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The battle for Broca's region

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The battle for Broca's region

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The intense effort to characterize Broca's region has produced many views on its anatomy and function. Here, we present the leading approaches and consider ways to adjudicate among them empirically. Anatomically, we focus on the cytoarchitecture of Brodmann areas 44 and 45, which constitute Broca's region. Functionally, we discuss four views: action perception, working memory, syntactic complexity and syntactic movement. We compare these views, reflect on how they can be distinguished experimentally and review relevant aphasia and functional magnetic resonance imaging (fMRI) studies. Although no single hypothesis accounts for all of the data, the role of Broca's region in language comprehension is best explained by the syntactic movement account. This conclusion opens the door for an attempt to define general principles for the neural representation of linguistic knowledge.

Introduction

In the old days of neuropsychology, the living was easy. Functional anatomy was based on investigations with brain-damaged patients, whose lesions were identified through postmortem procedures, or later by low-resolution scans; the analysis of behavioral deficits was limited to intuitively formulated modalities that translated into simple error-inducing experiments. These days are gone. Advances in anatomy and imaging, and progress in (psycho)linguistics have brought dramatic changes to our practices.

The approaching 150th anniversary of Paul Broca's landmark essay on the 'seat of the faculty of language in the brain' is a good time to take stock [1]. The intense effort to characterize the brain region named after Broca has produced a large number of experimental results and many ideas about its anatomy and function. It has also produced puzzles and debates. Here, we present the main current approaches and consider ways to adjudicate among them empirically, so that progress can be made.

Broca had several leading ideas: as a phrenologist, he believed that mental abilities are separable and that language is a special faculty – functionally individuated, neurologically distinguishable, left lateralized and localizable in a single region. Thanks to his pioneering effort, and to the work of other 19th century neurology giants (Wernicke, Lichteim, Hughlings-Jackson, and even Freud), a new functional neuroanatomy emerged, in which language was viewed as a collection of activities (speaking, listening, repetition, naming, reading and writing) that were attributed to several connected left-hemispheric loci [2,3] (Figure 1).

The success of this model made aphasiology the flagship of a burgeoning neuropsychology. Although psycho- and neuro-linguists later refined these distinctions, to fit better what we know today about linguistic ability and functioning, the traditional view still forms the basis of the diagnostic schema featured in almost every neurology textbook [4,5].

Below, we consider the current state of evidence concerning the linguistic functions of Broca's region. If cognitive neuroscience is engaged (in part) in the identification of pieces of cognition with brain pieces, then we had better have a clear notion of what the pieces are (or at least of what they should be). Thus, we focus on central aspects of linguistic knowledge and practice, and their neuroanatomical substrate. Methodologically, we commend a multimodal approach, the main methods of which are reverse engineering through investigations with brain-damaged patients and activation detection through fMRI in healthy subjects. The lesion study method avails the experimenter of a relatively unconstrained testing environment, and the analysis of aberrant behavior detects functions that crucially rely on a given, albeit imprecisely described, anatomically inhomogeneous area. Functional imaging offers greater anatomical precision, yet the measurement instruments constrain testing at times, and the signal obtained indicates the participation of an area, rarely proving its crucial role in a task. We seek to combine the two approaches.

The anatomy of Broca's region

Functional localization is contingent on a modular view of brain anatomy. Unless we assume that the brain is anatomically parcelated and demarcate sharp borders that delineate 'areas', precise functional anatomy is impossible. Brain parcelation currently relies on cytoarchitectonic border marking: the cortical ribbon exhibits 'cytoarchitecture' – different lamination and cell-packing density patterns at different loci. These patterns are stable, up to points of abrupt change – borders of cortical areas. Brodmann hypothesized that each cytoarchitectonic area corresponds to a function [6]. This radical modular view is now embraced by brain mappers, who use Brodmann's division extensively.

