannot be transparently derived from their parts (e.g. idiomatic phrases, such as *kick the bucket*).

[1] A terminological distinction must be made between the notion of a "mental lexicon", which is simply a storage place, and the way the term "lexicon" is often used in linguistic theories. Most linguistic theories assume an organization in which syntactic computations draw words from the "lexicon" (Anderson, 1992; Chomsky, 1965, 1970; Di Sciullo & Williams, 1987; Jackendoff, 1997; Lieber, 1992). However, the nature of this "linguistic" lexicon is controversial, as to whether it is a simple storage place (the mental lexicon) or whether, in addition, rule-based computations are carried out there (Anderson, 1992; Chomsky, 1970; Di Sciullo & Williams, 1987; Lieber, 1992; Spencer, 1991). In this paper the term "lexicon" is used solely to refer to the "mental lexicon"—that is, a repository of stored information.

Many regularities can also be found in language. These regularities can be captured by rules of grammar. The rules constrain how lexical forms and abstract symbols or features (e.g. *walk*, *-ed*, *Verb*, *Past-Tense*) can combine to make complex representations. The rules crucially allow us to interpret the meanings of complex forms even if we have not heard or seen them before. Thus, in the sentence "*Clementina glicked the plag*", we know that Clementina did something in the past to some entity. The rules specify not only the sequential order (precedence) of lexical items, but also their hierarchical relations, e.g. that a verb phrase (*glicked the plag*) can contain a noun phrase (*the plag*). Such rule-governed behavior is found at various levels in language, including in the structure of phrases and sentences (syntax), and of complex words such as *walked* or *glicked* (morphology). Importantly, the rules and constraints are a type of mental knowledge in that they underlie our individual mental capacity to produce and comprehend complex forms. It is often argued that aspects of the ability to learn, represent and compute the rules and constraints that underlie grammar depend on innately-specified mental constructs (Chomsky, 1995). The learning of grammatical knowledge, and the knowledge itself, are generally not available to conscious access (Fodor, 1983); that is, they are implicit. It has been argued that grammatical processing is not influenced by other cognitive domains; that is, the underlying system is "straight-through", or "informationally encapsulated" (Fodor, 1983; Frazier & Fodor, 1978). Moreover, at least certain aspects of grammatical processing are fast as well as automatic, in that they are not under conscious control but are rather triggered by the linguistic stimulus (Fodor, 1983; Friederici, 2002).

The two language capacities interact in a number of ways. First, the grammar combines lexical items into complex structures. Second, even though certain representations of complex linguistic structures that have idiosyncratic meanings (e.g. idioms) may be stored in the lexicon, their structures still generally follow the rules of grammar. Third, although "regular" (i.e. transparent; derivable) complex representations (e.g. *walked*; *the cat*) could be computed anew each time they are used (e.g. *walk* + *-ed*), and must be if they are new (e.g. *glicked*), they could in principle also be stored in the mental lexicon after being encountered. Finally, a general pattern observed in languages is that idiosyncratic, exceptional forms and meanings are selected preferentially over general, derivable ones (the "Elsewhere" principle; Halle & Marantz, 1993; Kiparsky, 1982; Pinker, 1984), suggesting that stored lexical items take precedence over those composed by the mental grammar.

3. Declarative and procedural memory

The declarative and procedural memory systems have been intensively studied in humans and in several animal models, including monkeys and rodents. The demonstration of numerous double dissociations has shown that the two systems are largely independent from each other, though they interact in a number of ways (Eichenbaum & Cohen, 2001; Mishkin et al., 1984; Poldrack & Packard, 2003; Schacter & Tulving, 1994; Squire & Knowlton, 2000). As will be seen, the two memory systems share a number of characteristics with the two language capacities. Importantly, research has begun to elucidate the specific computational, developmental, anatomical, cellular, molecular and

other aspects of these two systems across species. These findings lead to highly specific predictions about language.

3.1. Declarative memory

The "declarative" memory system (Eichenbaum & Cohen, 2001; Mishkin et al., 1984; Schacter & Tulving, 1994; Squire & Knowlton, 2000) has been implicated in the learning, representation, and use of knowledge about facts ("semantic knowledge") and events ("episodic knowledge"). It is important for the very rapid learning (e.g. based on a single stimulus presentation) of arbitrarily-related information – that is, for the associative binding of information (Cohen, Poldrack, & Eichenbaum, 1997; Eichenbaum & Cohen, 2001; Squire & Knowlton, 2000). It has been argued that the information learned by this system is not informationally encapsulated, being accessible to multiple mental systems (Squire & Zola, 1996). Moreover, at least part of this knowledge can be consciously ("explicitly") recollected.

Declarative memory depends, first of all, on medial temporal lobe structures: the hippocampal region (the dentate gyrus, the subicular complex, and the hippocampus itself), entorhinal cortex, perirhinal cortex, and parahippocampal cortex (Squire & Knowlton, 2000; Suzuki & Eichenbaum, 2000). The hippocampus projects to midline diencephalic nuclei, in particular the mammillary bodies and portions of the thalamus. These structures also play an important role in declarative memory, though they are less well studied than the medial-temporal lobe. The medial temporal structures are hierarchically organized: evidence from non-human primates indicates that the hippocampal region is heavily connected with entorhinal cortex, which is strongly connected with both the perirhinal and parahippocampal cortices, which are in turn connected extensively with temporal and parietal neocortical regions (Suzuki & Amaral, 1994).

The medial-temporal complex appears to subserve several related memory functions, including the encoding, consolidation and retrieval of new memories (Buckner & Wheeler, 2001; Eichenbaum & Cohen, 2001; Squire & Knowlton, 2000). Memories eventually (in humans, over months to years) become largely independent of the medial temporal lobe structures, and dependent upon neocortical regions, particularly in the temporal lobes (Hodges & Patterson, 1997; Squire, Clark, & Knowlton, 2001). Different regions of the temporal lobes may be specialized for different types of knowledge (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Ungerleider, & Haxby, 2000). It has been posited that medial temporal lobe structures associate or "bind" inputs from cortical regions, which together store an entire memory (Alvarez & Squire, 1994; McClelland, McNaughton, & O'Reilly, 1995).

The term "declarative memory system" is used here to refer to the entire system involved in the learning, representation and use of the relevant information (Eichenbaum, 2000), not just to those brain structures underlying the learning of new memories. Indeed, other brain structures also play a role in this system, although the precise regions and functions are still not entirely clear. First of all, prefrontal regions have been implicated in numerous studies (Buckner & Wheeler, 2001; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Ventrolateral prefrontal cortex (VL-PFC), which corresponds to the inferior frontal gyrus and Brodmann's areas (BA) 44, 45 and 47 (Damasio, 1995), plays a role in the encoding of

new memories and the selection or retrieval of declarative knowledge (Buckner & Wheeler, 2001; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner et al., 1998). Two functionally and anatomically distinct sub-regions have been implicated: posterior/dorsal inferior frontal cortex (BA 6/44) is strongly implicated in aspects of phonology, whereas anterior/ventral inferior frontal cortex (BA 45/47) is more important for semantics (Fiez, 1997; Poldrack, Wagner et al., 1999). Their precise roles may be closely related to working memory (Buckner & Wheeler, 2001; Moscovitch, 1992). Indeed, neuroimaging studies show that VL-PFC is consistently activated in working memory tasks (Smith & Jonides, 1999), and, within the same subjects, in both retrieval and working memory tasks (Braver et al., 2001). Additionally, anterior frontal-polar cortex (BA 10) is implicated in the retrieval of memories, or in the monitoring of that retrieval (Buckner & Wheeler, 2001). This area is also associated with working memory (Braver et al., 2001; McLeod, Plunkett, & Rolls, 1998). Finally, evidence suggests that portions of the cerebellum are involved in searching, retrieving or otherwise processing declarative memories (Desmond & Fiez, 1998; Ivry & Fiez, 2000).

The declarative memory system is closely related to the "ventral" stream system (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). This system is rooted in inferior and lateral temporal-lobe structures. It underlies the formation of perceptual representations of objects and their relations. These representations underlie the recognition and identification of objects and the long-term storage of knowledge about objects (Goodale, 2000). The ventral system is thus a memory-based system, feeding representations into long-term (declarative) memory, and comparing those representations with new ones. It has also been argued that humans are conscious of aspects of ventral stream functioning (Norman, 2002).

The declarative memory system has been intensively studied not only at functional and neuroanatomical levels, but also at cellular and molecular levels (Curran, 2000; Lynch, 2002). Acetylcholine in particular plays an important role in declarative memory and hippocampal function (Freo, Pizzolato, Dam, Ori, & Battistin, 2002; Packard, 1998). Thus, levels of choline acetyl transferase, the synthesizing enzyme for acetylcholine, correlate with declarative memory abilities (Baskin et al., 1999). Pharmacological manipulations of the cholinergic system in normal, healthy adults have also implicated acetylcholine in declarative memory (Nissen, Knopman, & Schacter, 1987; Rammsayer, Rodewald, & Groh, 2000). For example, acetylcholine esterase inhibitors, which prolong the activity of acetylcholine at the synapse, improve declarative memory (Ballard, 2002; Hammond, Meador, Aung-Din, & Wilder, 1987).

