The representation of grammatical categories in the brain

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Language relies on the rule-based combination of words with different grammatical properties, such as nouns and verbs. Yet most research on the problem of word retrieval has focused on the production of concrete nouns, leaving open a crucial question: how is knowledge about different grammatical categories represented in the brain, and what components of the language production system make use of it? Drawing on evidence from neuropsychology, electrophysiology and neuroimaging, we argue that information about a word's grammatical category might be represented independently of its meaning at the levels of word form and morphological computation.

Understanding how words are represented and retrieved in the brain will be crucial to any eventual neurobiological theory of language. The problem goes beyond determining how neural circuits encoding a particular conceptual representation are mapped to a unique and arbitrary set of representations for sounds, letters, or gestures: although this might suffice for the production of isolated words, it fails to specify how words are combined into phrases and sentences. How do we know, for example, that '*the singing are birds*' is not a well-formed alternative to '*the birds are singing*'? (And why are such exchanges rare even among speech errors? [1]) The most obvious answer is that *bird* and *sing* belong to different grammatical categories – noun and verb, respectively – with different syntactic roles, and that this information is encoded in the brain and accessed during the course of language production.

Even though grammatical categories are not created equal [2], most research in the area of lexical access has used the production of concrete nouns as a proxy for word production in general. Therefore, it is not too surprising that our current picture of the cortical organization of lexical knowledge leaves little room for mechanisms that might be sensitive to differences between words of different categories. A recent review of neuroimaging studies of lexical access parcels the left perisylvian cortex into areas involved in retrieving word forms from concepts and in various stages of phonological processing [3], but sheds little light on the question of how and where the brain processes a word's grammatical role.

This picture might change as more researchers use neuroscientific methods to address finer-grained questions about the representation of words in the brain. To date, however, experiments on the retrieval of grammatical category information have yielded conflicting results. Although electrophysiological measures have suggested that nouns and verbs are processed by distinct neural generators, neuroimaging has turned up little evidence for an anatomical distinction. The neuroimaging results have led some to argue that words are stored in distributed networks, in which categorical distinctions are not explicitly represented [4] – a conclusion that is at odds with what is known from the study of patients with language deficits following brain damage.

Are we at an empirical impasse? In our view, little progress will be made unless there is a clear understanding of what is at issue. Many researchers have treated the noun–verb distinction as essentially a question of word meaning. We argue that it is likely to prove more productive to focus on category specific processes at the levels of word form and inflectional morphology, where evidence from neuropsychology suggests that nouns and verbs have separate and distinct neural representations.

As the case reports on which we base our argument have primarily investigated language production, we will focus on output processes, although we assume that similar representations are invoked in comprehension. Likewise, we will confine our discussion to nouns and verbs, leaving out mention of other grammatical categories (adjective, preposition, etc.) – both for the sake of brevity and because nouns and verbs are the categories most often at the heart of discussion.

Evidence from neuropsychology: an overview

Perhaps the best reason to believe that *some* part of the brain is sensitive to the distinction between nouns and verbs comes from the voluminous literature on patients with grammatical category-specific deficits [5–13] (see Fig. 1 for examples). The vast majority of these reports suggest that left-hemisphere language areas are split by grammatical category roughly along anterior–posterior lines: the retrieval of nouns seems to be dependent on structures in the temporal lobe, whereas verb retrieval depends more on prefrontal areas [11,12].

However, there are cases of patients with grammatical category selective impairments whose lesions do not conform to this pattern. One patient studied by de Renzi and di Pellegrino [14] suffered massive frontal damage but

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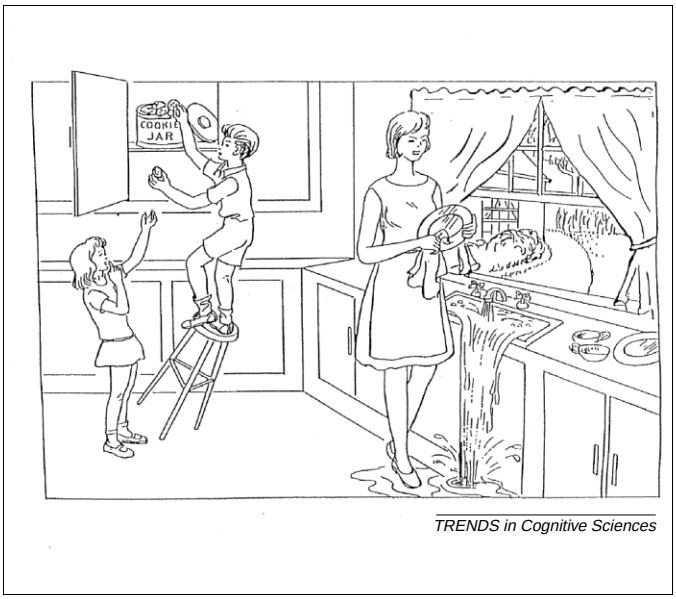