Yet current technology cannot glean cytoarchitectonic information from a living human: MR brain images detail only topography [7] and do not guarantee precise localization of function because of individual variation in cytoarchitectonic organization. As Box 1 shows, Talairach and Tournoux's solution, encoding Brodmann's century-old
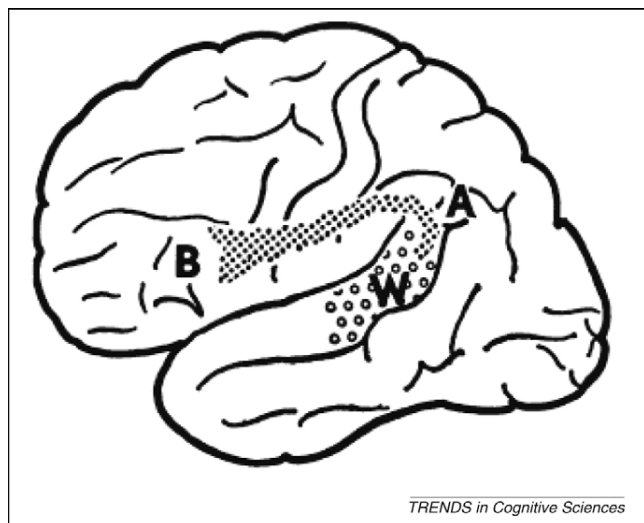
Figure 1. The traditional view of brain–language relationships. The 19th century neurological schema, revived by Norman Geschwind [(1970) The organization of language and the brain. *Science* 170, 940–944], attributes language production to the Left Inferior Frontal Gyrus or Broca's region (B); comprehension, to the Superior Temporal Gyrus and its vicinity – Wernicke's area (W); and the arcuate fasciculus (A) as the 'cable' connecting the other 2 'centers'. Reprinted with permission from AAAS.

map of one hemisphere, is imprecise. Modern computational methods have moreover identified great individual variation in cytoarchitecture, leading to the construction of probability maps, which might be our best current localization tool. We thus examine Brodmann's areas 44 and 45 from the perspective of the probability maps of Amunts *et al.* [12].

The functions of Broca's region

That Broca's region supports language processing is beyond doubt. But what exactly are its linguistic functions? To obtain an answer, we must first ask what proper linguistic functioning and subsequent successful communication presuppose. At a minimum, mastery of linguistic tools is required: knowledge of phonemes and words, and of rules governing their distribution and combination; knowledge of grammatical rules that allow their combination into phrases and sentences; knowledge of interpretive rules that extract meaning from these; and, finally, knowledge of conversational principles that guarantee appropriate linguistic behavior. Mechanisms that implement this knowledge in use must also be available.

All this is not controversial. There is less agreement in the community that studies brain mechanisms that support these functions. Focusing on comprehension functions of Broca's region, we identify linguistic and non-linguistic views. There are four current contenders: action perception (AP), working memory (WM), syntactic complexity (SC) and syntactic movement (SM) (Table 1).

Some of these positions are more nuanced than Table 1 indicates. We simplify for brevity and clarity, attempting to set up distinguishing predictions that can be tested experimentally. Importantly, Broca's region might well be multi-functional. Still, a prudent research strategy pursues the best account available and attempts to extend and refine it. Thus we argue that, although a single hypothesis cannot

Box 1. Cytoarchitectonic probability maps of Broca's region

How can we tell where Broca's region is? It is often identified by visual inspection of the topography of the brain – either by macrostructural landmarks (i.e. sulci) or by the specification of coordinates in a particular reference space. The commonly used Talairach and Tournoux atlas [8] projects Brodmann's cytoarchitectonic map (including 47 areas) on to a template brain. The result is a good, yet imprecise tool: first, Brodmann's parcelation was based on subjective visual inspection of cytoarchitectonic borders, rather than objective measurement. Second, Brodmann analyzed only one hemisphere of one brain. Today, great inter-hemispheric and inter-subject cytoarchitectonic variability is well recognized; third, the Talairach and Tournoux atlas was created by projecting Brodmann's cytoarchitectonic borders of that half brain on to the visible cortical surface. Today, it is well recognized that approximately two-thirds of each area [9] are located deep inside sulci. These problems leave much room for error. Because the resolution of current MRI technology does not enable visualization of cytoarchitecture, and group averaging of anatomical scans blurs or obfuscates sulci, methods to obtain better anatomical parcelation information of MRI scans are required.

The Jülich brain mapping project has developed computational, observer-independent, methods for the determination of cytoarchitectonic borders [10,11] and applied them to ten postmortem brains. Among the areas mapped were the two parts of Broca's region (Brodmann areas [BA] 44 and 45), which exhibited considerable variability across brains in terms of shape, size and position relative to sulcal and gyral structure.

