A NEUROCOGNITIVE PERSPECTIVE ON LANGUAGE: THE DECLARATIVE/ PROCEDURAL MODEL

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What are the psychological, computational and neural underpinnings of language? Are these neurocognitive correlates dedicated to language? Do different parts of language depend on distinct neurocognitive systems? Here I address these and other issues that are crucial for our understanding of two fundamental language capacities: the memorization of words in the mental lexicon, and the rule-governed combination of words by the mental grammar. According to the declarative/procedural model, the mental lexicon depends on declarative memory and is rooted in the temporal lobe, whereas the mental grammar involves procedural memory and is rooted in the frontal cortex and basal ganglia. I argue that the declarative/procedural model provides a new framework for the study of lexicon and grammar.

Language depends on two mental capacities: a memorized 'mental lexicon' and a computational 'mental grammar'^{1,2}. The mental lexicon is a repository of stored information, including all idiosyncratic, wordspecific information. It includes those words with arbitrary sound-meaning pairings, such as the non-compositional word 'cat'. It is also thought to contain other irregular word-specific information, such as any arguments that must accompany a verb ('devour' must be accompanied by a direct object), and any unpredictable forms that a word takes ('teach' takes 'taught' as its past tense). The mental lexicon might also comprise complex linguistic structures, such as phrases and sentences, the meanings of which cannot be derived transparently from their parts (for example, idiomatic phrases such as 'kick the bucket').

But language also consists of regularities, which can be captured by the rules of grammar. The rules constrain how lexical forms can combine to make complex representations, and allow us to interpret the meanings of complex forms even if we have not heard or seen them before. For example, in the sentence 'Clementina glicked the plag', we know that Clementina did something in the past to some entity. The meaning can be derived from rules that underlie not only the sequential order of lexical items, but also their hierarchical relations. In this example, an abstract representation for the verb phrase 'glicked the plag' contains a representation for the noun phrase 'the plag'. This grammatical ability to derive meaning from any well-formed complex structure underlies the incredible productivity and creativity of human language. Such rule-governed behaviour is found at various levels in language; for example, in phrases and sentences (syntax), and in complex words such as 'walked' or 'glicked' (morphology). Importantly, the rules are a form of mental knowledge, in that they underlie our individual capacity to produce and comprehend complex forms. Moreover, the rules underlie mental operations that manipulate words and abstract representations in the composition of complex structures. The learning and use of the rules and operations of grammar are generally implicit (subconscious), and it has been argued that such grammatical knowledge is not available to other cognitive operations - it is 'informationally encapsulated'3. Last, although complex representations ('walked') could be computed anew each time they are used ('walk' + '-ed'), and certainly must be if they have not been previously encountered ('glicked'), they could, in principle, also be stored in the mental lexicon after being constructed.

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The declarative/procedural model

The neurocognitive bases of the mental lexicon and the mental grammar have been the focus of many studies^{2,4-7}, which have concentrated on several issues including separability (do lexicon and grammar depend on distinct or shared neurocognitive correlates?), computation (what computational mechanisms underlie the learning, representation and processing of the two language capacities, and how is linguistic knowledge represented?), domain specificity (are the neurocognitive correlates of lexicon and grammar dedicated only to language, or do they subserve other functions?), and the identification of their neural correlates (can we localize their neural circuitry to particular brain structures; what is the temporal order in which these structures participate during language processing, and how do they interact?).

Several models have attempted to address these issues. Here I focus on one model — the declarative/procedural model — and compare its claims and predictions with those of competing models. The basic premise of the declarative/procedural model is that aspects of the lexicon/grammar distinction are tied to the distinction between two well-studied brain memory systems — declarative and procedural memory — that have been implicated in non-language functions in humans and other animals^{8,9}.

The declarative memory system¹⁰⁻¹² has been implicated in the learning, representation and use of knowledge about facts (semantic knowledge) and events (episodic knowledge). This memory system seems to be closely related to the ventral visual stream¹³. It might be particularly important for learning arbitrarily related items - that is, for the associative/contextual binding of information. The knowledge might be explicitly (consciously) recollected, and might not be informationally encapsulated, but accessible to multiple mental systems11. Declarative memory is subserved by regions of the medial temporal lobe - in particular, the hippocampus - which are largely connected with temporal and temporoparietal neocortical regions¹⁴. The medial temporal lobe is required to consolidate (and possibly to retrieve) new memories, although they eventually become independent of the medial temporal lobe and depend on neocortical regions, particularly those in the temporal lobe^{15,16}. Other brain structures are also part of this system. Anterior prefrontal cortex might underlie the selection or retrieval^{17,18} of declarative memories, whereas portions of the right cerebellum might be involved in searching for this knowledge¹⁸.