Fig. 1.

EBA: 'Oh Lordy, she's making a mess. She let the thing go, and it's getting on the floor. They're stealing something. He's falling; he's gonna hurt himself. She's cleaning these things. She's looking at him falling, and she's gonna get some of the stuff he's giving her.'

CH: 'Okay, the boy is, his cookies, he is, uh, his sister is look for him cookies, but he is going to fall out of his stool because his legs are not bent that way. And his mother is, all the time her dishes are bein'…and his mother is, she has got this [k ʌ sɪt] and her faucet is never really on that, and then he has a tree, but he is, I don't know.'

Samples of oral production from two patients asked to describe the picture shown. EBA is relatively more impaired at naming nouns than verbs, and uses only generic nouns (like '*stuff*') in her spoken description of the picture. CH, by contrast, has difficulty retrieving verbs, and the verbs that he does produce often occur in ungrammatical contexts ('*is look for him cookies*'). Cookie Theft picture reproduced with permission from Ref. [43].

still produced verbs better than nouns in speech. The same is true of patient JR [15], whose lesion bypasses those portions of the temporal lobe thought to be implicated in noun production [16]. At the same time, some patients with apparently verb-specific deficits have no trace of frontal damage [17]. These 'exceptions' to the anterior–posterior rule imply that several brain regions could be sensitive to the differential processing of nouns and verbs, perhaps at distinct stages of word retrieval.

What is a 'grammatical category'?

The possibility that distinctions between nouns and verbs at different levels of representation are mapped onto different cortical areas poses a problem for researchers trying to identify the locus of impairment in individual cases. It also presents a wealth of opportunity for those interested in charting the cortical layout and cognitive architecture of language functions. To exploit this opportunity, we must be able to define the levels of representation at which grammatical category might be relevant.

Are nouns and verbs distinguished at the semantic level?

There is good intuitive reason to believe that the distinction between nouns and verbs is captured at least in part by differences in word meaning [18,19]. Prototypically, nouns refer to objects or entities, whereas verbs refer to actions. The action-object distinction has been invoked frequently to account for apparently grammatical category specific deficits in neuropsychology [8,11], and derives some of its force from the felicitous observation that verb deficits seem to result from damage to parts of the brain adjacent to those involved in motor planning, whereas noun deficits result from damage to areas associated with the processing of sensory and other semantic features of objects. Computational models have been used to quantify this intuition, showing that when words are rated for their sensory and motor associations, nouns and verbs segregate partly along that dimension [20]. Moreover, verbs referring to actions tend to cluster with motor-related nouns, such as names of tools.

Another class of semantic accounts hinges on the observation that nouns and verbs differ along continuous semantic dimensions like concreteness [21,22] and imageability [23]. On these hypotheses, noun or verb production might be impaired following brain damage because of an inability to access information about the meaningful features of concrete words (noun deficits) or abstract words (verb deficits). As we will argue, it is unlikely that either of these kinds of semantic explanation is sufficient to account for grammatical category specific deficits.

Is grammatical category encoded at the level of lexical form?

It is possible that distinctions between grammatical categories are reflected in the organization of the lexicon; that is, that features like noun and verb are associated with word forms, independent of semantics. Some of the most striking evidence for the representation of grammatical category at this level comes from the study of patients with modality specific impairments (Box 1).

Another way of approaching the problem is to use production tasks controlled explicitly for semantic variables. When this has been done, the results show that semantic factors do not tell the whole story. One patient who is impaired at producing verbs shows *better* performance with highly agentive action verbs [24], contrary to what meaning-based accounts (and computational models that ostensibly support them) seem to predict. This patient also shows no difficulty naming tools compared with naming nouns that have more 'sensory' associations. Likewise, Berndt and colleagues have shown that grammatical category and imageability contribute independently to word production deficits [25] (Fig. 2). Such studies suggest that grammatical category may be an intrinsic property of representations at the form level.