The discovery of this variability (the extent of which is greater in these areas than in others) led to the construction of probability maps, built for localizing activation clusters in MRI scans. A template brain was selected, to which an image of each of the ten brains was warped, but not before the voxels that a given cytoarchitectonic area inhabits in each brain were marked. Thus for area 44, for example, the template brain contains its markings for all ten brains, and individual variation for it can be quantified. Moreover, the template brain has voxels marked for $0 \le n \le 10$, where n designates the number of brains in which this voxel is part of BA 44. This is the probability map for BA 44. This map is used to test and quantify the degree of overlap between an activation cluster and this area, with a resulting localization precision that is the highest currently available.

account for all of the available results, the SM approach, explicated in Box 2, fares better than others and points to fruitful directions.

The picture from aphasia

For over a century, researchers believed Broca's region to be entrusted with only productive language functions, and they focused on the more noticeable aspects of the deficit in Broca's aphasia – non-fluency, agrammatic production and repetition problems. Views diverged: some argued that Broca's region serves grammatical functions [13,14]; others [15,16] tended to follow Hughlings-Jackson and maintained that the proximity of Broca's region to supplementary motor areas suggests that the language deficit in Broca's aphasia is a manifestation of a more generalized motor deficit.

Controlled experimentation on receptive language in aphasia started in the 1970s, and led to important discoveries regarding the role of Broca's region in comprehension, and to continued debate [17]. The current picture seems intimately connected to syntactic variables, which do not easily lend themselves to analysis in action terms: patients seem to experience a syntactically selective comprehension deficiency for sentences that involve SM – an

Table 1. The main positions on the functions of Broca's region.

	Action perception (AP) [43,44]	Working memory (WM) [45–47]	Syntactic complexity (SC) [48–50]	Syntactic movement (SM) [51–53]
What Broca's region supports	Mechanisms that associate action observation and execution.	Verbal WM.	The processing of complex input.	The computation of syntactic movement in reception.
Evidence	(a) Homologous regions in the monkey are pre-motor, store motor commands, are connected to F5 and contain mirror neurons. (b) In humans, it is connected to areas homologous to the monkey's F5. (c) Speech perception and production seem related in a manner similar to action perception and execution.	(a) In fMRI, this region is activated by tasks that tax WM incrementally. (b) The n-back task, requiring comparisons between two members of a sequence that are separated by an increasing number of interveners, activates this area incrementally.	The processing of complex linguistic objects taxes this region more than the processing of simpler ones.	(a) Broca's aphasic patients fail to comprehend sentences with movement and succeed in sentences without movement. (b) In healthy subjects, sentences with movement (but not without) activate this region.
Domain	General	General	Specific	Specific

operation displacing an argument from its 'canonical' position (in which it gets interpreted for its semantic function with respect to a predicate, Box 2). Figure 2 summarizes the results of dozens of experiments with Broca's aphasic patients, involving binary-choice, sentence-to-picture matching tasks. SM (depicted by a red arrow) correlates with a performance drop to chance level.

This rich picture has led to the view that Broca's region houses mechanisms responsible for SM. Subsequent growth in data pointed to cross-linguistic stability but considerable individual variation [18,19]. Quantitative analyses of a large dataset later indicated that the movement effect is robust [20]. Corresponding failures in real-time processing have been documented [21,22]. Importantly, other grammatical and cognitive abilities remain intact in these patients [23–25].

This pattern has two intriguing exceptions: the first is comprehension of relative clauses (Figure 2, Box 2). Relative clauses modify nouns – the bracketed clause in *The cat that [chased the dog] was big* describes a particular cat that functions both as its subject and as subject of the main clause (blue).

Sometimes, however, for example see Figure 3a, *the cat* functions as the object of the relative clause. In this case, it is movement-displaced (red arrow). English or Hebrew speaking patients successfully comprehend the former type but fail on the latter (Figure 2a). Yet Chinese patients present an exactly opposite pattern (Figure 2d) [26]. On reflection, these results become highly structured, because English and Chinese relative clauses have mirror-image structure: in English, *the cat* precedes the relative, but follows it in Chinese. The direction of movement in these

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Box 2. Syntax

A theory of grammatical representation seeks structure in linguistic objects. The complexity and richness of the linguistic signal force a modular approach to grammar, which fits the modular approach to the neural representation of cognition. The idea is that form and meaning are determined by a set of independent rules and constraints, applying either in tandem, or sequentially. Semantic rules interpret this structure, yielding meanings.

