Morphology, language and the brain: the decompositional substrate for language comprehension

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This paper outlines a neurocognitive approach to human language, focusing on inflectional morphology and grammatical function in English. Taking as a starting point the selective deficits for regular inflectional morphology of a group of non-fluent patients with left hemisphere damage, we argue for a core decompositional network linking left inferior frontal cortex with superior and middle temporal cortex, connected via the arcuate fasciculus. This network handles the processing of regularly inflected words (such as *joined* or *treats*), which are argued not to be stored as whole forms and which require morpho-phonological parsing in order to segment complex forms into stems and inflectional affixes. This parsing process operates early and automatically upon all potential inflected forms and is triggered by their surface phonological properties. The predictions of this model were confirmed in a further neuroimaging study, using event-related functional magnetic resonance imaging (fMRI), on unimpaired young adults. The salience of grammatical morphemes for the language system is highlighted by new research showing that similarly early and blind segmentation also operates for derivationally complex forms (such as *darkness* or *rider*). These findings are interpreted as evidence for a hidden decompositional substrate to human language processing and related to a functional architecture derived from non-human primate models.

Keywords: language; morphology; regular inflection; neural decomposition

1. INTRODUCTION

The fundamental challenge for cognitive neuroscience is to construct explanatory accounts of the major human cognitive systems in a neurobiological framework. Most such systems—vision, attention, emotion and memory—have direct non-human precursors, so that studies of these processes in other species can provide a relatively direct input to our understanding and analysis of their human equivalents. A recent example of this is the way that the emerging story about the ventral visual object processing stream in non-human primates (e.g. Ungerleider & Mishkin 1982) has proved to be informative and predictive in constructing a neurobiologically rooted account of human visual object perception (e.g. Simmons & Barsalou 2003; Tyler *et al*. 2004).

Human language, in contrast, stands in a more ambiguous and less direct relationship to its neurobiological precursors. Non-human primates have well-developed systems for processing complex auditory objects, including conspecific vocal calls. Furthermore, as will be seen later, recent research into the properties of these networks is proving to be influential and informative in thinking about the neurofunctional architecture of the homologous human systems. Nonetheless, no matter how well we understand, for example, macaque systems

for processing conspecific vocal communication, these are not remotely comparable to human language in their range of expressive capacities. Human language has functional properties that go far beyond those exhibited by the macaque or closer primate relatives. The focus of this chapter will be on one hypothesis about the nature of this difference—that it lies in the grammatical aspects of human language function—which we will investigate in the context of regular inflectional morphology, a major source of grammatical information during language comprehension and production.

In developing this hypothesis, nonetheless, an important constraint will be the view of the basic architecture of primate auditory processing systems that has emerged from recent research in this domain (Kaas & Hackett 1999; Romanski *et al*. 1999; Rauschecker & Tian 2000; Petkov *et al*. 2006), and is shown in figure 1. This represents the application to auditory object processing of the dorsal/ventral processing stream model long established for primate visual processes. Neuroanatomical and neurophysiological evidence clearly shows that at least two major processing streams leave macaque auditory cortex (itself a close homologue of the human equivalent), with the dorsal stream leaving posteriorly and looping round to connect to areas in inferior frontal cortex. The ventral stream travels forward, down the superior temporal gyrus, and also connects to inferior frontal areas.[1] This division into processing streams, which has been taken up in detail in the human domain (e.g. Hickok & Poeppel 2000; Scott & Johnsrude 2003),

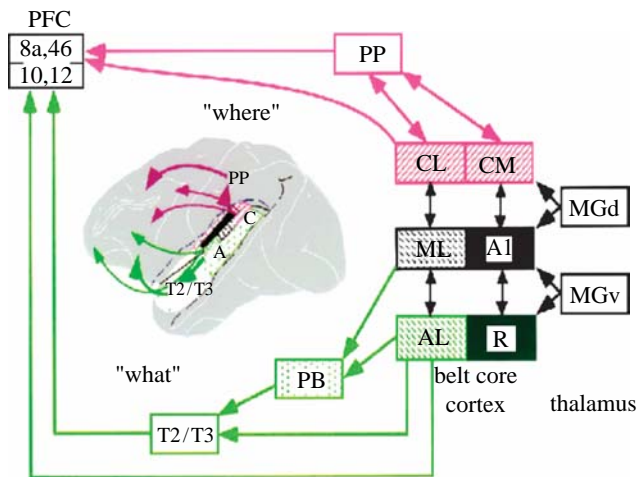* Author for correspondence (w.marslen-wilson@mrc-cbu.cam.ac.uk).