Are grammatical categories really morphological processes?

In a few cases, it seems unlikely that grammatical category selective processing impairments arise because of an inability to retrieve stored properties of words, whether semantic or phonological. Two patients we have studied present with complementary deficits in producing nouns and verbs on a variety of tests [16]. Interestingly, both patients fare poorly at using words of the impaired category in morphological transformation tasks, in which they must complete sentence frames such as '*every day, he judges; every day, they…*' or '*these are judges, this is a…*'. (In both cases the correct response is '*judge*'.) Even more

Box 1. Modality specific grammatical category deficits

Several patients present with selective problems in producing words of one category (nouns or verbs) in one modality of output (speech or writing but not both) – despite the fact that the target words are exactly the same across modalities. These deficits can occur in the aftermath of stroke [10,44] (Fig. I) or during the course of degenerative diseases [28] (Fig. II).

Modality specific deficits place important constraints on theories about the architecture of the language production system. To begin with, spoken and written word forms must be represented independently, at a level that is sensitive to differences in the processing of nouns and verbs; most likely, they are accessed directly from semantics [45]. The implications for functional neuroanatomy are less clear, but one recent study has reported two patients whose impairments in writing verbs were linked to hypoperfusion in left posterior frontal cortex. When blood flow was restored, written naming of verbs improved to ceiling [29].

Do modality specific deficits prove that grammatical category is represented at the word-form level? This would seem the most parsimonious account – such deficits clearly cannot arise because the store of semantic representations has been damaged. Nevertheless, a semantic explanation cannot be ruled out. Assume that the semantic system is organized in a way that coarsely reflects the noun–verb distinction, whether along lines of actions and objects or abstract and concrete concepts. These cases can then be explained by postulating a disconnection between semantic representations and output representations in one or the other modality. The difficulty in distinguishing between a lexical account and a semantic disconnection account of modality specific deficits underlines once again the problem of determining what kind of information about grammatical category must be represented in the brain.

Fig. I. Patient KSR, whose stroke resulted in a large lesion in left perisylvian cortex, presents with a modality specific double dissociation: he is impaired at writing nouns relative to verbs, but has more difficulty producing verbs than nouns in speech. Reproduced with permission from Ref. [44].

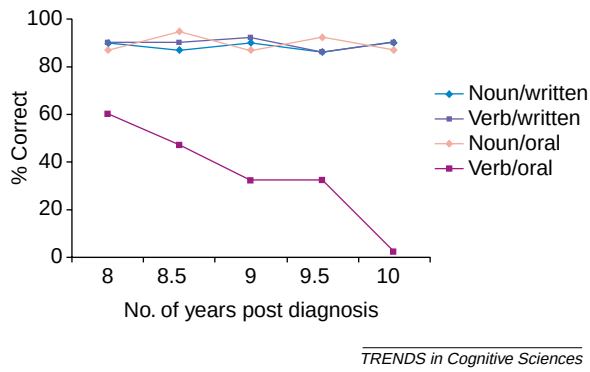

Fig. II. Longitudinal performance of primary progressive aphasic patient MML in tasks involving the written and oral naming of nouns and verbs, from ~8 years to 10.5 years following diagnosis. Oral naming of verbs deteriorated steadily (purple plot), whereas the production of written verbs and nouns in both modalities remained unaffected. Redrawn with permission from Ref. [28].

interestingly, the same dissociations obtain when the transformation is performed with nonce words (‘*he wugs*’; ‘*these are wugs*’), which have no stored meaning.