Evidence also suggests that the declarative memory system is affected by estrogen (Phillips & Sherwin, 1992; Sherwin, 1988), perhaps via the modulation of acetylcholine (Packard, 1998; Shughrue, Scrimo, & Merchenthaler, 2000). Declarative memory abilities and medial temporal-lobe function are linked to estrogen, via organizational effects in utero, and/or activational effects later on. Estrogen improves declarative memory in women (Maki & Resnick, 2000; Sherwin, 1998) and men (Kampen & Sherwin, 1996; Miles, Green, Sanders, & Hines, 1998), and strengthens the cellular and molecular correlates of long-term hippocampal learning (McEwen, Alves, Bulloch, & Weiland, 1998; Woolley & Schwartzkroin, 1998). Testosterone, which is the main source of estrogen in men, also improves their memory (Cherrier et al., 2001). Women with Turner's

syndrome, who do not produce estrogen, have worse declarative memory (which improves with estrogen therapy; Ross, Roeltgen, Feuillan, Kushner, & Cutler, 2000) and smaller hippocampi than control subjects (Murphy et al., 1993). During declarative memory tasks, increased estrogen (i.e. hormone replacement therapy) in healthy post-menopausal women leads to greater blood flow activation changes in medial temporal lobe regions, including the hippocampus (Maki & Resnick, 2000; Resnick, Maki, Golski, Kraut, & Zonderman, 1998).

3.2. Procedural memory

The "procedural memory" system (Eichenbaum & Cohen, 2001; Mishkin et al., 1984; Schacter & Tulving, 1994; Squire & Knowlton, 2000) subserves the learning of new, and the control of established, sensori-motor and cognitive "habits", "skills", and other procedures, such as riding a bicycle and skilled game playing. The system is commonly referred to as an "implicit memory system" because both the learning of the knowledge, and the knowledge itself, are generally not available to conscious access. Note that I use the term "procedural memory" to refer *only* to one type of implicit, non-declarative, memory system (Squire & Knowlton, 2000), *not* all non-declarative or implicit memory systems. Moreover, and analogously to how I use the term "declarative memory", the term "procedural memory" is used here to refer to the entire system involved in the learning, representation and use of the relevant knowledge, not just to those parts of the system underlying the learning of new memories.

Although procedural memory is less well understood than declarative memory, its functional characteristics and neural bases are beginning to be revealed. Functionally, the system may be characterized as subserving aspects of the learning and processing of context-dependent stimulus-response rule-like relations (Knowlton, Mangels, & Squire, 1996; Packard & Knowlton, 2002; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; White, 1997; Wise, Murray, & Gerfen, 1996). The system seems to be especially important for learning and processing these relations in the context of real-time sequences – whether the sequences are serial or abstract, or sensori-motor or cognitive (Aldridge & Berridge, 1998; Boecker et al., 2002; Doyon et al., 1997; Graybiel, 1995; Howard & Howard, 1997; Saint-Cyr, Taylor, & Lang, 1988; Willingham, 1998). Learning in the system is gradual, in that it occurs on an ongoing basis during multiple presentations of stimuli and responses – unlike the fast learning subserved by the declarative memory system. The relations are rule-like in that they are rigid, inflexible, and not influenced by other mental systems (Mishkin et al., 1984; Squire & Zola, 1996). Thus, this system, unlike declarative memory, appears to be informationally encapsulated (Squire & Zola, 1996). The rules apply quickly and automatically, in that the response is triggered by the stimulus rather than being under conscious control. The procedural system plays a role not only in learning and processing new sequences but also in the coordination of innate ones, such as "grooming sequences" in rodents, which follow a stereotyped sequence of "syntactic chains" that combine up to dozens of actions into a predictable order (Aldridge & Berridge, 1998). Intriguingly, although fixed linear sequences and possibly probabilistic sequences can be learned by monkeys, apes and humans, hierarchical structure is apparently commonly used and easily learned only by humans, though it has been observed in apes (Conway & Christiansen, 2001).

The procedural memory system is composed of a network of brain structures. The system is rooted in frontal/basal-ganglia circuits, with a likely role for portions of parietal cortex, superior temporal cortex and the cerebellum (De Renzi, 1989; Heilman, Watson, & Rothi, 1997; Hikosaka et al., 2000; Mishkin et al., 1984; Rizzolatti, Fogassi, & Gallese, 2000; Schacter & Tulving, 1994; Squire & Zola, 1996).

The basal ganglia are a set of sub-cortical structures, including the neostriatum, globus pallidus, sub-thalamic nucleus, and substantia nigra (Wise et al., 1996). In primates the neostriatum is composed of two structures: the putamen and the caudate nucleus. The putamen is particularly important for motor functions, whereas the caudate appears to underlie aspects of cognition (Alexander et al., 1986; Middleton & Strick, 2000a). Dorsal aspects of these structures (the dorsal striatum) play an important role in procedural memory, whereas ventral aspects (the ventral striatum) may be more important in affective (emotional) memory (Packard & Knowlton, 2002). The basal ganglia have been implicated in a number of functions, including implicit procedural learning in general (Eichenbaum & Cohen, 2001; Mishkin et al., 1984; Schacter & Tulving, 1994; Squire & Knowlton, 2000); stimulus-response learning (Packard & Knowlton, 2002; White, 1997), in particular of egocentric (body-centered) sensori-motor relations (White, 1997); probabilistic rule learning (Knowlton et al., 1996; Poldrack, Prabhakaran et al., 1999); sequence learning (Aldridge & Berridge, 1998; Boecker et al., 1998; Doyon et al., 1997; Graybiel, 1995; Peigneux et al., 2000; Willingham, 1998); reinforcement learning (in the dorsal striatum; cf. reward-based, in the ventral striatum) (Doya, 2000; Packard & Knowlton, 2002; White, 1997); real-time motor planning and control (Wise et al., 1996), particularly that which involves precise timing (Penhune, Zattore, & Evans, 1998) and the selection or switching among multiple motor programs (Haaland, Harrington, O'Brien, & Hermanowicz, 1997); mental rotation (Podzebenko, Egan, & Watson, 2002); interval timing and rhythm (Meck & Benson, 2002; Schubotz & von Cramon, 2001); and the context-dependent rule-based selection (Peigneux et al., 2000; Wise et al., 1996) and maintenance in working memory (Menon, Anagnoson, Glover, & Pfefferbaum, 2000) of and the real-time shifting (of attention, or focus) between sets, functions or programs. Importantly, these apparently disparate functions appear to be quite intimately related (Meck & Benson, 2002; Wise et al., 1996), although the precise nature of their relations and interactions are not yet understood.

The basal ganglia, in particular the neostriatum, receive input projections from multiple cortical areas, especially in frontal cortex, but also from other structures, including the medial temporal lobe (Alexander & Crutcher, 1990; Middleton & Strick, 2000b; Wise et al., 1996). The basal ganglia send outputs via the thalamus to neocortex, largely in frontal regions (Middleton & Strick, 2000b). The basal ganglia structures themselves are highly interconnected. Perhaps most importantly, the neostriatum projects to both the "direct" and the "indirect" pathways within the basal ganglia. The two pathways have opposing effects on the basal ganglia's outputs to frontal cortex via the thalamus. The direct pathway inhibits, whereas the indirect pathway disinhibits, the *inhibitory* projections from the basal ganglia to the thalamus. Thus, the direct pathway ultimately results in the *disinhibition*, and the indirect pathway in the *inhibition*, of the excitatory projections from thalamus to frontal cortex. So, frontal cortical activity is disinhibited by the direct pathway, and inhibited by the indirect pathway. The posited selection and set

shifting functions of the basal ganglia may be attributed to the interaction between the direct and indirect pathways: a given cortical "set" or "program" can be disinhibited, while the rest are inhibited (Young & Penney, 1993). Imbalances between the two pathways can lead to the excessive inhibition or disinhibition of the functions that depend on the frontal cortical regions to which the basal ganglia project. This is thought to explain the inhibited/suppressed and disinhibited/unsuppressed motor and other behaviors found in Parkinson's, Huntington's and other diseases affecting the basal ganglia (Young & Penney, 1993). The two pathways are modulated by dopaminergic projections from the substantia nigra to the neostriatum. Indeed, it is this bundle of neurons which degenerates in Parkinson's disease. These nigrostriatal dopaminergic neurons appear to have a role not only in the real-time modulation of the direct and indirect pathways, but also in the reinforcement learning functions of the basal ganglia, specifically in memory consolidation (Doya, 2000; Packard & Knowlton, 2002; White, 1997).