Figure 1. Ventral and dorsal auditory object processing streams in the macaque brain. The dorsal stream (red) connects caudolateral (CL) and caudomedial (CM) regions in auditory cortex to prefrontal cortex (PFC) either directly or via posterior parietal cortex (PP). The ventral stream (green) connects mediolateral (ML) and anterolateral (AL) regions in auditory cortex to PFC, via parabelt cortex (PB) and areas T2/T3 in the anterior superior temporal gyrus (reprinted with permission from Rauschecker & Tian 2000, copyright 2000 National Academy of Sciences).

Figure 2. Classical Broca–Wernicke neurological diagram of the human language system. Note the absence of a ventral processing stream.

has major implications for the characterization of human language function.

Cognitive approaches to the functional structure of the system for mapping from sound to meaning (and vice versa) have typically assumed that a single unitary process (or succession of processes) carries out these mappings. However, the neurobiological evidence suggests that the underlying neural system is not organized along these lines, and that multiple parallel processing streams are involved, extending hierarchically outwards from the auditory cortex. In this respect, speech and language analysis might be brought into closer alignment with long held assumptions about the organization of primate perceptual processing systems, where separable sub-processes analyse different aspects of the sensorimotor environment.

A recent report (Gil-da-costa *et al*. 2006) brings the apparent parallels between macaque and human functional architecture even closer (see also Ghazanfar & Miller 2006). This was a positron emission tomography (PET) activation study on awake monkeys, where the subjects heard a mixture of species-specific vocal calls and acoustically matched non-biological sounds. The vocal calls were found to preferentially activate areas in the macaque brain (ventral premotor cortex and temporo-parietal cortex) that are argued to be homologues of two key language areas (Broca's and Wernicke's, respectively) in the classical view of the human system (figure 2). This was despite the absence of hemispheric lateralization in these data, contrary to earlier studies (e.g. Poremba *et al*. 2004). Gil-da-costa *et al*. (2006) argue that this joint involvement of temporal and frontal cortex reflects the need to embed the interpretation of conspecific calls in the context of their social and environmental significance. Since macaques and human branched off from each other about 25 Myr ago, these parallels imply a distant common ancestor whose
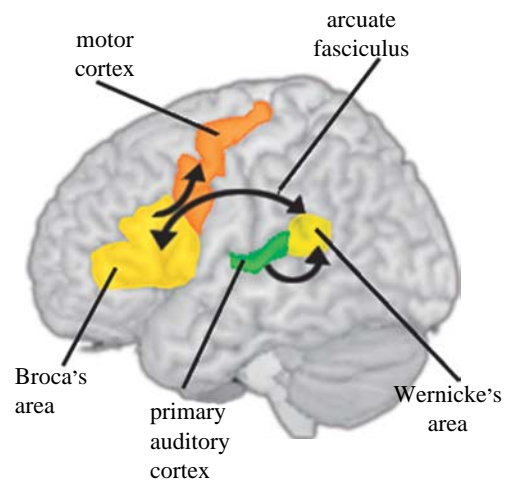
brain already possessed key organizational features that would eventually develop, in the human case, into the substrate for complex language function. These ancient architectural and functional commonalities bring into even sharper focus the question of how human language nonetheless differs so sharply in its apparent properties from those of our evolutionary relatives.