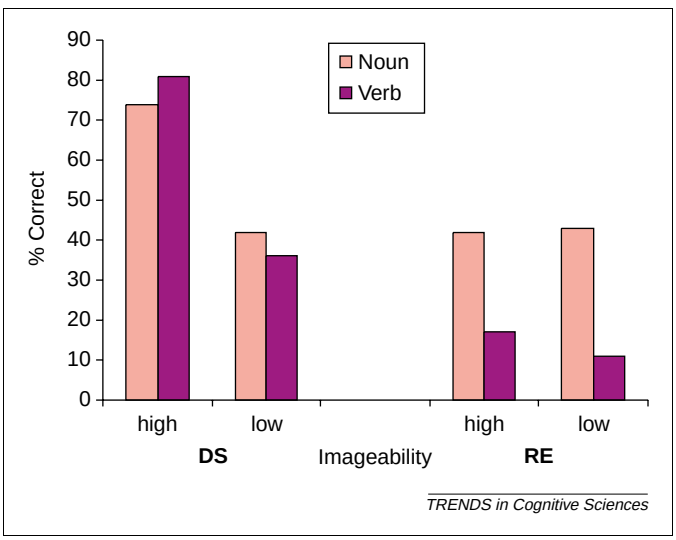

Fig. 2. Berndt and colleagues [25] devised a sentence-completion task in which the target word varied in grammatical category (noun or verb) and imageability (high or low). Shown here are proportions of correct responses on this task given by two patients. Patient DS showed a significant imageability effect in sentence completion, but no effect of grammatical category. On the other hand, patient RE showed an effect of grammatical category, but no effect of imageability. Redrawn with permission from Ref. [25].

These patterns of performance suggest that some part of the brain is sensitive to grammatical categories, not as stored features of words, but as computational processes, the output of which is words in forms appropriate to their syntactic context. In other words, formal grammatical category distinctions can be captured by inflectional morphology.

It is true that the deficits in these patients persist in tasks like repetition and picture naming, which appear not to involve morphological computations. This ceases to be mysterious, however, if one posits that the morphological system cannot be bypassed in the course of lexical output – that is, that *all* words are inflected, at least in languages that possess such machinery. (It happens that English morphological affixes often have no phonological content, as in the case of the third person plural marker for verbs. In languages such as Vietnamese, which lack morphological inflection, grammatical category distinctions can be captured only at the level of word form, or semantics.) One can even imagine a morphological account of modality specific deficits, as morphological structure is realized at the output level.

Grammatical categories and the brain

Although the picture painted by the data we have reviewed is still patchy, we can begin to discern an outline of how information about a word’s grammatical role might be represented in the brain.