The procedural memory system^{10–12} has been implicated in learning new, and controlling well-established, motor and cognitive skills. Learning and remembering these procedures is largely implicit. It has been argued that the procedural system is informationally encapsulated, having relatively little access to other mental systems¹¹. (Note that I use the term 'procedural memory' to refer to only one particular brain memory system¹¹ and not to all non-declarative or implicit memory systems.) The system is rooted in portions of the frontal

cortex (including Broca's area and the supplementary motor area), the basal ganglia, parietal cortex and the dentate nucleus of the cerebellum^{10–12,19–22}. This system might be related to the dorsal visual stream¹³ and is important for learning or processing skills that involve action sequences²³. The execution of these skills seems to be guided in real time by the posterior parietal cortex, which is densely connected to frontal regions¹³. Inferior parietal regions might serve as a repository for knowledge of skills, including information about stored sequences²⁰. Similarly, the basal ganglia are also densely connected to the frontal cortex²⁴. Basal ganglia circuits seem to be arranged in parallel and are functionally segregated; each of them projects through the thalamus to a particular cortical region, largely in the frontal cortex²⁴.

According to the declarative/procedural model, the declarative memory system underlies the mental lexicon, whereas the procedural system subserves aspects of mental grammar. So, declarative memory is an associative memory that stores not only facts and events, but also lexical knowledge, including the sounds and meanings of words. Learning new words relies largely on medial temporal lobe structures. Eventually, the knowledge of words becomes independent of the medial temporal lobe and dependent on other neocortical areas, particularly those in temporal and temporoparietal regions. The temporal lobe might be particularly important for storing word meanings, whereas temporoparietal regions might be more important in storing word sounds. Lexical memory is not informationally encapsulated, but is accessible to multiple mental systems.

On the other hand, procedural memory subserves the implicit learning and use of a symbol-manipulating grammar across subdomains that include syntax, morphology and possibly phonology (how sounds are combined). The system might be especially important in grammatical-structure building — that is, in the sequential and hierarchical combination of stored forms ('walk' + '-ed') and abstract representations into complex structures. The learning of rules should depend on parts of the system that are involved in procedural learning. One or more circuits between the basal ganglia and particular frontal regions might subserve grammatical processing and perhaps even finer distinctions, such as morphology versus syntax. From this point of view, the frontal cortex and basal ganglia are 'domain general', in that they subserve non-linguistic and linguistic processes, but contain parallel, 'domain-specific' circuits.

It is important to note that the model does not assume that all parts of the two memory systems subserve language. At least in the procedural system, and probably also in the declarative system, parallel circuits are posited to have analogous computational functions in language and in other domains. Similarly, the model does not assume that these two memory systems are the only systems that underlie lexicon and grammar. Other neural structures and other cognitive or computational components might be important for both capacities. INFLECTIONAL MORPHOLOGY The modification of a word to fit its grammatical role. For example, 'sang' and 'walked' are inflected in the past tense.

DERIVATIONAL MORPHOLOGY The creation of new words. For example, the nouns 'solemnity' and 'toughness' are derived from the adjectives solemn and tough, respectively.

Comparison with other models

The declarative/procedural model is similar in certain respects to other 'dual-system' models^{1,2,25}. These models hold that lexicon and grammar are separable and subserved by distinct cognitive systems^{1,2,26}. The learning, representation and processing of words and other arbitrary information in a rote or associative memory is subserved by one or more systems that might be specialized for and dedicated to these functions^{1,3,27}. It has been claimed that the use of stored words might depend on left temporal and temporoparietal structures⁷. The learning, knowledge and processing of grammar are also subserved by one or more systems that are dedicated to their linguistic functions. The grammar manipulates symbols

Box 1 | Dual-system models and regular/irregular morphology

All dual-system models assume that regular (default) forms are computed by rules that manipulate symbols representing their parts, whereas the use of irregular (non-default) forms involves form-specific stored representations. However, the models differ in the specific aspects of these claims.

Regular forms

⁶Piece-based' theories, such as the declarative/procedural model, assume that affixes are stored lexical items that are combined with stems^{25,29,134}. Some piece-based theories assume that pieces are put together anew each time they are used^{9,25,29,134}. For example, 'walked' is the real-time product of a function combining two arguments — 'walk' and '-ed'. Other piece-based theories posit that forms are combined from pieces and then stored as whole words¹³⁵, with or without more-specific representation of part–whole structure. So, 'walked' is listed as a whole word but could also contain information specifying its constituent parts 'walk' and '-ed'.

Other dual-system theories deny the piece-based computation of complex words. These posit that, unlike phrases and sentences, the parts of complex words do not exist as separate pieces, but are specified by relations that capture regularities among words. For example, 'walked' is related to 'walk' by an affixation function that takes 'walk' as its only argument. The controversy between real-time computation and memorized representations also exists among these theories. Although it is sometimes assumed that regular complex words are computed anew whenever they are used¹³⁶, it is alternatively claimed that the representations of existing forms are stored^{137,138}.