The functional answer, unsurprisingly, must lie in the grammatical domain—the powerful and flexible set of devices that every human language possesses, for organizing the flow of linguistic information and its interpretation—and for which there is no convincing evidence in any non-human communication system (Hauser *et al*. 2002). Language is more than a string of social signals or a list of symbols that stand for things and events in the world—this much, arguably, it may have in common with its primate ancestry. These semantic and referential aspects of linguistic communication, conveyed primarily by content words and morphemes, are embedded in a profusion of linguistic devices that indicate the grammatical relationships between these words, the temporal properties of the events being described, aspects of the speaker's attitude towards the addressee and many other similar functions.

The focus of this chapter is on the neural systems that underpin one particular aspect of these grammatical functions (cf. Ullman in press). Combining research on brain-damaged patients with neuroimaging studies of normal adults, we will argue for a specific left hemisphere (LH) fronto-temporal sub-system, tuned to the properties of grammatical morphemes. This may constitute a separate decompositional processing stream, as part of the complementary streams of processing activity underlying human language function. We begin with a sketch of the linguistic environment in which these linguistic devices occur, since understanding their functional role is critical to asking the right questions about how the neurocognitive system supports them.

2. GRAMMATICAL MORPHEMES IN ENGLISH: LINGUISTIC BACKGROUND

Human linguistic communication requires two kinds of information to be conveyed between speakers and

listeners: semantic information, about meanings and their instantiation in the world; and a wide range of syntactic information, specifying grammatical relationships, tense, aspect and so forth. These different kinds of linguistic information are associated with specific lexical entities, called *morphemes*, which are defined as the minimal meaning-bearing linguistic elements. These are assembled together, in different ways in different languages, to convey the necessary mix of semantic and syntactic cues to the intended meaning as the speech input is heard over time (or as a written text is read).

In a language like English, a high proportion of semantic and syntactic morphemes can occur as phonologically separate entities—as individual words like *the* or *dog*—so that the distinction between word and morpheme is neutralized. Nonetheless, this is by no means the case for the language as a whole, with the frequent occurrence of complex words made up of the combination of different morphemes, especially those involving bound morphemes. These latter are grammatical affixes, like {-ness} or {-s}, which cannot occur as words on their own, but only in combination with content word stems, as in forms like *darkness* ({dark} + {-ness}) or *smiles* ({smile} + {-s}). In common with many other languages, English has two modes of affixal word combination—*inflectional* and *derivational morphology*, where a stem is combined with a derivational or an inflectional morpheme (as in the *darkness* and *smiles* examples). Here, we will focus primarily on inflectional morphology, which is exclusively syntactic in its function, as opposed to derivational morphology (to which we return at the end of the paper), whose primary role is lexical in nature, creating new words in the language.

Inflectional morphology is the combination of a stem with one or more inflectional affixes—in English, examples are regular noun plurals (*cats*—{cat} + {-s}) and the regular past tense (*walked*—{walk} + {-ed}). Although the precise definition of an inflectional morphological process is controversial, there are some core properties of inflectional morphology that are generally accepted and of critical significance to a proper neurocognitive approach. First, inflectional morphology does not, by definition, create new words requiring new lexical entries. Rather, the prototypical inflectional functions—marking number, tense, aspect, gender, case and so forth—produce new forms of the same word and not new different words. Inflectional variants like *cat* and *cats* or *walk* and *walked* are not listed as separate headwords in standard dictionaries. If inflectional morphemes do modify the semantics of a word—as in the noun plural—they do not change the basic meaning of the stem to which they attach, nor do they change its grammatical category.

The second key characteristic of inflections is that they are responsive, in a regular and predictable way, to the properties of the grammatical environment in which they occur (e.g. Anderson 1992; Bickel & Nichols 2006). This is clear, for example, where inflectional morphemes express agreement—as in the third person singular {-s} for English verbs (*he walks*), or, in many other languages, when morphological case is used to express the grammatical role of a noun as subject, object, indirect object and so forth. Similarly, the presence of the regular past tense in English verbs

(*they walked*) is dictated by the role of the verb in the context of the utterance and its wider temporal and aspectual properties. The information carried by the inflection is not just about the stem itself, but about the processes of phrasal and sentential interpretation to which that stem relates.