Importantly, the various connections within the basal ganglia contain parallel and largely functionally segregated "circuits" (i.e. channels) (Alexander & Crutcher, 1990; Alexander et al., 1986; Middleton & Strick, 2000a,b). Each circuit receives projections at the neostriatum – some circuits primarily at the caudate, others at the putamen – from a particular set of cortical and sub-cortical structures. Each circuit then follows the split between the direct and indirect pathways, and projects via the thalamus to a particular cortical region, largely in frontal cortex. This cortical output area in turn projects back to the portion of the neostriatum that receives inputs for that circuit. Thus, there is at least in part a closed loop with feedback. For example, a basal ganglia "motor circuit" projects to frontal motor areas, a "prefrontal" circuit projects to prefrontal regions, and other circuits project to other frontal areas. The different basal ganglia circuits have similar synaptic organizations, suggesting that similar neuronal operations might be performed at comparable stages of each circuit (Alexander, Crutcher, & DeLong, 1990; Middleton & Strick, 2000b). Thus, the various parallel circuits of the basal ganglia seem to perform analogous computations; these are applied to different sets of information from different domains, depending on the particular set of input regions and frontal cortical output destinations of a given circuit (Middleton & Strick, 2000b). So, if the basal ganglia play a role in grammar, that role should be computationally analogous to that which the structures play in other domains, with the grammar-subserving circuits possibly projecting to somewhat different frontal cortical regions (e.g. in Broca's area) than other circuits.

Certain frontal cortical regions are also critical for procedural memory, in a manner which seems to be closely related to the functions of the basal ganglia. In the macaque, the basal ganglia project via the thalamus to pre-motor regions, including the supplementary motor area (SMA) and the general region of area F5 (Middleton & Strick, 2000a,b). F5 is a well-studied ventral pre-motor region that is a likely homologue of human BA 44 in Broca's area (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) (Broca's area is defined here as a portion of human inferior frontal cortex, including and perhaps limited to cortex corresponding to BA 44 – pars opercularis – and BA 45 – pars triangularis; Amunts et al., 1999). Each of these frontal regions plays an important role in the procedural memory system.

First of all, pre-motor regions (Harrington et al., 2000; Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994), including SMA (Jenkins et al., 1994) and pre-SMA

(rostral SMA) (Boecker et al., 1998; Hikosaka et al., 1996), are implicated in motor sequence learning in humans. Motor sequence learning in macaques also depends on SMA and pre-SMA (Hikosaka et al., 2000). Lateral pre-motor cortex and SMA are also involved in mental rotation (Jordan, Heinze, Lutz, Kanowski, & Jancke, 2001; Kosslyn, Di, Thompson, & Alpert, 1998; Podzebenko et al., 2002), and lateral pre-motor and pre-SMA regions are implicated in aspects of timing or rhythm (Schubotz & von Cramon, 2001).

Broca's area is another critical component of the procedural memory system. Evidence suggests that motor sequence learning depends on left inferior frontal cortex (Peigneux et al., 1999), including Broca's area (Conway & Christiansen, 2001; Dominey, Hoen, Blanc, & Lelekov-Boissard, in press), and its right homologue (Doyon, Owen, Petrides, Sziklas, & Evans, 1996). Broca's area in humans seems particularly important for learning sequences which contain abstract and potentially hierarchical structure, as opposed to fixed linear sequences (Conway & Christiansen, 2001; Dominey et al., 2003; Goschke, Friederici, Kotz, & van Kampen, 2001). Broca's area has also been implicated in mental rotation tasks (Jordan et al., 2001; Podzebenko et al., 2002), the processing of non-motor sequences, including musical sequences (Maess, Koelsch, Gunter, & Friederici, 2001), and sequences of phonological material in working memory (Smith & Jonides, 1999). A recent study suggests that the manipulation of sequential information engages posterior Broca's area, independent of the type of information that is manipulated (Gelfand & Bookheimer, 2003). More generally, evidence suggests a close link between working memory and sequence learning and processing. These two functions share much of their circuitry: like sequence learning and processing, working memory involves Broca's area, SMA, and other pre-motor regions (Ivry & Fiez, 2000; Smith & Jonides, 1999), as well as regions in other structures (see below). It has been suggested that Broca's area, and perhaps VL-PFC more generally, may subserve particular functions that are important for working memory, including the selection and comparison of maintained information (Petrides, 1996; Petrides, Alivisatos, & Evans, 1995), or the maintenance of information over a delay (D'Esposito et al., 1998; Smith & Jonides, 1997). Similarly, it has been argued that the role of this region in working memory is to recall or select and maintain information that is actually stored in temporal and temporo-parietal regions (Cowan, 1999; Ruchkin, Grafman, Cameron, & Berndt, in press). These functions appear to be closely related to the role of this region in the selection of declarative knowledge (see above). The functions also appear to be related to the view that frontal cortex underlies the inhibition of, excitation of, and switching between (and possibly learning of) sets, programs and rules (Knight & Grabowecky, 2000; Shimamura, 1995; Wise et al., 1996), and the inhibitory and excitatory control of posterior brain regions (Knight & Grabowecky, 2000; also see Passingham, 1993). It has additionally been suggested that these attentional set shifting and sequence coordination roles may depend upon the timing functions of frontal cortex (Knight & Grabowecky, 2000; Meck & Benson, 2002; Wise et al., 1996). Indeed, Broca's area also appears to play an important role in timing and rhythm (Fiez et al., 1995; Schubotz & von Cramon, 2001; Szelag, von Steinbuchel, & Poppel, 1997).

Within Broca's area, BA 44 plays an especially important role in a number of the functions described above. This region is also implicated in the observation of motor skills, and in the mental imagery of motion (Binkofski et al., 2000; Rizzolatti & Arbib,

1998; Rizzolatti et al., 2000). Intriguingly, F5 – the monkey homologue of BA 44 – contains "mirror neurons", which fire not only at the execution of particular learned sequential motor skills (i.e. each neuron discharges with specific goal-oriented movement sequences), but also during the observation of (and even the sound of) the same action sequences (Kohler et al., 2002; Rizzolatti, Fogassi, & Gallese, 2001). Evidence suggests that human BA 44 also has this mirror function (Rizzolatti et al., 2001). It has been suggested that in humans such neurons may play a role in language, in particular in language comprehension (Rizzolatti & Arbib, 1998).

Portions of parietal cortex also play an important role in the procedural system. Anatomical studies of macaques show that parietal cortex projects heavily to, and reciprocally receives projections from, frontal cortex, with specific parietal regions connecting to specific frontal regions (Petrides & Pandya, 1984; Wise, Boussaoud, Johnson, & Caminiti, 1997). Macaque area F5, which corresponds to the BA 44 area in humans (see above), receives strong input from a number of parietal regions (Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Petrides & Pandya, 1984), especially macaque area AIP (Gallese, Fogassi, Fadiga, & Rizzolatti, 2001; Matelli, Luppino, Murata, & Sakata, 1994) – which is a probable homologue of human anterior intraparietal sulcus (Culham & Kanwisher, 2001) – and macaque area PF (also referred to as area 7b) (Matelli et al., 1986; Petrides & Pandya, 1984; Rizzolatti, Luppino, & Matelli, 1998) – which is likely homologous to the human anterior inferior parietal lobule (supramarginal gyrus; BA 40) (Nishitani, Uutela, Shibasaki, & Hari, 1999), or possibly to part of the superior parietal lobule (BA 7) (Culham & Kanwisher, 2001; Milner, 1996).

In monkeys, AIP neurons discharge during hand movements, with the majority of neurons preferring specific types of hand grips (Sakata, Taira, Mine, & Murata, 1992). AIP neurons also contains neurons that are tuned to the specific shapes to be grasped (Sakata & Taira, 1994). Similarly, AIP's human homologue, the anterior intraparietal sulcus, is activated during visually-guided grasping (Binkofski et al., 1998; Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997) and reaching (Culham & Kanwisher, 2001), by the physical manipulation of objects (Binkofski et al., 1999), by mental rotation (Harris et al., 2000; Podzebenko et al., 2002), by the observation of hand movements made by others (Iacoboni et al., 1999), and by passively looking at manipulable objects, namely tools (Chao & Martin, 2000).

Monkey area PF is connected not only with frontal area F5, but also with parietal area AIP (Nishitani et al., 1999). Area PF is related to hand manipulation and eye movements, and may code the orientation of body parts (Nishitani et al., 1999). Like frontal area F5, area PF contains mirror neurons (Gallese et al., 2001; Rizzolatti et al., 2001). Human superior parietal lobule (BA 7), one possible homologue of PF, is strongly related to attention (Perry & Zeki, 2000). Human inferior parietal lobule, and the supramarginal gyrus (BA 40) in particular, another likely homologue of PF, has been implicated in a number of functions, including attention (Perry & Zeki, 2000), mental rotation (Harris et al., 2000; Podzebenko et al., 2002), and the execution and recognition of motor skills (Heilman et al., 1997). According to one view, inferior parietal regions may serve as a repository of stored knowledge of motor skills, including information of stored sequences (Heilman et al., 1997). This region has also been strongly implicated in phonological processing, including in working memory tasks (Ivry & Fiez, 2000).

Intriguingly, circumscribed portions of the temporal lobes also appear to play a role in the procedural memory system. In macaques neurons that respond to the observation of movement, though *not* to movement itself (that is, they are not mirror neurons), are found in the anterior superior temporal sulcus – a region which is connected to both frontal area F5 and parietal area PF (Rizzolatti et al., 2001). In humans, superior temporal regions in more posterior areas, including the superior temporal sulcus, have been implicated in the storage of information about motion, in contrast to more ventral temporal regions, which appear to underlie the storage of information about visual form (Martin et al., 2000).