Irregular forms

Because the application of an irregular transformation is, by definition, arbitrary, all dualsystem models claim that each word is associated with some type of stored information regarding any irregular transformations. Theories differ as to how the information is represented, what type of information is stored, and with which irregular items it is stored. Some models suggest that any memorized irregulars are stored as symbols in a rote memory^{29,48}. All such models admit that 'suppletive' forms (utterly idiosyncratic, as in go-went) must be stored. However, it has been argued that subregularities that are found among many irregular transformations (for example, the shared pattern in sing-sang, spring-sprang and ring-rang) can be captured by rules of grammar^{29,139}. Although memorized representations that link the stems of irregulars to their individual rules must exist, the irregular morphological forms themselves are suggested to be rule products that are computed anew each time they are used. These rule products can be computed by morphophonological 'stem-readjustment rules' for forms that undergo stem changes (dig-dug or sing-sang) and/or affixation rules. Last, several dual-system models, including the declarative/procedural model, claim that irregulars are represented and processed in a distributed associative memory that is at least partially productive, therefore allowing the generation of new irregulars (for example, spling-splang). So, the system learns the mappings of individual morphologically complex forms (sing-sang), learns patterns common to the mappings of different forms (sing-sang, spring-sprang, ring-rang), and can then generalize these patterns to new forms (spling-splang). Moreover, some of these models²⁵, including the declarative/procedural model, assume that the representations of forms can be structured, reflecting the morphophonological and phonological part-whole structures of words.

representing lexical forms and abstract representations, combining them to construct complex linguistic structures. These structures are often suggested to be composed from their parts every time they are used^{2,28,29}. Grammar has been claimed to depend on the left frontal cortex, particularly on Broca's area and adjacent anterior regions^{30,31}. So, the declarative/procedural model shares several features with other dual-system models. Their differences will become clearer when I discuss the specific predictions made by each of them.

'Single-system' theories posit that the learning and use of the words and rules of language depend on a single computational system that has a broad anatomical distribution^{32,33}. According to this view, there is no categorical distinction between non-compositional and compositional forms. Instead, rules are only descriptive entities, and the system gradually learns the entire statistical structure of language, from the arbitrary mappings in non-compositional forms to the rule-like mappings of compositional forms. Modern connectionist theory has offered a computational framework for the singlesystem view. It has been argued that the learning, representation and processing of grammatical rules and lexical items take place over many interconnected, simple processing units. Learning occurs by adjustments to the weights of connections on the basis of statistical contingencies in the environment^{4,34}.

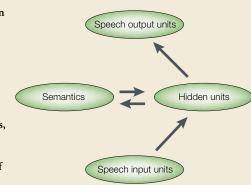
Deciding between these competing perspectives has been problematic, partly because tasks that probe for lexicon or grammar usually differ in ways other than their use of the two capacities. For example, it is difficult to match measures of grammatical processing in sentence comprehension with measures of lexical memory. For this reason, much recent research has focused on the distinction between regular and irregular morphology, especially in English past tense9,25,34,35. This offers a comparison between two otherwise well-matched types of linguistic form. The application and construction of irregular past-tense forms is not entirely predictable (compare, for example, bring-brought, sing-sang and come-came), and must therefore depend on memorized representations9,25,29. Regular past tenses follow a simple rule, the affixation of '-ed', which is the default transformation for the past tense. Regular past tenses could therefore be rule products. This distinction between regular and irregular forms is found across languages, in both inflectional morphology and derivational MORPHOLOGY. So, the irregular/regular distinction offers a relatively simple and well-studied cross-linguistic approach for examining the neurocognitive correlates of lexicon and grammar.

Predictions of the models

Dual-system models predict that representations of irregulars are stored in lexical memory, whereas regulars are grammatical rule products (BOX 1). Single-system models argue that all forms are learned, represented and processed in an associative memory, which can be modelled by a connectionist network. Whereas early connectionist models focused on the phonological mappings between stem and past tense^{34,36}, a recent

Box 2 | A single-system model of regular/irregular morphology

Double dissociations between regular and irregular forms have posed a problem for single-system language models, but a recent model³⁵ has tried to go beyond this limitation. The model contains distinct representations for semantics, and for input and output phonology, each being subserved by a separate set of units. These units (ellipses), and the pathways between



them (arrows), are assumed to be neuroanatomically distinct, and can therefore be lesioned independently. Although the model claims distinct representations and pathways, it is a single-system model in that it assumes a uniformity of processing mechanisms. All representations and pathways underlie the computation of both regular and irregular morphological forms. It is suggested that the inconsistent phonological patterns of irregulars result in their computation relying more on semantics than on phonology. Regulars, by contrast, do not show this bias, and novel verbs actually show the opposite pattern, relying for their computation on phonology but not on semantics.

Simulations of damage to the semantic representation led to worse performance in producing irregular rather than regular or novel past tenses. Simulations of damage to output phonology led to worse performance in producing novel rather than regular and irregular past tenses, but no difference between regulars and irregulars. So, the model revealed double dissociations between irregular and novel verbs but, crucially, not between irregular and regular forms, even from lesions to output phonology. The results from this simulation do not fit the empirical data from patients. For example, several reports^{8,68–72,74} have revealed a consistent pattern of worse performance by patients with anterior aphasia in processing regular than irregular past tenses over five classes of task: production, reading, judgement, writing and repetition.

single-system model attempted to integrate semantic and phonological knowledge, which are assumed to be linked to temporal lobe and frontal lobe structures, respectively³⁵ (BOX 2).