We will argue in this paper that these two functional properties—of meaning preservation and context sensitivity—are directly reflected in the properties of the neurocognitive language system. Regularly inflected forms, such as *joined*, *treats* or *agreed*, are not stored or processed as whole forms, since their morphemic components are relevant to different aspects of the interpretation process and their lexical content—the semantic and syntactic properties of the stem—is fully recoverable from the representation of the stem on its own. This means that access to lexical content is via the stem (*join*, *treat* and *agree*), which in turn requires morpho-phonological parsing of the complex form in order to separate the stem from its affix. This decompositional access process, consistent with the psycholinguistic functions of regularly inflected forms in English, seems to apply early and automatically to all potentially decomposable inputs and may be specifically dependent on the dorsal processing network linking posterior temporal lobe regions to LH inferior temporal cortex.

This emphasis on the morphological decomposition of regular inflected forms clearly allies the account presented here with the 'Words and Rules' (e.g. Clahsen 1999; Pinker 1999) and the procedural/declarative (e.g. Ullman 2004) approaches, in distinction to non-decompositional, usually connectionist approaches, which deny the existence of separable stem and inflectional morphemes and argue instead that inflected forms are processed and represented as overlapping whole forms sharing certain semantic and phonological similarities (e.g. Rumelhart & McClelland 1986; McClelland & Patterson 2002). Unlike Pinker and colleagues, however, we do not assume that the presence or absence of grammatical morphemes implicates differences in the nature of mental computation, while our treatment of inflectional morphology cuts across Ullman's declarative/procedural dichotomy.[2]

Our initial evidence for a decompositional scenario, as laid out in §3, comes from neuropsychological research on patients with LH damage which affects primary grammatical functions. These patient data make explicit what are the core, neurally irreplaceable functions of the LH grammatical processing system and demonstrate the separability of the systems processing stem morphemes from those involved in the access and analysis of regular inflectional morphemes.

3. NEUROPSYCHOLOGICAL EVIDENCE FOR STEM-BASED ACCESS AND OBLIGATORY DECOMPOSITION

A linked set of experiments demonstrate, first, that the neurocognitive processes mediating access for isolated stems (and any other lexical entity that is accessed as a non-decomposed whole form) are separable from those mediating access for complex forms made up of a stem and an inflectional affix—as in cases like *joined*
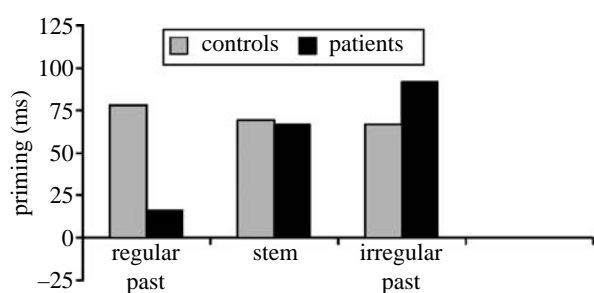
Figure 3. Priming effects (the difference in milliseconds between responses to targets following related versus unrelated prime words) for non-fluent patients and controls in an auditory–auditory semantic priming task for three types of prime word—regularly inflected past tenses (regular past); uninflected stems (stem); and irregularly inflected past tenses (irregular past). For details, see Longworth *et al.* (2005).

or *agreed*, analysable, respectively, as {*join*} + {*-ed*} and {*agree*} + {*-ed*}. The first of these experiments (Marslen-Wilson & Tyler 1997; Tyler *et al.* 2002*a*) used auditory–auditory immediate repetition priming to demonstrate a selective impairment for the decompositional aspects of inflectional morphology. Left hemisphere non-fluent patients, typically with damage that included inferior frontal regions, showed normal priming for irregular past-tense pairs like *found/find*, but significantly reduced priming for regular pairs like *joined/join*.[3] The significance of the English irregulars here is that they are fully matched to the regulars in terms of their general syntactic and semantic properties, but do not require (or allow) segmentation into a stem + affix format. An irregular past tense like *found*, given its idiosyncratic and unpredictable surface form, must be learned, stored and accessed as a whole form—in the same way as morphologically simple forms like *sound* or *round*.[4] The fact that priming is intact for these irregular forms indicates that the impairment for the regulars is specific to their decompositional properties.