The cerebellum has traditionally been implicated in the coordination of skilled movement and in the control of balance, as well as in motor learning (Ivry & Fiez, 2000). More recent evidence suggests that portions of the cerebellum subserve procedural memory, in particular in motor sequencing (Desmond & Fiez, 1998; Eichenbaum & Cohen, 2001; Hikosaka et al., 2000; Ivry & Fiez, 2000; Mostofsky, Goldberg, Landa, & Denckla, 2000; Squire & Knowlton, 2000). Some evidence suggests that the cerebellum may be involved in the modification of performance of learned sequences, rather than in the learning of those sequences (Seidler et al., 2002). Within the cerebellum, the dentate nucleus (Hikosaka et al., 2000) as well as portions of the cerebellar hemispheres and the vermis (Desmond & Fiez, 1998) play important roles in learning procedures, especially of motor sequences. The cerebellar hemispheres and vermis, especially regions at least partly overlapping those that also underlie sequence learning, have also been implicated in verbal working memory and in the retrieval or search of information from declarative memory (Desmond & Fiez, 1998). The cerebellum has additionally been implicated in imaged hand movements and in mental rotation (Ivry & Fiez, 2000; Podzebenko et al., 2002). The cerebellum has important timing functions, and seems to be involved in mental coordination and the control of attention, and in error detection and error-based learning (Doya, 2000; Ivry & Fiez, 2000). Studies of macaques have shown that, analogously to the basal ganglia, the cerebellum projects via the thalamus to frontal cortex, with each cerebellar region projecting (via the thalamus) to particular frontal regions. Intriguingly, in macaques the dentate nucleus projects via the thalamus to ventral pre-motor cortex (Middleton & Strick, 2000a), suggesting that in humans it might project to BA 44 in Broca's area.

The procedural system, and parietal cortex in particular, is closely related to the "dorsal" stream system (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). This system is rooted in posterior parietal structures, and the frontal pre-motor regions to which they are heavily connected. The system underlies the transformation of visual information into an egocentric framework that enables the execution of motor programs, such as grasping and otherwise manipulating an object. It has been argued that the main function of this system is the analysis of visual input for visually-guided motor behavior.

3.3. Interaction of the two memory systems

The declarative and procedural memory systems interact in a number of ways. In sum, together the systems form a dynamically interacting network which yields both cooperative and competitive learning and processing, such that memory function may be optimized (Poldrack & Packard, 2003).

First, brain structures which underlie procedural memory also perform context-dependent selection and maintenance (in working memory) of knowledge stored in declarative memory. Note that it is only a terminological issue as to whether we consider these structures to be part of the procedural system which plays a role in declarative memory, or vice versa, or simply (and most reasonably) brain structures that play particular roles in both systems.

Second, although there appear to be striking separations of function among the different brain areas involved in the two brain systems, it does not appear to be the case that all parts of each lobe subserve only one or the other system. In particular, we have seen that superior aspects of the temporal lobe may play some function in the procedural system, perhaps as a storage repository of procedural knowledge, and that the same or nearby areas of VL-PFC play related roles in declarative and procedural memory.

Third, the two systems can complement each other in acquiring the same or analogous knowledge, including knowledge of sequences. As was initially shown in patient H.M., the declarative memory system need not be intact for the procedural memory system to learn (Corkin, 1984; Eichenbaum & Cohen, 2001; Squire & Knowlton, 2000). However, when both systems are undamaged they can complement each other. Thus, in motor sequence learning in humans, both systems can be used cooperatively to learn the task, optimizing learning in some cases (Willingham, 1998). When the declarative memory system is able to acquire knowledge, it may do so initially, thanks to its rapid learning abilities, while the procedural system gradually learns the same or analogous knowledge (Packard & McGaugh, 1996; Poldrack & Packard, 2003). Note that if a given sequence that is normally learned and processed by the procedural system is memorized in declarative memory, its structure will likely be constrained by the rules governing the sequence in procedural memory. Interestingly, the time-course of this shift from declarative to procedural memory can be modulated pharmacologically (Packard, 1999).

Fourth, animal and human studies suggest that the two systems can also interact competitively (for reviews, see Packard & Knowlton, 2002; Poldrack & Packard, 2003). This leads to what one might call a "see-saw effect", such that a dysfunction of one system leads to *enhanced* learning in the other, or that learning in one system depresses functionality of the other. Animal studies show that damage to medial-temporal lobe structures, including the hippocampus, can enhance basal-ganglia-based procedural learning (McDonald & White, 1993; Packard, Hirsh, & White, 1989; Schroeder, Wingard, & Packard, 2002). Conversely, damage to the neostriatum in the basal ganglia can facilitate learning in declarative memory (Mitchell & Hall, 1988). A similar pattern has been found in human lesion (Halbig et al., 2002) and neuroimaging studies (Dagher, Owen, Boecker, & Brooks, 2001; Jenkins et al., 1994; Poldrack & Packard, 2003; Poldrack et al., 2001; Poldrack, Prabhakaran et al., 1999).

The see-saw effect may be explained by a number of factors. In rodents there are direct anatomical projections from the medial temporal lobe (entorhinal cortex) to the dorsal striatum (Sorensen & Witter, 1983). Stimulation of both entorhinal and hippocampal neurons leads to mainly inhibitory responses in both the dorsal and ventral striatum (Finch, 1996; Finch, Gigg, Tan, & Kosoyan, 1995). Conversely, stimulation of the caudate (in cats) reduces the occurrence of hippocampal spikes (La Grutta & Sabatino, 1988; Sabatino, Ferraro, Liberti, Vella, & La, 1985). Several studies have suggested that lesions

to the hippocampus can result in increased dopamine transmission in the portion of the striatum to which the hippocampus projects (Jaskiw, Karoum, & Weinberger, 1990; Lipska, Jaskiw, Chrapusta, Karoum, & Weinberger, 1992). Neurochemically, acetylcholine appears to play a role in the interaction (Packard & Knowlton, 2002), perhaps by enhancing function of the hippocampus (see above), which could in turn inhibit function of the striatum via the projections described above. Moreover, acetylcholine can also directly inhibit the function of the neostriatum (Calabresi, Centonze, Gubellini, Pisani, & Bernardi, 2000). Because acetylcholine function can be enhanced by estrogen, particularly in the hippocampus (see above), it is plausible that estrogen may also contribute to the see-saw effect.

A recent and quite elegant series of neuroimaging experiments of healthy adults nicely demonstrates interactions between the two brain memory systems (Poldrack et al., 2001; Poldrack, Prabhakaran et al., 1999). Procedural learning – probabilistic rule learning – was shown to yield not only activation in the caudate nucleus, but also *deactivation* in the medial temporal lobe. Moreover, across subjects, the degree of activity in the caudate nucleus correlated negatively with the degree of activity in the medial temporal lobe. That is, subjects with higher caudate activity had lower medial-temporal activity, and vice versa. This suggests that individuals vary with respect to their relative dependence on the two systems. Moreover, this relationship changed over the course of learning. During early training the medial temporal lobe structures were activated while the caudate was not, whereas as learning progressed, the medial temporal structures became deactivated, while caudate activation increased. These experiments suggest some sort of competitive interaction between the two systems. Moreover, they strengthen the view that early in learning declarative memory can play a particularly important role compared to procedural learning, and that over time this balance shifts to the opposite direction. Thus, with increased dependence on procedural memory for a given function, there may be a decreased dependence on declarative memory, even if that system played a role initially in the same function. As we will see below, evidence suggests a similar pattern in language learning.

4. The declarative/procedural model

We have seen above that there are a number of striking commonalities between the functional characteristics of grammar/lexicon on the one hand, and of declarative/ procedural (DP) memory and their underlying brain structures on the other. These commonalities lead to the basic claim of the DP model: the brain systems which subserve declarative and procedural memory play analogous roles in language as in their non-language functions. So, the DP model predicts common or related computational, processing, anatomic, physiological and biochemical substrates for the language and non-language functions.

4.1. The lexical/declarative memory system

According to the DP model, the brain system underlying declarative memory also underlies the mental lexicon. This system subserves the acquisition, representation and use not only of knowledge about facts and events, but also about words. It stores all arbitrary, idiosyncratic word-specific knowledge, including word meanings, word sounds, and

abstract representations such as word category. It includes, among other things, representations of simple (non-derivable) words such as *cat*, bound morphemes such as the past-tense suffixed *-ed*, "irregular" morphological forms, verb complements, and idioms. It can also contain stored complex forms and abstract structures that are "regular" in that they can *also* be composed or derived by the grammatical/procedural system. As with idiosyncratic knowledge, the likelihood of these "regular" representations being memorized should increase with item-related factors such as their frequency, and subject-related factors such as the individual's lexical/declarative memory abilities. The system supports a superpositional associative memory, which allows for generalizations across representations. For example, the memorization of phonologically similar stem-irregular past tense pairs (e.g. *spring–sprang*, *sing–sang*) may allow for memory-based generalization to new irregularizations, either from real words (*bring–brang*) or from novel ones (*spling–splang*). This ability to generalize could underlie some degree of productivity within the memory system.