The declarative/procedural model predicts that irregular forms are stored in declarative memory. This is an associative memory of distributed representations, over which the phonological and semantic mappings of the transformations are learned, stored and computed (BOX 1). The procedural system, by contrast, is suggested to subserve the composition of regular forms from their parts in real time ('walk'+'-ed'). The computation of a morphologically complex form involves the parallel activation of the two systems; the declarative system tries to compute a form in associative memory, while the procedural system attempts to compute a rule product in real time37. As the memory-based computation proceeds, a continuous signal is sent to the rule-processing system, indicating the probability of the successful retrieval of a form from declarative memory. This signal prevents the procedural system from carrying out its computation. So the computation of 'dug' blocks the computation of 'digged'. If a memorized form is not retrieved, then the rule can apply, resulting in over-regularization errors such as 'digged'^{8,37-40}. In addition, the successful computation

of a form by the procedural system should inhibit the memorization of that form in declarative memory, therefore decreasing the likelihood of memorizing regular forms. However, any regular form can, in principle, be memorized. The likelihood of memorization should increase with factors such as the frequency with which the item is encountered or individual variation in learning abilities of the declarative memory system.

The different theoretical perspectives make specific predictions about the issues that I have discussed above, allowing the theories to be distinguished empirically.

Separability. The declarative/procedural model and other dual-system models posit that lexicon and grammar are subserved by separable cognitive systems, with at least partially distinct neural correlates. So, these models predict DOUBLE DISSOCIATIONS between the two language capacities. Single-system models do not invoke separate underpinnings for lexicon and grammar, and therefore do not predict such double dissociations.

Computation. The declarative/procedural model assumes that language involves an associative memory system and a symbol-manipulation system. This assumption is consistent with other dual-system models, although many such models adopt the distinct perspective that lexical memory is a rote list of words (BOX 1). According to the declarative/procedural model, psychological markers of associative memory, such as FREQUENCY EFFECTS and phonological-similarity effects⁴⁰⁻⁴³, should be found with memorized lexical items including irregular forms, but not with regular and other complex linguistic forms that are rule-computed in real time. By contrast, single-system models predict associative memory effects for all linguistic forms.

Domain generality. According to the declarative/procedural model, but not to other dual- or single-system models, lexicon and grammar are subserved by distinct systems, each of which underlies a specific set of nonlanguage functions. Only the declarative/procedural model predicts associations in learning, representation and processing, among irregular forms, non-compositional lexical items, facts and events. Similarly, only this model predicts associations between regular forms, aspects of syntax and other domains of grammar, and motor and cognitive skills.

Localization. The declarative/procedural model makes specific claims about links between the two language capacities and sets of specific brain structures on the basis of the roles of these structures in the two memory systems. Certain dual-system models predict similar links, but they do not make the particular neuro-anatomical claims of the declarative/procedural model. Single-system models do not predict the same function–structure associations.

As I discuss next, these predictions are supported by evidence from several languages, obtained using a range of methodological approaches in children and adults.

DOUBLE DISSOCIATION A double dissociation is observed when two different tasks lead to complementary patterns in behaviour or brain activation. Task X is normal in patient A but not patient B, whereas task Y is normal in patient B but not in A. Similarly, in scanning healthy subjects, task X leads to activation in one brain area but not another, whereas task Y shows the opposite pattern.

FREQUENCY EFFECTS Words stored in memory are remembered better and faster if they have been more frequently encountered.

Psycholinguistic evidence

Frequency effects⁵ are expected for representations stored in the lexicon, but not for representations that are constructed by mental rules in real time. Several studies have found frequency effects for irregular but not for regular past-tense forms^{40,41,43–45}. A similar contrast has been found between irregular and regular plurals in German^{46,47}. These data indicate that the representations of irregular but not regular past tenses are retrieved from memory^{9,43}. However, frequency effects for some regular past tenses, such as those in which stems rhyme with the stems of irregulars (for example, glide–glided; compare with hide–hid and ride–rode), indicate that at least some regular forms can be stored^{9,40}.

If multiple stored representations share distributed memory traces, then strengthening one representation will strengthen all of them (BOX 1). Such distributedfrequency (phonological-similarity) effects have been found for real and novel irregular past tenses (for example, spring–sprang and spling–splang), but not for real or novel regular past tenses (walk–walked and grock–grocked)^{40,42,43,48}. Analogous contrasts between regular and irregular forms have been found for adjectival past-tense inflection in Japanese⁴⁹. These contrasting phonological-similarity effects support the declarative/procedural and other dual-system models in which irregulars, but not regulars, are represented in a distributed associative memory.

These effects indicate that representations of irregular, but not regular, forms are generally memorized. However, real-time rule processing can also be examined directly. One widely used method is PRIMING⁵. Studies of English past tense, and German participles and plurals, have consistently shown that a target word stem ('walk') is consistently primed as much by its regular inflected form ('walked') as by itself ('walk'); this is not the case for irregulars^{50–52}. This indicates that regulars but not irregulars are decomposed into their stems, as predicted by dual-system models.