Syntactic structure is determined by properties of the participating words and by rules that combine these into phrases and sentences. Words reside in the mental lexicon as sound–meaning pairs, annotated for syntax-relevant properties. Phrase structure rules (or **MERGE**) analyze sentences into hierarchical, tree-like structures the units of which are lexical and phrasal categories (e.g. noun [N], verb [V], adjective [A], noun phrase [NP], verb phrase [VP], adjective phrase [AP]). **MERGE** combines a verb like *run* or *sleep* with a noun, creating a well-formed sentence (*John ran, Mary slept*). The lexicon lists these verbs as intransitive (objectless), excluding a **MERGE** operation that creates ungrammatical strings like *John ran Mary*, or *Mary slept a bed*. Congruence between these knowledge sources (lexicon, **MERGE**) works to ensure that sentences are well-formed at a basic, 'canonical,' level.

Natural language consists of more complicated phenomena. Elements in a sentence are not always found in 'canonical' positions. Certain elements might be displaced by **MOVEMENT**. In the question–answer pair Figure Ia,b, the verb *contact* assigns the same semantic roles to its arguments (arrows). **MOVEMENT** links the original and new positions of a displaced element, thereby guaranteeing that *the senator* is the recipient of action, whether or not it is displaced.

The recursive nature of **MERGE** enables syntactic complexity, for example sentences embedded within other sentences. Both complex

sentences (Figure Ic,d) embed a bracketed and *italicized* relative clause within a main clause.

In Figure Ic, *the cat*, which the relative modifies, is subject of both clauses (hence called a subject relative clause). Yet in Figure Id, *the cat* is displaced, standing in a **MOVEMENT** relation with the object position of the relative ← (hence called object relative clause). The complex sentences in Figure Ic,d thus manifest a **MOVEMENT** contrast.

Finally, **BINDING** governs the relation between anaphora (*him, himself*) and expressions with which they share reference (e.g. **Barack** looked at **himself** in the mirror; **the candidate** asked **her** husband to help **her**).

(a) Which senator did Hilary contact ◄ ?

(b) Hilary contacted the senator.

(c) The cat that [chased the dog] was big

(d) The cat that [the dog chased ◄] was big
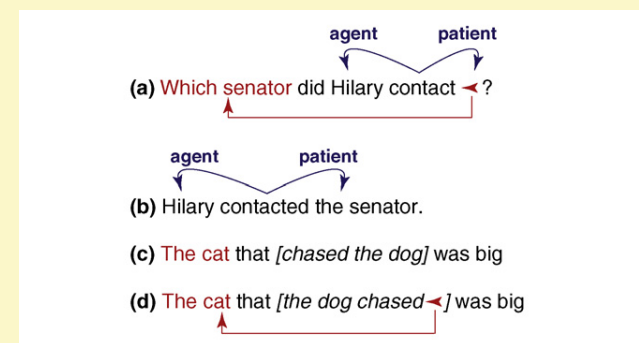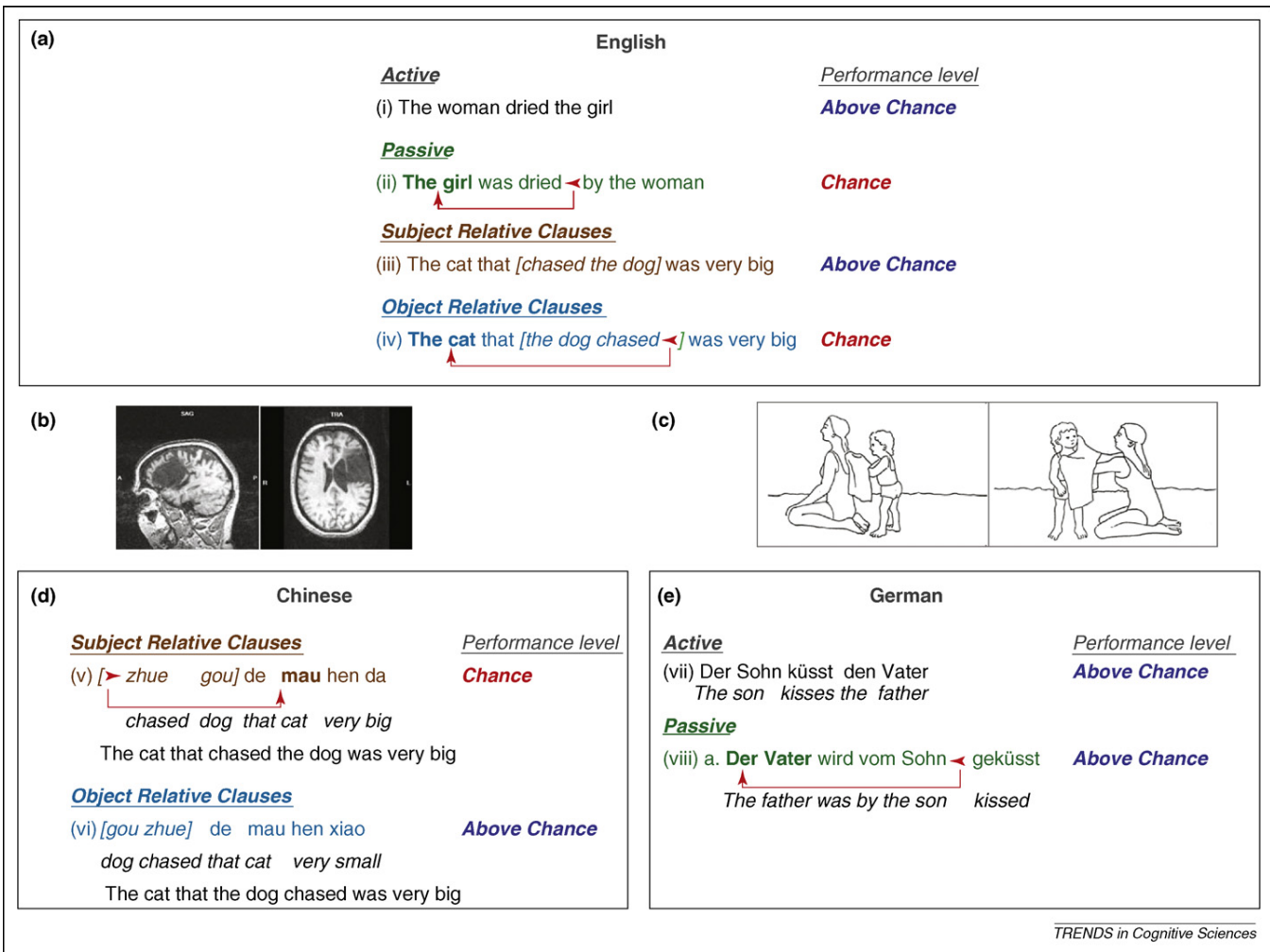
Figure I.