This inference is strengthened by the results of a subsequent experiment with similar patients using a semantic priming task (again auditory–auditory), where prime and target are semantically rather than morphologically related (Longworth *et al.* 2005). Here, we contrasted regular past tense pairs (*blamed/accuse*), verb stem pairs (*hope/wish*) and irregular past tense pairs like *shook/tremble*. This is a task where successful priming requires rapid access to the meaning of the prime, followed by equally rapid access to the form and meaning of the target, such that the semantic relatedness between the two can be accessed and used to facilitate responses to the target. The fact that these LH patients show unimpaired priming for the stem pairs and the irregular past pairs (figure 3) is a confirmation that they retain apparently normal and effective systems for mapping stems and whole forms onto lexical representations of form and content. At the same time, the absence of semantic priming for the regularly inflected pairs, in the same patients, confirms their problems with forms requiring decompositional processing.[5]

What these results also mean is that the regular inflected 'whole form' cannot be stored as the perceptual target for lexical access. If the access route

for *joined* were via a representation of *joined* as a whole form, then there would be no reason for access to fail here when it was succeeding for other whole-form representations like *found* or stem representations like *hope*. This, in turn, means that inflected regular forms must be subjected to some form of morpho-phonological parsing, which breaks down the surface full form into its stem + affix components. Without such decomposition, the full inflected form is an ill-formed input to the lexical access process, not matching fully with any stored representation.

Further work with the same type of LH non-fluent patients sheds additional light on these decompositional processes, showing them to be applied early and obligatorily to the speech input and highlighting the priority that the system seems to assign to the detection of inflectional morphemes and their separation from their stems. The evidence for this comes from an auditory same–different task, where patients were presented with two successive words (or non-words), spoken in a male and a female voice, and asked to judge whether the second word/non-word in each pair was the same as the first (Tyler *et al.* 2002*b*).

Successful performance in this apparently simple task requires the participant to construct a stable internal representation of the first stimulus heard, so that this can be held in memory for comparison with the second member of the pair. The pattern of successes and failures for the non-fluent patients indicates the importance of morpho-phonological parsing in constructing these representations. The patients had problems not only with regularly inflected real words—in pairs like *played/play*—but also with any other stimulus pairs—even non-words like *snade/snay*—that ended in the characteristic phonetic pattern associated with regular inflectional morphology in English and which were therefore potentially decomposable. This pattern—the presence of a coronal consonant (d, t, s, z) that agrees in voice with the preceding phoneme—holds without exception for the two dominant regular inflectional paradigms in English, the past tense {-d} and the {-s} inflection. We have labelled this the English *inflectional rhyme pattern* (IRP).

In the experiment, we compared performance on real regular pairs (*played/play*)[6] with two other sets that shared this IRP. These were pseudo-regular pairs like *trade/tray*, where *trade* is homophonous with the potential but non-existent past tense of the noun *tray*, and non-word regular pairs like *snade/snay*, where neither is a word in English, but where *snade* could be the past tense of the (non-existent) stem *snay*. These three sets contrast with two sets of word/non-word pairs which are matched to the inflectional sets in terms of consonant–vowel (CV) structure, with the final phoneme being dropped in the second member of the pair, but where this final phoneme is not a possible inflectional affix in English—as in pairs like *claim/clay* or *blane/blay*. Although *claim* contains the imbedded word *clay*, much as *trade* contains *tray*, it cannot be interpreted as a morphologically complex form and does not invite morpho-phonological parsing and decomposition. For the non-word *blane*, there is similarly no indication that it is the inflected form of a potential real stem.
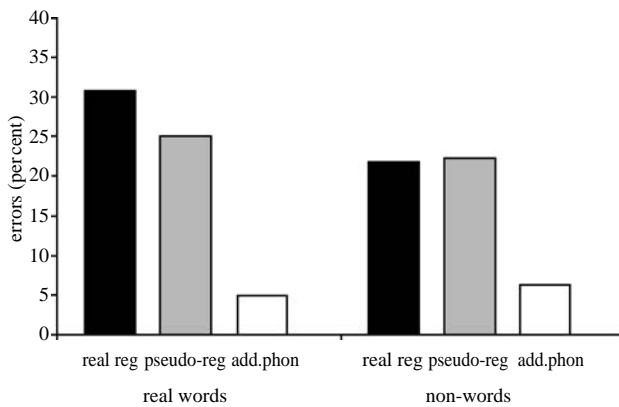
Figure 4. Per cent error rates (for different pairs only) for non-fluent patients in a same–different judgement task, comparing real regular, pseudo-regular and additional phoneme pairs in real word and non-word conditions (data replotted from Tyler *et al.* 2002*a*).