The real-time composition of regulars has also been tested by examining the limited storage capacity of working memory. The number of items that it is possible to hold actively in mind is relatively small. If regular complex words ('walked') are composed in real time from multiple independent pieces ('walk' and '-ed'), then maintaining them in working memory would involve maintaining each of their constituent pieces. By contrast, for forms that are associated with a single memorized representation (irregulars), one should need to maintain only one element. It should therefore be possible to retain fewer forms that are composed from two or more independent pieces than forms that are not. Indeed, performance in a working memory task was worse for regular than for irregular past tenses53. The results support the real-time composition of regulars from their stems and affixes.

Evidence from developmental disorders

Specific language impairment. This term is often assigned to developmental language disorders that do not have any other apparent social, psychological or neurological cause⁵⁴. Although specific language impairment (SLI) is a

heterogeneous disorder, homogeneous groups of people with SLI have been identified54, including groups with a hereditary form of the disorder that is accompanied by syntactic deficits^{55,56}. Processing of past tense was examined in two such groups45,57,58, both of which failed to produce novel regular forms (for example, plam-plammed) and over-regularizations (dig-digged), indicating that they were unable to apply the '-ed' suffix productively. Both groups showed frequency effects for regular as well as irregular past-tense forms^{45,57,58}. These data indicate that subjects with SLI had difficulty in learning grammatical rules and were therefore forced to memorize regular as well as irregular forms45,57,58. Motor-skill performance and brain abnormalities were probed in one of the groups. Consistent with an underlying deficit of the procedural memory system, they showed impairments in performing motor sequences⁵⁹ and abnormalities in frontal cortical regions, including the left supplementary motor area and Broca's area, and in the caudate nucleus of the basal ganglia⁶⁰. These findings link the rule of '-ed' affixation for regular verbs to syntax and procedural memory.

Williams' syndrome. People with WILLIAMS' SYNDROME might have spared syntactic abilities but abnormal lexical retrieval^{61,62}. Children and adults with the disorder have more difficulty producing irregular than regular past tenses (dig–dug versus look–looked) and plurals (mouse–mice versus rat–rats). Most of their errors are over-regularizations (digged, mouse)^{62,63}. These results help to dissociate irregular from regular forms, and link irregulars to lexical memory and regulars to syntactic abilities.

Neurological evidence

Aphasia. There are at least two fundamental classes of APHASIA — anterior and posterior^{6,64–66}. Anterior aphasia is associated with damage to left frontal regions - in particular, to Broca's area and nearby cortex --- the basal ganglia and portions of inferior parietal cortex^{64,65}. People with anterior aphasia typically show AGRAMMATISM, but are relatively spared in their use of non-compositional words. Anterior aphasia is also linked to IDEOMOTOR APRAXIA^{6,20}. Posterior aphasia, in turn, is associated with damage to left temporal and temporoparietal regions. People with posterior aphasia show impairments in the production, reading and recognition of word sounds and meanings. These patients tend to produce syntactically well-structured sentences and do not omit morphological affixes such as '-ed'6. Posterior aphasia is also linked with semantic impairments in non-language domains, but not with motor deficits^{64,67}.

People with anterior aphasia are worse at producing^{8,68}, reading out loud^{8,68–73}, writing to dictation⁷⁴, repeating⁷¹ and judging⁶⁸ regular versus irregular pasttense forms. These patients also have more difficulty in reading^{69,70} and writing⁷⁴ regular compared with irregular plurals. Patients with posterior aphasia show the opposite pattern: worse production^{8,68}, reading⁶⁸ and judgement⁶⁸ of irregular past tenses. Similar double dissociations have been found with a priming task^{75,76}. In Japanese, the

PRIMING

A word is recognized faster if it has been primed by an earlier presentation of the same word.

WILLIAMS' SYNDROME A hereditary developmental disorder characterized by cognitive impairment (usually mild mental retardation), distinctive facial features and cardiovascular disease.

APHASIA

Language impairments acquired as a result of stroke or other brain injury.

AGRAMMATISM

Syntactic and morphological impairments in production and comprehension, including those in the use of free and bound grammatical morphemes (auxiliaries, determiners, and affixes such as '-ed').

IDEOMOTOR APRAXIA An impairment in the expression of motor skills. Patients with ideomotor apraxia have problems with imitation, pantomime and tool use.