Figure 2. The picture from aphasia. **(a)** English sentences of various types are presented (about 10–20 tokens per type) to patients with lesions in Broca's region **(b)**, concurrent with two drawings **(c)** – one depicts the content of the sentence; the other depicts its reversal (in terms of roles). The patient's task is to point to the correct picture. Syntactic movement [depicted by a red arrow in (a)] correlates with a performance drop to chance level. Apparent exceptions: **(d)** The Chinese counterparts of English relative clauses reveal the opposite performance pattern [26]. **(e)** German and Dutch patients (n_{Ger} = 18; n_{Du} = 40) perform above chance on passive sentences, which are also derived by movement [27]. See main text for discussion.

two languages is reversed, leading to opposite performances (Figure 2a,d).

The second apparent exception to the pattern is that English patients comprehend passive sentences at chance levels (Figure 2a). Yet German and Dutch patients comprehend the passive well in their native language (Figure 2e) [27]. Again, this performance contrast can be deduced from a cross-linguistic movement difference: a movement-displaced noun crosses the verb (blue) in English passive (Figure 3b) but not in German (Figure 3c). The consequence of this cross-linguistic contrast is a performance difference (Figure 2a,e).

Action perception, a unified theory of the functional role of the language and the motor cortices, must deal with
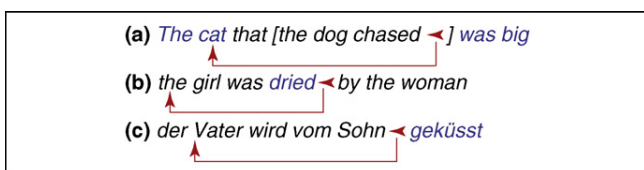

Figure 3.

these intriguingly complex patterns, for which a movement-based explanation seems feasible. Although it is difficult to see how AP would handle these facts, SC and WM are still in the running: SC maintains that movement increases the complexity of sentences and leads to chance performance; WM, based mostly on memory studies with the *n-back* task, maintains that any dependency relation between non-adjacent positions in a sentence requires linking, for which WM is needed. A lesion to the tissue supporting WM thus results in deficient performance.