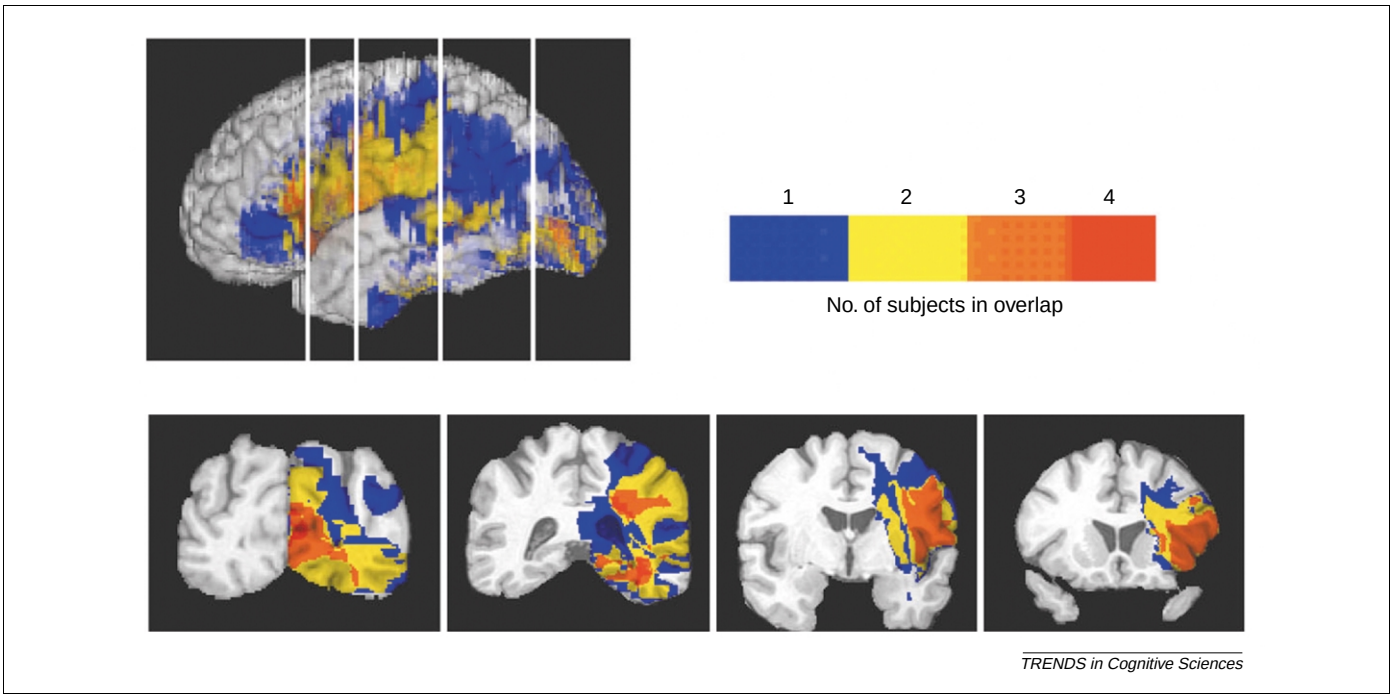

Fig. 3. Areas of lesion overlap in 13 subjects with disproportionate impairments in action naming, relative to naming of concrete entities. The figure shows three regions of maximal overlap: (1) the left frontal operculum, underlying white matter, and anterior insula; (2) the left mesial occipital cortex; and (3) the paraventricular white matter underneath the supramarginal gyrus and posterior temporal region. The color bar indicates the number of subjects in the overlap. Reproduced with permission from Ref. [26].

Semantics

Semantic information about words can be represented in a distributed network, in which the organization of features patterns along some dimension(s) related to meaning and not along lines of grammatical category in the formal sense. Damage to this network might produce deficits that resemble grammatical category specific deficits in the measure to which the poles of the affected dimension mirror the distinction between nouns and verbs. Studies of naming deficits in aphasic patients suggest that semantic information about objects is localized in parts of the middle and inferior temporal lobe [11], whereas semantic properties of actions depends on other frontal and posterior cortical structures [17,26] (Fig. 3).

Lexical status

Grammatical category might affect the organization of knowledge about stored lexical items, such that noun and verb word forms are stored in or retrieved by different parts of the brain. Few concrete proposals have been made regarding the cortical localization of knowledge about grammatical category at the form level, but reports of patients whose deficits are thought to occur at this level show that retrieval of verbs can be compromised by damage affecting parts of the left frontal-parietal cortex [27–29].

Inflectional morphology

Finally, the contrast between patients JR and RC [16] suggests that different neural circuits are engaged when nouns and verbs are used in an appropriate syntactic context (Fig. 4). Lesion analyses suggest that these circuits are located in the left frontal cortex. Difficulties with verbal morphology might stem from damage to part of the left midfrontal gyrus superior to Broca's area, whereas nominal morphology seems to depend on more inferior neural structures. Alternatively, it could be the case that a unitary morphological processing system in the left frontal cortex receives segregated streams of input from other cortical areas that are sensitive to a word's grammatical status.

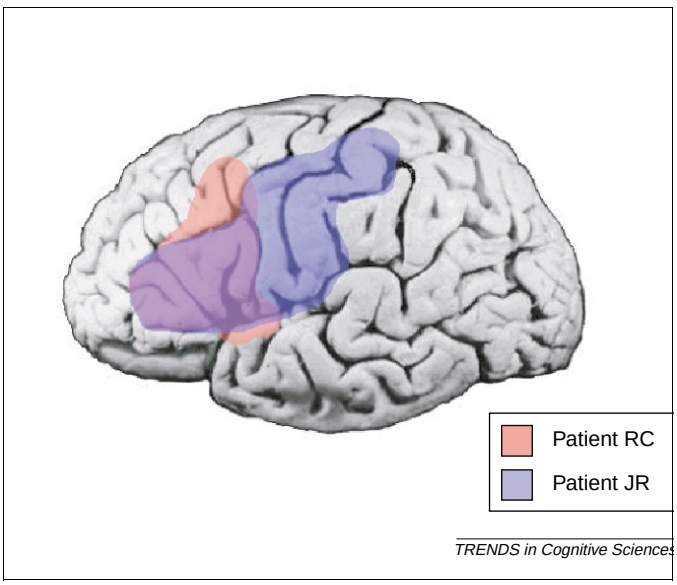

Fig. 4. Brain regions implicated in naming of nouns and verbs. Patient RC (lesion shown in red) is relatively impaired at naming verbs, and presents with a lesion primarily affecting the left posterior frontal lobe and underlying structures. Patient JR (lesion shown in blue) is more impaired at noun production; he suffered a left middle cerebral artery infarction with damage extending from the frontal lobe posteriorly, including the sensory strip and the angular and supramarginal gyri. The left temporal lobe is largely spared, with the possible exception of the first temporal gyrus near the pole.