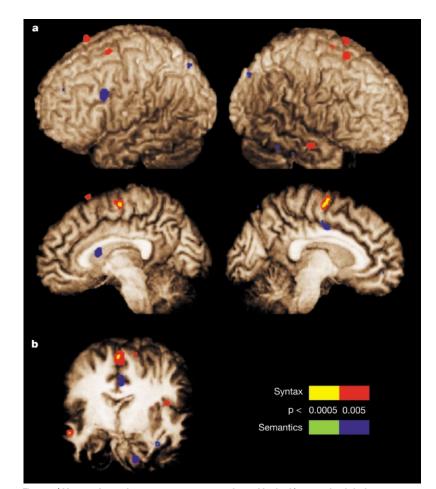


Figure 1 | Haemodynamic responses to syntactic and lexical/semantic violations detected by fMRI. Haemodynamic responses averaged over 14 subjects in a functional magnetic resonance imaging (fMRI) study. **a** | Syntactic violations elicited greater blood-oxygenlevel-dependent (BOLD) activations than semantic violations, primarily in bilateral superior frontal gyrus, corresponding to Brodmann areas (BA) 6 and 8, including the supplementary motor area. Additional activations were observed in the left insula and right anterior superior temporal sulcus. **b** | Semantic anomalies yielded a different pattern of activation, with substantially more temporal and temporoparietal involvement than syntactic anomalies, in the angular gyri bilaterally (BA 39), the right middle temporal gyrus (BA 21), and left hippocampus and parahippocampal gyrus. Additional activations were found in dorsolateral prefrontal cortex and medial foci. Reproduced with permission from REE 103 © 2001 Plenum Publishing Corporation.

double dissociation between people with anterior and posterior aphasia has been found in a judgement task of regular and irregular forms in derivational morphology⁷⁷. The findings link irregular forms to lexical and non-linguistic semantic memory, and to temporal/temporoparietal cortex, and link regular forms to syntax, motor skills, and left frontal cortex and the basal ganglia.

Neurodegenerative disease. Alzheimer's disease largely affects structures in the temporal lobe, leaving frontal cortex (particularly Broca's area and motor regions) and the basal ganglia relatively spared⁷⁸. Temporal-lobe dysfunction might explain the impairments of patients with Alzheimer's disease in learning new and using established lexical and conceptual knowledge^{79–81}. These patients are relatively spared at acquiring and expressing motor and cognitive skills^{79,82–84}, and aspects of syntactic processing^{85,86}. In the morphology domain, investigations of past

tense have found that error rates in object naming and in fact retrieval correlate with error rates in producing irregular but not regular forms^{8,87}. Patients with severe deficits in object naming or fact retrieval make more errors in producing irregular than regular past tenses. Similarly, Italian patients with Alzheimer's disease have greater difficulty in producing irregular than regular present tense and past participle forms in Italian⁸⁸.

Semantic dementia is associated with severe degeneration of inferior and lateral regions of the temporal lobe. The disorder results in the loss of lexical and non-linguistic conceptual knowledge⁸⁹, with spared motor, syntactic and phonological abilities⁹⁰. Patients with semantic dementia yield a pattern like that of patients with Alzheimer's disease. They have more trouble producing and recognizing irregular than regular past tenses, and the degree of their impairment on irregular forms correlates with their performance on an independent lexical memory task⁹¹. The data link irregular forms to stored words and conceptual knowledge, and to inferior and lateral temporal lobe regions.

Parkinson's disease is associated with the degeneration of dopamine neurons, especially in the substantia nigra of the basal ganglia. Loss of dopamine leads to the suppression of motor activity (hypokinesia) and difficulty in expressing motor sequences^{19,92,93}. It might also account for the impairments of patients with Parkinson's disease in acquiring motor and cognitive skills^{83,94}, and in grammatical processing95-97. By contrast, the temporal lobe remains relatively undamaged in these patients, and the use of words and facts remains relatively intact, if dementia is not present^{80,83,93}. In fact, non-demented patients with Parkinson's disease that suffer from severe hypokinesia show a pattern opposite to that found among patients with Alzheimer's disease, making more errors when producing regular versus irregular past tenses. The level of right-side hypokinesia, which reflects degeneration of the left basal ganglia, correlates with error rates in the production of regular but not irregular forms. Intriguingly, left-side hypokinesia is not accompanied by the analogous correlations with error rates in the production of any type of past tense, underscoring the role of left structures in the use of grammatical rules^{8,87}.

Although Huntington's disease is also associated with degeneration of the basal ganglia, it involves different structures than those affected in Parkinson's disease; in particular, regions of the caudate nucleus. This degeneration leads to unsuppressible movements (hyperkinesia) instead of the hypokinesia that characterizes people with Parkinson's disease⁹². In the language domain, patients with Huntington's disease also show the opposite pattern of abnormalities to that found in Parkinson's disease^{8,87}. Patients with Huntington's produce forms like 'walkeded' and 'dugged', but not analogous errors on irregular verbs like 'dugug' or 'keptet', indicating that these errors are not attributable to articulatory or motor deficits. Instead, the data point to unsuppressed '-ed' suffixation. The finding that the production rate of these over-suffixed forms correlates with the degree of chorea, across patients, strengthens this conclusion. The findings in Parkinson's and Huntington's diseases strongly implicate frontal cortex and the basal ganglia in '-ed' suffixation. More generally, they support the hypothesis that these structures underlie the expression of grammatical rules, as well as movement, and indicate that they have a similar function in the two domains.