The results show a striking divergence between the inflectional sets and the additional phoneme sets. Although patients perform worst on the real regulars, they also perform remarkably poorly on the pseudo-regular and non-word regular sets, while being close to normal on the two additional phoneme sets. These effects show up significantly in their response times, but can be seen most dramatically in the pattern of errors (defined as a failure to detect a difference; figure 4). In the context of near-zero error rates for the age-matched controls (means of 1.7% for non-words and 0.6% for real words), the patients fail to detect a *played*/*play* difference over 30% of the time, with error rates well above 20% for the pseudo-regular and the non-word conditions. In contrast, they make less than 5% errors on the matched additional phoneme conditions.[7]

This pattern of deficits gives us a kind of 'negative image' of the properties of the underlying intact system for processing regular inflectional forms in English. First of all, it confirms that this is a decompositional process, and that regular inflected forms are not treated or stored as whole forms. Otherwise, there would be no reason for a non-word like *snade* to create significant problems when *blane* does not. It is only in a decompositional context, where whole forms are not stored, that a string like *snade* needs to be analysed to determine whether it is a form like *played*—also not stored—which is an inflected form of a stem that does exist and which is stored.

Second, and relatedly, this potential internal structure seems to be signalled by the presence of a specific acoustic–phonetic pattern in the input, that triggers morpho-phonological parsing processes independent of the actual lexical status of the string being decomposed. It is this that selects out *snade* for analysis, in contrast to items like *blane*—or indeed items like *trade* in contrast to *claim*. This tuning of the parsing process to the distributional properties of English inflectional morphemes, and the fact that such parsing evidently operates blindly and obligatorily, vividly brings out the priority that the system must place on the identification of inflectional morphemes in the speech stream.

This neuropsychological behavioural data illuminates for us, therefore, the functional outlines of a hidden decompositional processing system that operates beneath the surface of the language

interpretation process. However, owing to the heterogeneous nature of the lesions involved and the size of the left perisylvian lesions in some of these patients, this patient group is only weakly informative about how these functions relate to specific brain systems. To move beyond this, in order to establish an adequate neuro-cognitive model of these phenomena, we need to: (i) map these processes onto an anatomically more specific neural substrate and (ii) carry out the appropriate tests, using behavioural and neuroimaging techniques, to evaluate these claims in the context of the undamaged brain. These goals are the focus of §4–7 of this paper.

4. TOWARDS A NORMAL NEUROCOGNITIVE MODEL
As we have shown above, behavioural priming tasks allow us to segment the damaged system in functional terms, with different kinds of priming relationships being differentially sensitive to different aspects of cognitive and psycholinguistic function. In tests with the non-fluent patients, for example, we see a selective impairment for stimuli containing a regular inflectional morpheme. In other experiments, we see selective impairments for semantic priming, in patients with semantic disorders (Marslen-Wilson & Tyler 1997; Tyler & Moss 1998).