Preliminary studies, with the aim of distinguishing between SM and WM, used sentences with reflexive binding (e.g. **Mama Bear** *touched* **herself**). Like movement, these sentences require that two elements be linked for interpretation. In particular, the reflexive pronoun needs to be linked to the noun to which it refers (i.e. **Mama Bear**). The establishment of this link requires WM. A sentence verification task required the patients to judge whether Mama Bear touched herself or another character (naturally, controls were included). Six Broca's aphasic patients performed correctly, despite their movement failure, contrary to the prediction of a WM deficit account [28].

(a) Heute hat   der Opa   **dem Jungen**   *den Lutscher*   geschenkt
                     1   2   3
    Today has   the grandpa   the boy   the lollypop   given
    "Today, the grandpa has given the boy the lollypop"

(b) Heute hat **dem Jungen** der Opa ◄ *den Lutscher* geschenkt
                     2   1   ◄   3

(c) Heute hat **dem Jungen** *den Lutscher* der Opa ◄ ◄ geschenkt
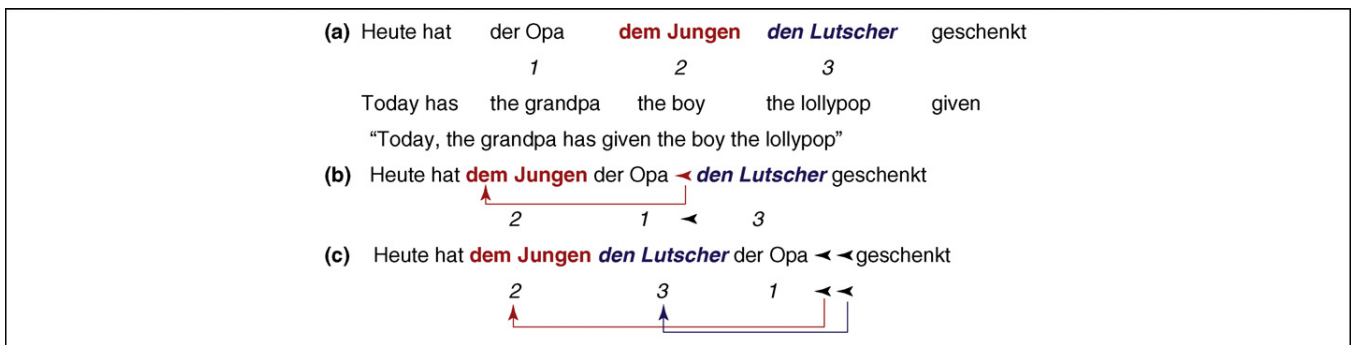   2   3   1   ◄ ◄

Figure 4.

Many questions remain, but this selective impairment pattern provides hints that favor SM.

The reverse engineering method has notable limitations: first, lesions are usually large, and they do not necessarily align with neuroanatomical borders; second, this method cannot discover the functional role of areas unaffected by stroke. These problems call for the use of other methods.

The picture from functional magnetic resonance imaging of sentence comprehension

Broca not only pioneered reverse engineering but also dabbled in imaging. A 'thermometric crown' that he invented measured temperature changes at different scalp positions, which he thought would index local changes in cerebral blood flow [29]. Current imaging methods seem to have realized his vision. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of language processing have created a rich picture, which is mostly consistent with the aphasia results. Results from different tasks repeatedly indicate that SM taxes Broca's region [30–32], whereas other aspects of syntax do not [33].

A move toward parametric designs in this field has recently begun, and this development makes results more comparable with studies of WM and SC. Parametric designs manipulate a variable at least twice by equal amounts and search for corresponding changes in a dependent variable. Friederici and colleagues made the first steps in this direction. They capitalized on the German 'scrambling' rule that displaces noun phrases in a declarative sentence, while keeping meaning more-or-less constant [34] (Figure 4).

An increased number of displacements correlated with greater activation in Broca's region (i.e. *Activation [Figure 4c] > Activation[Figure 4b] > Activation[Figure 4a]*). Yet it is difficult to determine whether this result supports SM, WM or SC. In an attempt to adjudicate among the approaches, we used a judgment task to compare two distinct syntactic dependencies – movement (10) and reflexive binding (11) – by parametrically increasing the distance between co-dependent elements, to detect corresponding activation increments, called linear effects (Box 3).