Amnesia. Bilateral damage to medial temporal lobe structures leads to an inability to learn new information about facts, events and words12. Importantly, neither phonological nor semantic lexical knowledge is acquired98,99, supporting the hypothesis that these structures underlie the learning of word forms, as well as meanings. The ANTEROGRADE AMNESIA seen after damage to the temporal lobe is accompanied by variable degrees of RETROGRADE AMNESIA. However, knowledge acquired a long time before the lesion tends to be spared¹². So, although medial temporal lobe structures underlie the learning of new lexical information, knowledge of words learned during childhood should be intact in adult-onset amnesia. As expected, our examination of the well-studied global amnesic H.M.¹⁰⁰ revealed that he did not differ from normal age- and education-matched subjects in syntactic processing tasks, or in the production of regular and irregular forms in past-tense, plural and derivational morphology.

Neuroimaging evidence

Haemodynamics. Several studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have investigated the pattern of brain activation during language processing. Lexical and semantic processing is strongly associated with activation in temporal/temporoparietal regions, including the medial temporal lobe (FIG. 1)16,101-104. In addition, selection or retrieval of lexical and semantic knowledge leads to activation in anterior prefrontal cortex¹⁷. By contrast, several tasks that are designed to probe syntactic processing preferentially elicit activation of Broca's area, the supplementary motor area (FIG. 1) and the left basal ganglia (caudate nucleus)^{102,105-109}. Interestingly, the processing of lexically stored syntactic knowledge (for example, wordspecific knowledge about what arguments a verb takes) is accompanied by activation of the temporal lobe¹⁰⁴.

Imaging studies have examined the production of regular and irregular forms in the English past tense^{110–112}, and in the German past tense and past participle¹¹³. These studies have found differential activation in frontal and temporal regions for the two forms, although the specific regions have varied across the studies⁹. A study of Finnish, a morphologically very rich and productive language, reported greater activation in Broca's area for regular morphologically complex words than for non-compositional words¹¹⁴, strengthening the view that this region underlies rule-based morphological processing.

Electrophysiology. Event-related potentials (ERPs) reflect the real-time electrophysiological activity of the brain elicited by cognitive processes that are time-locked to the presentation of target stimuli. Difficulties in semantic processing with lexical or non-linguistic stimuli elicit central/posterior bilateral negativities that peak

about 400 ms post stimulus (N400s), and depend on bilateral temporal lobe structures^{115–117}. Difficulties in rule-governed syntactic processing can yield early (150–500 ms) left anterior negativities (LANs)^{118,119}, which have been linked to rule-based automatic computations¹²⁰ and left frontal structures¹²¹. Intriguingly, difficulties in processing word-specific syntactic knowledge can elicit an N400 rather than a LAN¹²². Syntactic processing difficulties also tend to elicit late (600 ms) centroparietal positivities (P600s)¹²³. However, these positivities are associated with controlled processing¹²⁰ and posterior brain regions, and are not suggested to depend on the procedural system.

Several ERP studies have examined regular and irregular inflectional morphology in German^{124,125}, Italian¹²⁶ and English^{127–129}. All of these studies have found distinct ERP patterns for regular and irregular morphology. Although the specific results have varied, a trend has emerged. Whereas inappropriate regular affixation (anomalous addition^{124,125} or omission^{128,129} of the affix) can lead to a LAN, modification of irregular inflection tends to elicit a more central, N400-like negativity^{124,128,129}. Moreover, this LAN does not seem to differ in topography from the LAN that is elicited by syntactic anomalies^{128,129}, underscoring common neural mechanisms for regular morphology and syntax.

Whereas most ERP studies examine language during comprehension, a recent experiment probed regular and irregular past-tense production, and examined cortical localization of the scalp-recorded potentials¹³⁰. Regular past tenses elicited more frontal activation than irregular verbs, but irregular forms yielded more activity in left temporal lobe regions, strengthening the temporal lobe/frontal lobe dichotomy that is predicted by the declarative/procedural model.

Magnetoencephalography. In a MAGNETOENCEPHALOGRAPHIC investigation of regular and irregular past-tense production, DIPOLE MODELLING was used to localize sources of brain activity¹³¹. Dipoles were localized to a single left temporal/parietal region for both regular and irregular verbs, 250–310 ms after verb-stem presentation. Dipoles in left frontal regions were found only for regular verbs and only for times immediately after the left temporal/ parietal dipoles (310–330 ms). No dipoles were found in the right hemisphere. These results are consistent with a dual-system model in which temporal/parietalbased memory is searched for an irregular form, the successful retrieval of which blocks the application of a frontal-based suffixation rule⁸.

Conclusion

In summary, studies using different methodologies have examined the acquisition, computation, processing and neural bases of lexicon and grammar, focusing on irregular and regular morphology in several languages. These studies have tested the predictions of different single- and dual-system language models. The data largely conform to the dissociations and associations that are predicted by the declarative/procedural model, supporting its validity (BOX 3).

ANTEROGRADE AMNESIA The inability to store new information in long-term memory.

RETROGRADE AMNESIA Loss of or inability to recall information that was previously stored in long-term memory.

H.M.

Arguably the best-studied patient in the literature on memory, H.M. became amnesic after the bilateral resection of large parts of the temporal lobe in an attempt to treat epilepsy episodes. The analysis of H.M.'s amnesia provided a clear dissociation between declarative and procedural memory.