The brain structures that subserve declarative memory play analogous roles in lexical memory. Thus, medial temporal lobe structures underlie the encoding, consolidation and access or retrieval of new memories, which eventually rely instead on neocortical regions, especially in temporal and temporo-parietal areas. Inferior and ventral temporal regions are particularly important for representing non-linguistic conceptual knowledge and word meanings. They may also contain abstract lexical representations (Damasio et al., 1996). Superior temporal cortex may be particularly important for storing phonological representations, and perhaps other grammatical (syntactic, morphological) representations. Thus, this region may be related to both the procedural and declarative memory systems. Other brain structures, particularly those related to the procedural memory system, also play roles in declarative memory. These are described below. Acetylcholine and estrogen have important functions in lexical/declarative memory, likely in the learning and/or retrieval of new lexical knowledge.

4.2. The grammatical/procedural memory system

The brain system underlying procedural memory subserves the mental grammar. This system underlies the learning of new, and the computation of already-learned, rule-based procedures that govern the regularities of language-particularly those procedures related to combining items into complex structures that have precedence (sequential) and hierarchical relations. Thus, the system is hypothesized to have an important role in rule-governed structure building; that is, in the sequential and hierarchical combination – "merging" (Chomsky, 1995), or concatenation – of stored forms and abstract representations into complex structures. Procedural memory is assumed to play a role in all sub-domains of grammar which depend on these functions, including syntax; inflectional and derivational morphology – at least for default "regulars" (Pinker, 1999; Ullman, 2001a,c), but also for irregulars that appear to be affixed (Ullman, Hartshorne, Estabrooke, Brovetto, & Walenski, submitted); aspects of phonology (the combination of sounds); and possibly non-lexical (compositional) semantics (the interpretive, i.e. semantic, aspects of the composition of words into complex structures). Moreover, the computational nature of the system is likely to be similar across grammatical sub-domains – although this does not preclude the

possibility that these sub-domains maintain a certain degree of independence (see discussion below).

The system is a network composed of several brain structures. These are functionally related, highly inter-connected, and dynamically interactive: the basal ganglia, especially the caudate nucleus; frontal cortex, in particular Broca's area and pre-motor regions (including SMA and pre-SMA); parietal cortex, particularly the supramarginal gyrus (BA 40) and possibly the superior parietal lobule (BA 7); superior temporal cortex, probably in close relation with the declarative memory system; and the cerebellum, including the cerebellar hemispheres, the vermis, and the dentate nucleus.

The language-related functions of each of these structures is expected to be highly related to its non-language functions. Thus, the basal ganglia are posited to play a role in one or more aspects of the real-time selection and maintenance in working memory of, and switching between, sequentially and hierarchically structured elements in complex linguistic representations, and in the learning of rules over those representations. Grammar is learned and processed by one or more channels that run throughout the basal ganglia to the thalamus and thence to frontal cortex. These channels are parallel to and largely functionally segregated from other channels that undergo analogous computations but subserve other domains. The channel(s) subserving grammar might also subserve other domains, such as non-linguistic sequence learning; that is, they may be at least somewhat domain-independent. Alternatively, there may be one or more channels dedicated to grammar, and perhaps distinct (sub)channels for distinct grammatical sub-domains (e.g. syntax, morphology). Such channels and their frontal outputs may be considered domain-specific "modules" dedicated to grammar or its sub-domains. Though these hypothesized grammatical (sub)channels are domain-specific in that they underlie only grammatical processing, they are part of a domain-general procedural system, in which the same or analogous computations are performed on parallel and largely functionally segregated channels subserving other domains. This is a somewhat different view of modularity than is traditionally discussed in the study of language (Fodor, 1983).

The frontal cortical areas to which the basal ganglia project – in particular Broca's area, SMA and pre-SMA – also underlie aspects of grammar. Broca's area or portions thereof – especially BA 44 – may play an especially important role. Based on the functions of Broca's area in non-linguistic domains, this region is expected to subserve aspects of the selection and maintenance in working memory of elements in complex linguistic structures, and the learning and processing of rule-governed sequential and hierarchical patterns over those structures. These functions are, not surprisingly, quite related to the hypothesized functions of the basal ganglia in language, though Broca's area and the basal ganglia likely differ at least somewhat in their specific functions (Ullman, 2003; Ullman and Pierpont, in press).

Although the other structures that constitute the procedural system network are also expected to subserve language, their functional roles are perhaps less clear than those of the structures discussed above. Following evidence from their non-linguistic functions, the supramarginal gyrus and/or the superior parietal lobule may each play a role in attentional selection, which could be related to the selection functions described above. Parietal cortex may also play a role not only in sensori-motor transformations, but also in transforming structured representations stored in superior temporal regions to the dynamic

representations created by Broca's area. The cerebellum is expected to be involved in the search of lexical items, and possibly in the error-based learning of the rules that underlie the regularities of complex structures.

4.3. Interactions between the systems

The lexical/declarative memory system and the grammatical/procedural system are hypothesized to interact in several ways. First, the procedural system is hypothesized to build complex structures, and learn rule-governed patterns over those structures, by selecting lexical items from declarative memory, and maintaining and structuring those items together in working memory. Second, superior aspects of the temporal lobe may play a role in the storage of knowledge about procedural memory related relations of structured representations. Third, the same or similar types of knowledge can in at least some cases be acquired by both systems. The rapid lexical/declarative storage of sequences of lexical forms should provide a database from which grammatical rules can gradually and implicitly be abstracted by the procedural memory system. Moreover, in some cases explicit knowledge of the rules themselves may help guide processing, perhaps enhancing the procedural rule acquisition. Fourth, the two systems interact competitively in a number of ways. Access to a stored representation which has similar mappings to one which could be composed compositionally by the procedural system (e.g. an irregular vs. a regular past-tense form of the same verb) would block completion of the latter computation. Damage to the declarative system is expected to lead to enhanced learning and processing by the procedural system, and vice versa. Moreover, learning in one system may depress functionality of the other. It is possible that, at least under certain circumstances, enhancing acetylcholine or estrogen function in medial temporal lobe structures may result not only in improved lexical/declarative memory function, but also in suppressed grammatical/procedural function.

4.4. Further clarifications

The DP model is motivated by a set of commonalities between language functions on the one hand, and the functions of the memory brain systems on the other. However, the commonalities do *not* suggest, and indeed it is not the claim, that there are isomorphic (one-to-one) relations between lexicon and declarative memory, or between grammar and procedural memory. That is, it is *not* expected that all parts of the brain system underlying procedural memory subserve all aspects of the mental grammar, and similarly for declarative memory and the mental lexicon. First, there may be parts of each system that subserve non-language functions but which play no role in language, or a minimal role, or perhaps a role only in special circumstances (e.g. after breakdown). Indeed, this seems likely. For example, the declarative memorization of visual images clearly depends in part on cortical regions which may be specialized for and perhaps dedicated to visual processing, and thus are unlikely to be involved in the memorization of phonological word forms. Second and conversely, the DP model does *not* claim that *all* aspects of language depend upon the two brain memory systems. Other neural structures and other cognitive or computational components, perhaps even dedicated to language, may play an important role

in the two language capacities. Third, as we have seen above, structures with topographically segregated sub-regions (i.e. the basal ganglia, cerebellum, and possibly frontal cortex) may contain distinct sub-regions or circuits that subserve language and non-language functions (see above). On this view, the procedural memory system may be domain-independent in that it subserves many functions, but is also domain-specific in that each function is subserved by parallel and functionally segregated sub-components or modules. Fourth, as discussed above, even in the context of such topographic organization, there may be anatomical and functional specialization of sub-regions, such as in Broca's area.

4.5. Predictions

The predictions follow from the model described above. Most fundamentally, language and non-language functions that are posited to depend on the same brain systems should pattern together, showing similar computational, anatomic, physiological, biochemical and other characteristics. Moreover, this should apply not only to normal functioning, but also to the breakdown of these brain systems, and to recovery from this breakdown.

5. Comparison with other models

The DP model is proposed in the same spirit as, and is similar in a number of respects to, several other models and proposals (Dominey, 1997; Dominey et al., in press; Friederici, 1990; Greenfield, 1991; Lieberman et al., 1992; Rizzolatti & Arbib, 1998). These focus on the relation between grammar on the one hand, and implicit procedural memory, motor sequencing and hierarchical structure on the other. Some of these proposals are quite well-specified in certain respects. For example, Dominey and his colleagues have developed a computational model of the type of sequencing that may underlie both grammar and non-linguistic sequencing (Dominey et al., 2003). These models complement the DP model, specifying some aspects to a greater depth than the DP model, which in turn provides further specification in other dimensions, in particular the anatomical, physiological and biochemical substrates, and the functional roles in language played by those substrates.