Greater distance between the co-dependent elements increases both WM demands and complexity across dependency types. Yet if Broca's region is movement selective

(SM), it would only respond to increased movement distance. (Box 4)

As Figure 5 indicates, the evidence favors SM: a linear effect for movement by reflexive binding interaction was measured in Broca's region. The interaction was due to a positive linear effect of SM in Broca's region and absence thereof for reflexive binding. However, reflexive binding

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Box 3. Parametric designs of fMRI experiments

Creating minimal comparisons to ensure that any effect obtained is indeed due to the intended factor is a challenge. The 'subtraction method' is not always effective [35,36], because stimuli often differ in multiple correlated dimensions. Ben-Shachar *et al.* [31], for example, tested the claim that syntactic movement activates Broca's region using a contrast between Hebrew declarative (Figure Ia) and left-dislocated (Figure Ib) sentences (translated to English in Figure I).

The subtraction of the signal obtained for (a) from (b) revealed activation in Broca's region. Although consistent with other findings described in the text, activation might be due to other factors: syntactic movement here serves semantic focus, making (b) mean that **the professor from Oxford** received the red book (= a), but also that *he*, and no one else among the characters under consideration, was the one to receive it. We can enrich (a) so that it expresses the same meaning by imposing emphatic stress on **the professor from Oxford** introducing another confound: stress. Thus, (a) and (b) contrast in more than a single dimension – either stress or meaning. Teasing apart multiple factors, then, is exceedingly difficult if done through direct contrasts.

Parametric experimental designs come to our rescue. They enable us to nest a multivalued parameter within each condition and to distinguish the conditions neurologically by showing that a change in one parametric value, but not others, affects a given brain area. This enables an indirect comparison between conditions, without subtraction: we compare the slopes of the signal intensity curve obtained for each condition as a function of the change in value of the nested parameter (i.e. linear effects).

Braver *et al.* [37] sought to demonstrate that a load increase in verbal WM modulates a certain area, in a manner distinct from other WMs. A direct comparison was insufficient, so their subjects watched sequences of letter stimuli and sequences of other stimuli, with a variable task: subjects had to indicate whether the current letter is identical to a specified one (e.g. '*m*'), to the previous one, the 2-back one, or the 3-back one. The intensity curve in Broca's area for $0 \leq n \leq 3$ in the verbal WM task was different from that obtained for the non-verbal WM task, teasing the two WMs apart.
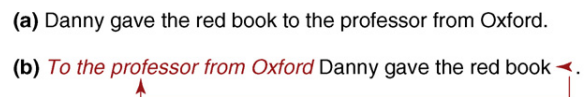
(a) Danny gave the red book to the professor from Oxford.

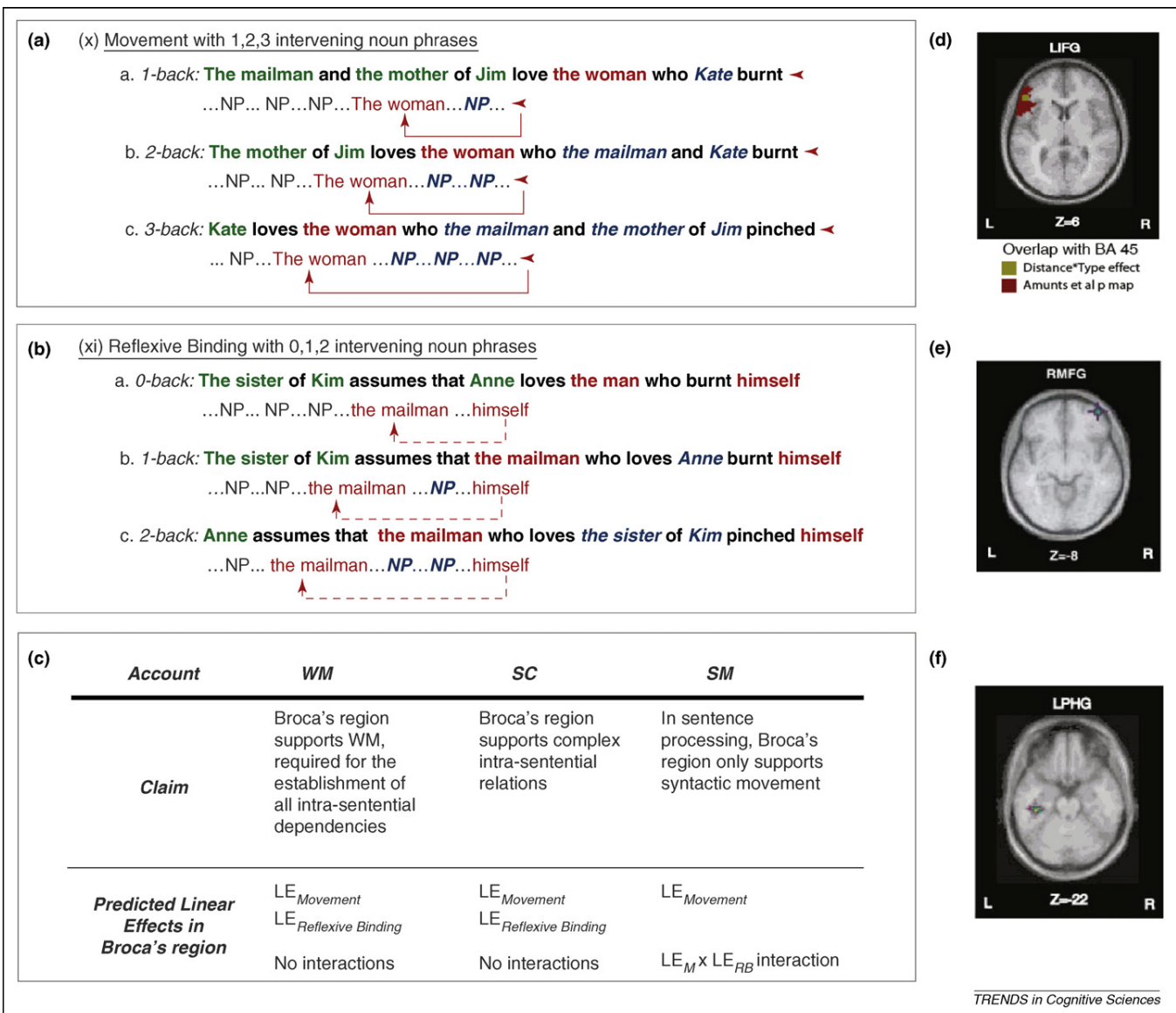(b) *To the professor from Oxford* Danny gave the red book ◄.