These possibilities regarding the cortical representation of grammatical category information are not mutually exclusive. It could well be the case that the semantic system is organized in a way that partially captures the distinction between nouns and verbs, that grammatical category is associated with stored word forms, *and* that neural mechanisms for morphological processing differ for words of different grammatical categories [30].

On the other hand, it might turn out that one (or more) of these levels is functionally irrelevant to the representation and retrieval of grammatical category information. For example, grammatical category might *not* be associated with stored word forms, but instead be assigned by morphological processes in ways that are constrained by a word's semantic representation (e.g. plural morphology is only applied to words specifying entities that can be individuated). Adjudicating among these possibilities should be a focus of future research.

Converging evidence

The sketch we have just described is motivated largely by neuropsychological data. What is wanted now is additional evidence from studies that reveal differences in processing nouns and verbs in the unimpaired brain. At least three techniques have been used to test specific hypotheses about the role of brain regions in processing words of different grammatical categories: event-related potentials (ERPs); neuroimaging (including positron emission tomography, or PET, and functional magnetic resonance imaging, or fMRI); and transcranial magnetic stimulation (TMS).

Numerous electrophysiological studies have suggested that distinct neural populations are engaged in the processing of nouns and verbs [31–36]. The most elegant of these have varied semantic factors along with grammatical category, and have found spatially and temporally distinct effects on ERPs of properties like motor and visual association, on the one hand, and grammatical status on the other [36]. Although the specificity of anatomical source localization in ERP remains controversial, these results at least seem to confirm the anterior–posterior distinction that emerges from the aggregate of lesion studies.

Converging evidence from neuroimaging studies, however, is conspicuously lacking. The few studies that have directly compared noun and verb generation have found that both tasks activate a patchwork of cortical regions in the left hemisphere, including parts of prefrontal, temporal and parietal cortex [37,38]. For example, Warburton and colleagues found that verbs produced greater activation than nouns throughout this area, but no region was found to be more highly activated for nouns [37]. Although this study has been criticized for using tasks that might not be equivalent in processing demands across categories [4,39], other paradigms have not produced clearer results: lexical decision and semantic categorization tasks appear to activate similar perisylvian regions for nouns and verbs [4,40,41].

These data have been interpreted as supporting the hypothesis that nouns and verbs are represented in an undifferentiated cortical network [4]. However, the failure of neuroimaging studies to replicate the dissociations observed in patients might be more a function of the specific questions that are asked than of the organization of lexical knowledge in the brain. It is not clear that tasks like lexical decision and semantic categorization require subjects to tap into specifically grammatical knowledge about stimulus items; if they do not, we might not expect to see metabolic differences in processing words as a function of their grammatical category, at least not at the resolution afforded by PET and fMRI.

We have tried to study questions about the cortical representation of nouns and verbs using tasks designed to engage grammatical processes. In particular, we have asked normal subjects to perform transformation tasks of the kind we have used with patients [16], which require the ability to manipulate grammatical information about nouns and verbs. When TMS is used to suppress a region in the left prefrontal cortex near Broca's area, production of morphologically inflected abstract and concrete verbs – but not of nouns – is delayed. This disruption affects both real verbs and nonce words used as verbs, suggesting that the left prefrontal cortex is involved in processing verbs as grammatical objects [42].

Guidelines for future research

If questions about the representation of grammatical category knowledge are to be made empirically tractable, researchers must take care both to define the level of representation at which grammatical category is being investigated, and to choose tasks sensitive to computations at that level. For example, if the distinction between nouns and verbs is an essentially morphological one, it stands to reason that very little purchase will be gained on the issue of grammatical categories by studying subjects' behavior in a semantic classification task that requires little, if any, morphological computation. By using well-tailored tasks in complementary experimental methodologies, we stand to gain some understanding of how the building blocks of language are pieced together by the brain.

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