MAGNETOENCEPHALOGRAPHY A non-invasive technique that allows the detection of the changing magnetic fields that are associated with brain activity. As the magnetic fields of the brain are very weak, extremely sensitive magnetic detectors known as superconducting quantum interference devices, which work at very low, superconducting temperatures (-269 °C), are used to pick up the signal.

DIPOLE MODELLING A method to determine the location of the sources that underlie the responses measured in a magnetoencephalographic experiment. It provides an estimate of the location, orientation and strength of the source as a function of time after the stimulus was presented.

Box 3 | Some open questions

Although I argue that most of the available evidence supports the declarative/ procedural model, the data are not uniform in this regard. Even the relatively simple approach of studying regular and irregular morphology has failed to yield entirely consistent results, particularly in other languages, in which the contrast is not as well understood as in English²⁵.

Moreover, several issues remain to be further specified by the declarative/procedural model, including the following.

- What is the exact computational role of the procedural system and its parts? What particular functions do the different brain structures in the system underlie? Is the system involved in both structure building and learning rules?
- What specific regions in frontal and parietal cortex subserve these functions? Are inferior parietal structures involved in lexical as well as grammatical functions?
- The declarative/procedural model does not claim that these two brain systems are the only circuits underlying lexicon and grammar, let alone other aspects of language. What other circuits underlie these two language capacities, and how do they relate to the declarative and procedural systems?
- What types of regular and other complex structures are stored? What form do their representations take?
- Are there individual differences (for example, corresponding to sex differences) in the storage of complex forms?

• How similar are the linguistic and non-linguistic computations in each of the two systems? Do the similarities extend to the non-linguistic computations in other animals, such as non-human primates? Would this enable the development of an animal model of aspects of language?

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regions.

The declarative/procedural model has several implications. First, the numerous studies of the declarative and procedural memory systems in animals and humans are expected to help to elucidate the computational and neural bases of learning, representation and processing of lexicon and grammar. For example, the neuropharmacology of declarative memory and its underlying neural substrates132 should also pertain to language. Second, because language is a relatively wellunderstood cognitive domain, linguistic theory and related language disciplines will probably shed light on the workings of declarative and procedural memory. Third, the model has direct clinical implications. People with developmental or adult-onset disorders of the grammatical/procedural system should recover through the memorization of complex forms using lexical/declarative memory. Indeed, this is what subjects with SLI seem to do (see above)45,57,58. In addition, preliminary evidence indicates that people with anterior (but not posterior) aphasia memorize regular forms after the onset of their lesion¹³³. Such recovery could be stimulated with pharmacological and other therapeutic approaches derived from our current knowledge of the two memory systems. Last, the existence of brain systems that subserve language in humans, but are homologous to systems that are present in other animals, has implications for the evolution of language.

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Biography

Michael Ullman is a faculty member of the Department of Neuroscience and at the Georgetown Institute for Cognitive and Computational Sciences at Georgetown University, Washington DC. He holds secondary appointments in Linguistics, Psychology and Neurology. He received his Ph.D. from the Department of Brain and Cognitive Sciences at the Massachusetts Institute of Technology. His group examines the neural, psychological and computational underpinnings of language, focusing on the mental lexicon of memorized words and the mental grammar, which underlies rule-governed behaviour. He uses various methodological approaches, including neuroimaging, neuropsychology and psycholinguistics, to probe the structure of words (morphology), and phrases and sentences (syntax), in several languages, including English, Italian, Spanish and Japanese.

At a glance

- Several models have been proposed to account for the neurocognitive basis of the mental lexicon (a repository of stored words) and the mental grammar (which captures the regularities of language). The declarative/procedural model argues that lexicon and language depend on two neural systems that are intensively studied in the context of memory: declarative and procedural memory.
- The declarative/procedural model links lexicon with the declarative system and with brain structures in temporal/temporoparietal regions. On the other hand, the model links grammar with the procedural system, and with structures in the basal ganglia and frontal cortex.
- The declarative/procedural model makes a set of specific predictions about the neurocognitive basis of lexicon and grammar, regarding their separability, computation, domain generality and localization. These predictions, which have been thoroughly tested in the context of the use of regular versus irregular word forms (walk–walked versus go–went), have been helpful in contrasting this model with other competing perspectives.
- Several lines of evidence support the declarative/procedural model over alternative views. This evidence has come from psycholinguistic studies, the analysis of developmental disorders of language, neurological cases, haemodynamic studies and neurophysiological observations. Collectively, the data show a double dissociation. On the one hand, there is a link between lexicon, associative-memory markers, the knowledge of facts and events, and temporal/temporoparietal regions. On the other, there is a link between grammar, motor and cognitive skills, and structures in the frontal lobe and the basal ganglia.
- The declarative/procedural model has several implications. First, studies of declarative and procedural memory should help to elucidate the neural bases of lexicon and grammar, and vice versa. Second, the model has clinical implications for people with developmental or adult-onset disorders of grammar, as they might recover through the memorization of complex forms using the declarative system. Last, the existence of systems that subserve language in humans and are homologous to systems present in other animals has implications for the evolution of language.