Figure I.

Figure 5. The parametric fMRI study – stimuli, predictions and results. Santi and Grodzinsky [54] increased the distance between the two dependent elements by nesting a syntactic parameter – number of intervening noun phrases. We searched for a linear effect (LE) of the parametric manipulation. The three accounts contrast in prediction **(c)**, and we can thus distinguish between them empirically. In Broca's region, we found a linear effect for movement but not for reflexive binding. Precise anatomical localization through co-registration with the probability map of Amunts *et al.* confirmed that the interaction cluster is well within BA 45 **(d)**. Reflexive binding selectively activated the right middle frontal gyrus **(e)**. Both dependencies activated Parahippocampal Gyrus (PHG)/Fusiform Gyrus (FG) **(f)**. (d–f) reproduced with permission from [54].

provided greater activation in the right middle frontal gyrus. This rich picture provides hints for cerebral organization that aligns with (at least some) abstract syntactic principles.

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Box 4. Outstanding questions

1. **Exclusivity.** Is syntactic movement computed solely in Broca's region, or does it also involve other brain regions?
2. **Specificity.** How does the multifunctionality of Broca's region manifest anatomically, and what are the exact relationships between these functions?
3. **Uniformity.** Is Broca's region functionally uniform, given that cytoarchitectonically it is divided into several subregions (e.g. BA 44, 45 and the inferior frontal junction)?
4. **Semantic map.** Is the map for syntax the only linguistic map, given that there are preliminary hints suggesting that semantic composition is also divided into modules and can be localized neurologically [40–42]?

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Coda: a syntactic 'homunculus'? Multiple brain loci for syntax

What lessons can be learned from this short tour? And what can we hope for? The neuroscience of language currently sports clearly articulated, empirically distinguishable, hypotheses. Of these, evidence suggests a highly structured role for Broca's region in sentence analysis, favoring the SM view. However, this does not make non-linguistic results go away. Indeed, Broca's region might be multifunctional, most notably supporting language production [38] and WM [39]. Future work might find distinctions within Broca's region, corresponding to these (putatively separate) functions.

The results we have reviewed, including the possibility of a right hemispheric basis for certain syntactic components, lead to thoughts about neurological similarities between language and other neural systems: like the

sensory/motor homunculi, language might not be situated in the brain arbitrarily but, rather, organized syntacto-topically, such that abstract linguistic abilities are neurologically distinguished. This possible outcome – if true – would put language on a neurological par with other systems, which would be of major interest to neuroscientists and linguists alike.

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