The DP model is also largely, though not completely, compatible with many "dual-system" ("dual-mechanism") or multiple-system linguistic and psycholinguistic models of language (Bever, Sanz, & Townsend, 1998; Chomsky, 1995; Fodor, 1983; Fodor, Bever, & Garrett, 1974; Frazier & Fodor, 1978; Pinker, 1994, 1999). On these views, language is subserved by separable components. At the very least, the mental lexicon is assumed to be distinct from a "computational" mental grammar, which moreover is often claimed to be composed of several components (Chomsky, 1995). These theories also claim or assume that at least the grammatical component or components are domain-specific. As can be seen from the discussion above, all of these claims are compatible with the DP model. Thus, the DP model can be thought of as a neurocognitive model of aspects of these linguistic and psycholinguistic proposals. The neurocognitive model provides further specification in certain respects, particularly of the underlying brain structures and their functions, whereas the linguistic and psycholinguistic models provide much greater specification at the level of representation, computation and processing.

In contrast, the DP model is at least partially inconsistent with certain claims about the domain specificity of the neural basis of grammar. Thus, the DP model is not consistent with the particular claim (Grodzinsky, 2000) that Broca's area is dedicated to language and performs a different set of linguistic computations than are claimed by the DP model. The DP model is also not consistent with the claims made by certain connectionist models, in particular connectionist models that deny grammatical composition (Bates & MacWhinney, 1989; Joanisse & Seidenberg, 1999; MacDonald, Pearlmutter, & Seidenberg, 1994; Rumelhart & McClelland, 1986). These models also do not predict empirical associations among grammatical domains and procedural memory, or dissociations between these and lexical and declarative memory.

6. Empirical evidence

Here I examine neurocognitive evidence pertaining to the claims and predictions of the DP model in native (first) language. I focus on the relation between brain and cognition. For a discussion of purely behavioral (psycholinguistic) evidence from cognitively unimpaired individuals, see Pinker (1999), Ullman (2001a), or Pinker and Ullman (2002), among others. Three broad types of evidence are examined here. First, I provide brief overviews of hemodynamic (PET, fMRI) and electrophysiological (ERP) evidence from normal processing (i.e. in cognitively unimpaired individuals). For more in-depth reviews of this evidence, see, among others, Kaan and Swaab (2002), Kaan and Stowe (2002), and Friederici (2002). Second, I present evidence from developmental and adult-onset disorders that have traditionally been viewed as "language" disorders. I argue that the evidence suggests that these may be viewed as disorders affecting the brain structures of one or the other of the two brain memory systems. Third, evidence is presented that suggests that developmental and adult-onset disorders that have traditionally not been associated with language impairments in fact do affect language, and can also be profitably considered to be disorders of one or the other brain memory system.

6.1. Neuroimaging evidence from normal processing

6.1.1. Hemodynamics: PET and fMRI

Activation in temporal/temporo-parietal regions, including the hippocampus and other medial temporal lobe structures, is strongly linked to the representation and processing of both non-linguistic conceptual-semantic knowledge and lexical knowledge (Damasio et al., 1996; Martin et al., 2000; Newman, Pancheva, Ozawa, Neville, & Ullman, 2001). Activation in VL-PFC, and Broca's area in particular, has been elicited not only in a range of tasks related to procedural memory (see above), but also numerous tasks designed to probe syntactic processing, in both receptive and expressive language (Caplan, Alpert, & Waters, 1998; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Friederici, 2002; Indefrey, Hagoort, Herzog, Seitz, & Brown, 2001; Moro et al., 2001; Ni et al., 2000; Stromswold, Caplan, Alpert, & Rauch, 1996). Intriguingly, many of these studies have implicated BA 44 (pars opercularis) and the adjacent frontal operculum, suggesting that these regions play a particularly important role in grammatical processing, possibly related to aspects of

working memory (Friederici, 2002). Syntactic processing has been shown to elicit activation in SMA/pre-SMA (Caplan et al., 1998; Newman et al., 2001), the basal ganglia, specifically the caudate nucleus (Moro et al., 2001), and anterior superior temporal gyrus (Dapretto & Bookheimer, 1999; Meyer, Friederici, & von Cramon, 2000; Ni et al., 2000). Interestingly, processing of lexically stored syntactic knowledge (i.e. word-specific knowledge regarding which arguments a verb takes) has yielded inferior temporal lobe activation (Kuperberg et al., 2000).

6.1.2. Electrophysiology: event-related potentials (ERPs)

Event-related potentials (ERPs) reflect the real-time electrophysiological brain activity of cognitive processes that are time-locked to the presentation of target stimuli. Difficulties in lexical processing as well as non-linguistic conceptual-semantic processing elicit central/posterior bilateral negativities that peak about 400 ms post-stimulus ("N400s") (Kutas & Hillyard, 1980; Olivares, Bobes, Aubert, & Valdes-Sosa, 1994). Evidence from several empirical approaches suggests that N400s depend especially on temporal lobe structures, including in the medial temporal lobe (Kiehl, Laurens, & Liddle, 2002; Nobre, Allison, & McCarthy, 1994; Simos, Basile, & Papanicolaou, 1997), and possibly VL-PFC as well (Halgren et al., 2002; Kiehl et al., 2002). The N400 is posited to reflect declarative memory processes (Ullman, 2001b,c).

Anomalies in rule-governed syntax, morpho-syntax, or morpho-phonology can yield relatively early (150–500 ms) left anterior negativities ("LANs") (Friederici, Pfeifer, & Hahne, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991; Penke et al., 1997; Weyerts, Penke, Dohrn, Clahsen, & Münte, 1997). These LANs have been linked to rule-based automatic computations (Friederici, 2002; Friederici, Hahne, & Mecklinger, 1996) and left frontal structures (Friederici, Hahne, & von Cramon, 1998). LANs have also been elicited by difficulties in non-linguistic sequencing (Hoen & Dominey, 2000), and by the observation of incorrect tool use (e.g. incorrect positioning of a screwdriver with respect to the screw) (Bach, Gunter, Knoblich, Prinz, & Friederici, 2002). LANs are posited to reflect procedural memory processes (Ullman, 2001b,c). Syntactic processing difficulties also tend to elicit late (600 ms) centro-parietal positivities ("P600s") (Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992). These are associated with controlled processing (Friederici et al., 1996), and are posited to not reflect automatic aspects of procedural memory. Intriguingly, difficulties in processing word-specific syntactic knowledge (about verb arguments) can elicit an N400 rather than an LAN (Friederici & Frisch, 2000).

6.2. "Language" disorders

6.2.1. Developmental "language" disorders

6.2.1.1. Specific Language Impairment. The term Specific Language Impairment (SLI) is often assigned to developmental language disorders that do not have any apparent social, psychological or neurological cause (Leonard, 1998). SLI has generally been explained as an impairment specific to grammar (Clahsen, 1989; Rice & Oetting, 1993; van der Lely & Stollwerck, 1996) or as a processing deficit (Leonard, McGregor, & Allen, 1992),

specifically of working memory (Gathercole & Baddeley, 1993) or of brief stimuli and rapid sequences (Merzenich, Schreiner, Jenkins, & Wang, 1993; Tallal & Piercy, 1978). However, SLI may best be viewed as an impairment of procedural memory, resulting from the dysfunction of the brain structures underlying this system (Ullman & Gopnik, 1999; Ullman & Pierpont, in press).

SLI is strongly associated with grammatical impairments, including of syntax (Clahsen, Bartke, & Göllner, 1997; van der Lely, 1996), morphology (both morpho-syntax and morpho-phonology) (Leonard, Bortolini, Caselli, McGregor, & Sabbadini, 1992; Rice & Oetting, 1993; van der Lely & Ullman, 2001) and phonology (Gathercole & Baddeley, 1993). Lexical knowledge is relatively spared in SLI, as evidenced by spared recognition and comprehension in word learning tasks (Leonard, 1982; Weismer & Hesketh, 1996). In contrast, retrieval of lexical knowledge (word finding) is often difficult for people with SLI (Rapin & Wilson, 1978; Weckerly, Wulfeck, & Reilly, 2001), as might be expected if structures underlying procedural memory are involved in this function.

Contrary to traditional perspectives, SLI is also strongly associated with impairments of procedural memory (see Ullman & Pierpont, in press). First, motor deficits are widely observed in children and adults with SLI (Bishop, 2002; Hill, 2001; Owen & McKinlay, 1997). These include impairments of oral or facial praxis, limb praxis/coordination, and fine motor skills. People with SLI have particular difficulty on motor tasks involving complex sequences of movements, such as moving pegs, sequential finger opposition, rapid finger tapping and stringing beads. SLI is also associated with deficits of a number of other functions which depend upon the brain structures underlying procedural memory, including working memory (Gathercole & Baddeley, 1993), processing rapidly-presented sequences (Merzenich et al., 1993; Tallal, Stark, & Mellits, 1985), and mental rotation (Johnston & Weismer, 1983) and other "dynamic" mental imagery tasks involving the mental manipulation of images (Leonard, 1998). In contrast, "static" mental imagery appears to be spared in the disorder (Leonard, 1998). SLI is linked to abnormalities of the brain structures underling procedural memory, especially Broca's area, the basal ganglia (particularly the caudate nucleus), SMA and the cerebellum (Gauger, Lombardino, & Leonard, 1997; Jernigan, Hesselink, Sowell, & Tallal, 1991; Oki, Takahashi, Miyamoto, & Tachibana, 1999; Tallal, Jernigan, & Trauner, 1994; Vargha-Khadem et al., 1998). In contrast, declarative memory abilities often remain intact in SLI (Dewey & Wall, 1997; Merritt & Liles, 1987; also see Ullman & Pierpont, in press).