This behavioural selectivity can be used, together with whole brain structural magnetic resonance imaging (MRI) of patients' lesions, in a novel analysis procedure that allows us to pinpoint the brain areas that are most critical for the performance of the behavioural functions indexed by these tasks. This procedure correlates variations in behavioural performance on specific tasks with whole-brain voxel-by-voxel variations in MRI signal intensity (Tyler *et al.* 2005*a*). These variations in signal strength reflect variations in tissue density within each voxel, and these, relative to a population norm, reflect the integrity of the tissue involved. Lower signal intensity reflects damage to the brain, either directly (e.g. in the area affected by an infarct or following surgery) or indirectly, through effects of damage elsewhere on grey and white matter density in connected areas.

This is a much more sensitive technique than conventional lesion overlap methods and is proving remarkably successful in delineating highly specific brain–behaviour relationships (e.g. Tyler *et al.* 2005*c*; Bright *et al.* 2006). Here, we focus on the outcome of a study correlating structural MRIs for a sample of 22 brain-damaged patients with their performance on the same auditory–auditory repetition priming task described earlier, where a stem target is primed by a regularly inflected stem (*joined*/*join*), together with other priming conditions for irregular past tenses (*found*/*find*), semantically related pairs (*swan*/*goose*) and a phonological control condition (*clamp*/*clam*), matched to the regularly inflected pairs in amount of phonetic overlap between prime and target (Tyler *et al*. 2002*a*, 2005*a*). The patients tested, with predominantly LH lesions, were not pre-selected on the basis of their linguistic performance but simply according to the requirement that (i) they were able to have a structural MRI and (ii) they could perform the priming task, where lexical decision responses to the targets were required.
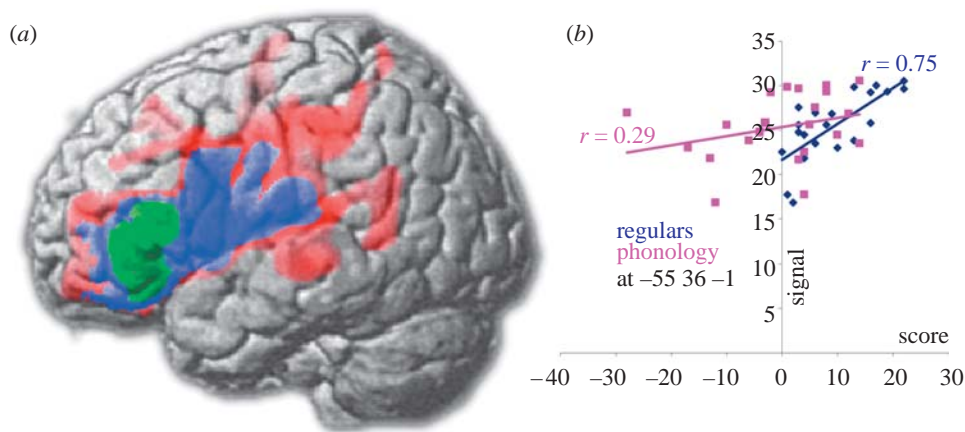
Figure 5. Structural correlates of regular inflection. (*a*) Three-dimensional reconstruction of a T1-weighted MRI image showing brain areas where variations in signal density (for grey and white matter) correlate with priming for regularly inflected words at three significance levels: $p < 0.001$ (green); $p < 0.01$ (blue); and $p < 0.05$ (red) voxel thresholds. The clusters shown survived correction at $p < 0.05$ cluster level adjusted for the entire brain. The statistical peak ($-55, 36, -1$) is in the LIFG (BA 47), and the cluster extends superiorly into BA 45. At lower thresholds, the cluster extends from Broca's to Wernicke's areas and includes the arcuate fasciculus. (*b*) The scatter plot showing the relationship between variations in signal intensity at the most significant voxel, and individual behavioural scores in the regular past tense condition and the non-morphological phonological overlap condition (reprinted with permission from Tyler *et al.* 2005*a*, copyright 2005 National Academy of Sciences).