Evidence suggests that people with SLI may shift their reliance from the impaired procedural memory system to the relatively spared declarative memory (for further discussion see Ullman & Pierpont, in press). For example, whereas in normally developing children and adults, frequency effects (indicating storage) for regular inflected forms are absent, inconsistent or weak, they have been consistently demonstrated in children and adults with SLI, in both past-tense and plural production (Oetting & Horohov, 1997; Ullman & Gopnik, 1999; van der Lely & Ullman, 2001). Moreover, children with SLI produce compounds with regular as well as irregular plurals in them (e.g. *mice-eater* and *rats-eater*), whereas normal children only produce compounds with irregular plurals (e.g. *mice-eater* vs. *rat-eater*) (van der Lely & Christian, 2000). These data suggest that while normal children retrieve only irregular past-tense forms from memory, children with SLI retrieve both past-tense types.

6.2.2. Adult-onset "language" disorders

6.2.2.1. Aphasia. The term "aphasia" generally refers to language impairments resulting from one or more focal lesions in the brain. Clusters of symptoms tend to co-occur in types (syndromes) of aphasia. Although there are a number of different adult-onset aphasia syndromes, several of these can be grouped into either of two larger categories, which are often referred to as non-fluent and fluent aphasia (Alexander, 1997; Damasio, 1992; Goodglass, 1993). It is argued here that non-fluent aphasia reflects, at least in part, damage to the brain structures underlying procedural memory. In contrast, it is posited that fluent aphasia entails damage to brain structures underlying long-term representations in declarative memory, although the damage also often extends to posterior areas involved in procedural memory, resulting in the accompaniment of particular types of impairments of the grammatical/procedural system.

Non-fluent aphasia is associated with lesions of left inferior (ventro-lateral) frontal regions, in particular Broca's area and nearby cortex, as well as the basal ganglia, portions of inferior parietal cortex, and anterior superior temporal cortex (Alexander, 1997; Damasio, 1992; Dronkers, Redfern, & Knight, 2000). Characteristic of anterior aphasia is "agrammatism": syntactic and morphological impairments in production and comprehension, and especially in the use of free and bound grammatical morphemes (e.g. auxiliaries, determiners, and affixes such as *-ed*) (Goodglass, 1993). Agrammatics have been shown to have more trouble with regular than irregular morphology, holding constant word frequency, length, and other factors, in both expressive and receptive language tasks (Pinker & Ullman, 2002; Ullman et al., 1997, in press). Agrammatism is also strongly associated with phonological impairments (Goodglass, 1993). Agrammatic speech can follow focal lesions that are relatively circumscribed to the left basal ganglia (Fabbro, Clarici, & Bava, 1996) or right cerebellum (Silveri, Leggio, & Molinari, 1994; Zettin et al., 1997). Non-fluent aphasics are relatively spared in their recognition and comprehension of non-compositional (simple) content words (e.g. nouns, adjectives) (Goodglass, 1993). As would be expected with damage to Broca's area and the basal ganglia if these structures play a role in lexical retrieval, agrammatics generally have difficulty retrieving content words, despite the spared recognition of these words (Alexander, 1997; Damasio, 1992; Dronkers et al., 2000; Goodglass, 1993).

Non-fluent aphasia is strongly associated with impairments of non-linguistic functions that depend on procedural memory and its underlying brain structures. Non-fluent aphasics typically have a range of motor impairments, from articulation to the execution of complex learned motor skills, particularly those involving sequences (ideomotor apraxia) (Alexander, 1997; De Renzi, 1989; Dronkers et al., 2000; Goodglass, 1993; Heilman et al., 1997). Non-fluent aphasics have also been shown to have impairments learning new motor sequences, especially sequences containing abstract structure (Conway & Christiansen, 2001; Dominey et al., 2003; Goschke et al., 2001). Non-fluent aphasia is also linked to deficits of working memory and impairments of timing in speech production and perception, (Goodglass, 1993; Szelag et al., 1997).

Fluent aphasia is linked to damage of left temporal and temporo-parietal regions, often extending to inferior parietal structures. Fluent aphasia is associated with impairments in

the production, reading, and recognition of the sounds and meanings of content words, as well as of conceptual knowledge (Alexander, 1997; Damasio, 1992; Dronkers et al., 2000; Farah & Grossman, 1997). In contrast, fluent aphasics tend to produce syntactically well-structured sentences, and to not omit morphological affixes (e.g. the past tense *-ed* suffix). Intriguingly, damage in and around inferior parietal cortex in fluent aphasia can lead to certain types of grammatical impairments (Goodglass, 1993), supporting a role for this region in the mental grammar. Nevertheless, in direct comparisons of regular and irregular morphology, fluent aphasics show the opposite pattern to that of non-fluent aphasics, with worse performance at irregulars (Ullman et al., 1997, in press).

6.3. "Non-language" disorders

6.3.1. Developmental "non-language" disorders

A number of developmental disorders are associated with impairments of procedural memory related functions, and with abnormalities of the brain structures underlying this system. These include dyslexia, Attention Deficit Hyperactivity Disorder (ADHD) and autism spectrum disorder. According to the DP model, in these disorders one should observe both grammatical difficulties and lexical retrieval impairments, though the particular characteristics of these language deficits may differ depending on the specific procedural memory dysfunction in each disorder.

Dyslexia and ADHD are both linked to impairments of motor function (Denckla, Rudel, Chapman, & Krieger, 1985; Diamond, 2000; Wolff, Cohen, & Drake, 1984) and working memory (Denckla, 1996; Gathercole & Baddeley, 1993). Both disorders yield deficits in the ability to accurately reproduce time intervals (Barkley, Koplowitz, Anderson, & McMurray, 1997; Goswami et al., 2002) and to maintain motor timing control (Diamond, 2000; Wolff et al., 1984). The cerebellum has been implicated in dyslexia (Nicolson, Daum, Schugens, Fawcett, & Schulz, 2002) and ADHD (Berquin et al., 1998; Castellanos, 2001). The basal ganglia, especially the caudate nucleus, is abnormal in ADHD (Castellanos, 2001; Diamond, 2000), and possibly in dyslexia (Georgiewa et al., 2002). Dyslexia and ADHD show high co-morbidity with SLI and with each other (Cohen et al., 2000; Denckla, 1996; Snowling, 2000). According to one study, approximately 55% of children with a specific reading disorder were found to have impaired oral language, and 51% of children with SLI had a reading disability (McArthur, Hogben, Edwards, Heath, & Mengler, 2000). Some studies document as high as a 45% rate of language impairment among children with ADHD (Tirosh & Cohen, 1998). Indeed, the most frequent psychiatric diagnosis among children with language impairments is ADHD (Cohen et al., 2000).

Autism spectrum disorder is associated with cerebellar abnormalities (Courchesne, Yeung-Courchesne, Press, Hesselink, & Jernigan, 1988; Rumsey, 1996) and with deficits of motor function (Bauman, 1992; Ohta, 1987), working – but not declarative – memory (Bennetto, Pennington, & Rogers, 1996), and procedural learning, especially of sequences (Mostofsky et al., 2000; Sigman & Ungerer, 1984). One of the defining characteristics of autism is a deficit in language (Rutter, 1978). In many cases expressive language ability never develops at all (Bailey, Phillips, & Rutter, 1996). Deficits have been reported in syntax (Ramondo & Milech, 1984; Van Meter, Fein, Morris, Waterhouse, & Allen, 1997) and morphology (Bartolucci, Pierce, & Streiner, 1980; Howlin, 1984; Pierce & Bartolucci,

1977). In contrast, knowledge of words and concepts are apparently not impaired (Tager-Flusberg, 1985; Whitehouse & Harris, 1984), though there may be impairments in the recall of this knowledge (Tager-Flusberg, 1985).

6.3.2. Adult-onset "non-language" disorders

6.3.2.1. Alzheimer's disease. Alzheimer's disease (AD) affects medial and neocortical temporal-lobe structures, leaving frontal cortex – particularly Broca's area and motor cortex – and basal-ganglia structures relatively intact (Arnold, Hyman, Flory, Damasio, & Hoesen, 1991). The temporal lobe dysfunction may explain AD patients' impairments in learning new and using established lexical and conceptual knowledge (Grossman et al., 1998; Nebes, 1997; Sagar, Cohen, Sullivan, Corkin, & Growdon, 1988). AD patients are relatively spared at acquiring and expressing motor and cognitive skills (Beatty et al., 1994; Gabrieli, Corkin, Mickel, & Growdon, 1993; Nebes, 1997; Saint-Cyr et al., 1988), and at aspects of syntactic processing (Bayles, 1982; Schwartz, Marin, & Saffran, 1979). AD patients with severe deficits at object naming or fact retrieval make more errors at producing past-tense forms of irregulars than of regulars or *-ed*-suffixed novel verbs. Across AD patients, error rates at object naming and at fact retrieval correlate with error rates at producing irregular but not regular or *-ed*-suffixed novel past tenses (Ullman, in press; Ullman et al., 1997). Similarly, Italian AD patients have greater difficulty producing Italian irregular than regular present tense and past participle forms (Cappa & Ullman, 1998; Walenski, Sosta, Cappa & Ullman, submitted).

6.3.2.2. Semantic dementia. Semantic dementia is associated with the progressive and severe degeneration of inferior and lateral temporal lobe regions. The disorder results in the loss of non-linguistic conceptual and lexical knowledge (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000), with spared motor, syntactic and phonological abilities (Graham, Patterson, & Hodges, 1999). Patients with semantic dementia yield a pattern like that of AD patients: they have more trouble producing and recognizing irregular than regular and *-ed*-suffixed novel past tenses, and the degree of their impairment on irregulars correlates with their performance on an independent lexical memory task (Patterson, Lambon Ralph, Hodges, & McClelland, 2001).

6.3.2.3. Parkinson's disease. Parkinson's disease (PD) is associated with the degeneration of dopaminergic neurons, especially in the basal ganglia (i.e. the substantia nigra). This causes high levels of inhibition in the motor and other frontal cortical areas to which the basal ganglia project. It is thought to explain why PD patients show suppression of motor activity (hypokinesia) and have difficulty expressing motor sequences (Dubois, Boller, Pillon, & Agid, 1991; Willingham, 1998; Young & Penney, 1993). It may also account for their impairments at acquiring motor and cognitive skills (Harrington, Haaland, Yeo, & Marder, 1990; Saint-Cyr et al., 1988), and at grammatical processing (Grossman, Carvell, & Peltzer, 1993; Illes, Metter, Hanson, & Iritani, 1988; Lieberman et al., 1992). PD patients also have trouble retrieving words (Dubois et al., 1991). In contrast, temporal-lobe regions remain relatively undamaged and the recognition of words and facts remains relatively intact in low- or non-demented PD patients (Dubois et al., 1991; Sagar et al.,

1988; Saint-Cyr et al., 1988). Severely hypokinetic PD patients show a pattern opposite to that found among AD patients, making more errors when producing regular and *-ed*-suffixed novel past-tenses than irregular past-tenses. Across PD patients, the level of right-side hypokinesia, which reflects left basal ganglia degeneration, correlates with error rates at the production of regular and *-ed*-suffixed novel forms but not irregular forms. Intriguingly, left-side hypokinesia, which reflects right basal ganglia degeneration, does not show the analogous correlations with error rates in the production of any past tense type, underscoring the role of left frontal/basal-ganglia structures in grammatical rule use (Ullman, in press; Ullman et al., 1997). Across PD patients, error rates at regular and *-ed*-suffixed novel past-tenses correlate with error rates at naming manipulated objects (e.g. tools), but not non-manipulated objects, suggesting a common neural basis for manipulated objects and *-ed*-affixation, as expected by the DP model (Ullman, 1999).

6.3.2.4. Huntington's disease. Although Huntington's disease (HD) is like PD in causing degeneration of the basal ganglia, it strikes different portions of these structures. Unlike in PD, this damage affects the indirect pathway, resulting in the disinhibition of frontal areas receiving basal ganglia projections (Young & Penney, 1993). This is thought to explain the unsuppressible movements (chorea, a type of hyperkinesia) found in patients with HD. Patients with HD show the opposite pattern to those with PD not only in the type of movement impairment (the suppressed movements of hypokinesia vs. the unsuppressed movements of hyperkinesia), but also in the type of errors on *-ed*-suffixed forms (Ullman, in press; Ullman et al., 1997). HD patients produce forms like *walkeded*, *plaggeded*, and *dugged*, but not analogous errors on irregulars like *dugug* or *keptet*, suggesting that these errors are not attributable to articulatory or motor deficits. Rather the data suggest unsuppressed *-ed*-suffixation. This conclusion is strengthened by the finding that the production rate of these over-suffixed forms correlates with the degree of chorea, across patients. These contrasting findings in PD and HD, linking movement and *-ed*-suffixation in two distinct types of impairments related to two types of basal ganglia damage, strongly implicate frontal/basal-ganglia circuits in *-ed*-suffixation. They support the hypothesis that these structures underlie the expression of grammatical rules as well as movement, and suggest that they play similar roles in the two domains.

6.3.2.5. Amnesia. Bilateral damage to medial temporal lobe structures leads to an inability to learn new information about facts, events, and words (Schacter & Tulving, 1994). Importantly, neither phonological nor semantic lexical knowledge is acquired (Gabrieli, Cohen, & Corkin, 1988; Postle & Corkin, 1998), supporting the DP hypothesis that these structures underlie the learning of word forms as well as word meanings. This "anterograde amnesia" is typically accompanied by the loss of this type of information for a period preceding the damage. However, knowledge acquired substantially before lesion onset tends to be spared (Schacter & Tulving, 1994). Thus, even though medial temporal lobe structures are posited to underlie the learning of new lexical information, knowledge of words learned during childhood should be largely intact in adult-onset amnesia. As expected, the examination of the well-studied amnesic H.M. (Kensinger, Ullman, & Corkin, 2001) revealed that he did not differ from normal age- and education-matched

control subjects at syntactic processing tasks, or at his production of regular or irregular forms in past-tense, plural and derivational morphology.

7. Conclusion

According to the DP model, the brain systems underlying two well-studied memory capacities, declarative and procedural memory, also subserve aspects of the mental lexicon and the mental grammar. Both brain systems play similar functional roles across language and non-language domains, which depend on common anatomical, physiological, and biochemical substrates. Evidence from neuroimaging (fMRI, PET, ERPs) and from developmental and adult-onset disorders supports this claim. Moreover, I have argued that certain developmental and adult-onset "language" disorders may be best viewed as disorders that affect brain structures underlying the memory systems.

The DP model has a number of implications in addition to those discussed above. First, our understanding of the two memory systems should lead to further predictions about language. For example, sex differences in language acquisition and processing can be predicted by independent knowledge of declarative memory. Women show an advantage over men at remembering verbal information in declarative memory (Golomb et al., 1996; Kimura, 1999). This effect is modulated by estrogen (see above). These data lead to the prediction that girls and women tend to memorize complex forms (*walked*) in lexical/declarative memory that boys and men tend to compose (*walk* + *-ed*) in the grammatical/procedural system (Ullman et al., 2002). Preliminary evidence supports this contention, and implicates estrogen in the effect (Estabrooke, Mordecai, Maki, & Ullman, 2002; Ullman et al., 2002, submitted).

Second, aspects of our existing understanding of language can be reinterpreted in the context of the DP model. For example, evidence suggests that in late second language learning – particularly after puberty – grammar is more difficulty to learn than lexical knowledge (Birdsong, 1999; Johnson & Newport, 1989). Under the DP model, this suggests that at later ages, especially after puberty, the grammatical/procedural system is less available than lexical/declarative memory (Ullman, 2001b). This may result from the attenuation of procedural memory, possibly due to increasing estrogen levels at puberty (directly or via testosterone; see above), which would be expected to enhance declarative memory, and possibly suppress the procedural system through the "see-saw" competition mechanism. The availability of the lexical/declarative system should allow it to compensate for the dysfunctional grammatical/procedural system, as has been found in SLI (see above). However, since practice should increase performance in procedural memory, late-language learners should tend to become native like with experience, showing an increased dependence on the grammatical/procedural system. Previous studies are consistent with this view of second language acquisition and processing (Ullman, 2001b). Morever, a recent fMRI study examining the acquisition of an artificial language in adulthood (Opitz & Friederici, in press) found that early during acquisition (i.e. at low proficiency) syntactic processing involves the hippocampus and cortical areas in the temporal lobe. Activation in these brain structures decreased across the experiment (as proficiency increased), while activation increased in Broca's area. This finding

suggests a shift from the declarative to the procedural system during late second language learning, similar to the non-linguistic procedural learning experiments discussed above (Poldrack et al., 2001; Poldrack, Prabhakaran et al., 1999).

Third, because language is a relatively well-understood cognitive domain, it is likely that linguistic theory and related language disciplines will shed light on aspects of the declarative and procedural memory systems. For example, the Elsewhere Principle (see above) suggests that even in non-language domains, declarative memory may hold precedence in certain contexts over procedural memory.

Fourth, the DP model suggests the feasibility of the development of animal models for the study of language: the model predicts that significant advances in our understanding of language can be made by investigating non-language functions, in particular by using a range of highly informative methods available only in animal models. Therefore, a reasonable and desirable research program would be to develop animal models of non-linguistic functions whose computational and neural substrates are expected to be shared with those of linguistic functions.

Fifth, the model has direct educational and clinical implications. For example, the neuropharmacology of declarative memory and its underlying neural substrates (Curran, 2000) should pertain to language as well. Moreover, as discussed above, people with disorders of the grammatical/procedural system may recover through the memorization of complex forms (e.g. *walked*) in lexical/declarative memory. Such recovery could presumably be encouraged with neuropharmacological and other therapeutic approaches motivated by existing knowledge of the memory systems (Ullman & Pierpont, in press). Finally, the existence of brain systems that subserve language and are homologous to systems in other animals has implications for the evolution of language.

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