The results for regular inflected primes (figure 5*a*) selectively pick out key areas of the perisylvian language system in the left inferior frontal gyrus (LIFG). At the highest statistical threshold ($p < 0.001$ voxel, $p < 0.05$ cluster levels), variations in priming performance for regular pairs correlate with variations in tissue density in Broca's area, with the maxima in BA 47, extending superiorly into BA 45. This is a part of the brain long thought to be implicated in grammatical aspects of linguistic performance (Grodzinsky 2000). The scatterplot in figure 5*b* gives the distribution of priming scores for the patient group at the peak voxel for this analysis, showing a strong positive correlation with signal intensity ($r = 0.75$, $p < 0.01$). As signal intensity diminishes with increasing damage, the size of the priming effect falls off. For comparison, the scores for the phonological control condition (*clamp*/*clam*) are also included. These do not correlate significantly with damage in these areas ($r = 0.29$, n.s.) and are significantly weaker than the effects for the regulars. Instead, performance on the phonological pairs correlates with a more medial LH area, the insula, known on independent grounds to be involved in aspects of phonological processing (Noesselt *et al.* 2003), and where a significant effect for the regulars is not seen.

What figure 5*a* also shows is that when the correlation with regular priming scores is plotted at a slightly lower statistical threshold ($p < 0.01$ voxel level), we see a more extensive region of the LH being implicated. This region included the left superior temporal gyrus, extending posteriorly from primary auditory cortex into the anterior extent of Wernicke's area (BA 41, 42) and anteriorly along the left superior temporal gyrus. When the threshold is reduced further ($p < 0.05$ voxel level), the cluster now includes all of Wernicke's area, looping around to include the arcuate fasciculus and including BAs 47, 44 and 45.

These patterns of correlation correspond closely both to the classical Broca–Wernicke–Lichtheim model of language function (figure 2), where the white matter

tract of the arcuate fasciculus connects superior temporal and inferior frontal regions, and to the dorsal route identified in more recent neurobiological accounts (figure 1). This is not only consistent with previous reports implicating damage to the dorsal route in impairments of regular inflectional morphology, but also allows us to make the stronger inference, given the selectivity of the priming task, that this impairment is specific to the decompositional aspects of regular inflection—especially since priming patterns for the irregulars correlate with quite different posterior temporo-parietal brain regions (Tyler *et al.* 2005*a*).

In terms of an initial statement of a neurocognitive model of the processing of spoken regularly inflected words in English, these results point to a core decompositional network involving LIFG and posterior left temporal regions, centred around the dorsal processing stream and less critically dependent on other processing streams—either the proposed ventral processing stream (Scott *et al.* 2000; Davis & Johnsrude 2003) or a potential third stream of processing (e.g. Rodd *et al.* 2005), possibly linked to an inferior temporal 'basal language area' (Price 2000). This dorsal decompositional network would be engaged in two types of interdependent processing activity triggered by a regularly inflected stem combined with an inflectional affix. These are processes of stem and affix access and of morpho-phonological segmentation of the original complex form.[8]

These functions are distributed over a partially left lateralized fronto-temporal language system, with some differentiation of function between frontal and temporal areas. Access to lexico-semantic content is likely to be mediated by temporal lobe structures, centred around the posterior superior and middle temporal gyri and linking sensory inputs to stem-based representations of morphemic form and meaning (cf. Binder *et al.* 2000; Wise *et al.* 2001). If these brain regions are intact, we see preserved phonological and semantic processing of both monomorphemic forms

(like *jump* or *dog*) and irregular forms (like *gave* or *taught*) that have to be accessed as whole forms. Note that considerable neuropsychological and neuroimaging evidence suggests that access for these morphologically simple forms is supported bilaterally, in RH and LH temporal lobes.

The successful access, in contrast, of regularly inflected forms requires a further left-lateralized process of morpho-phonological parsing, which segments potential complex forms into stems and grammatical affixes. This segmentation, on one hand, allows the isolated stem to access successfully the appropriate stem representation, and, on the other hand, allows the inflectional affix to access the representations and processes relevant to its successful interpretation. The processes supporting this parsing process seem to require intact left inferior frontal cortex and intact processing links between these areas and left superior and middle temporal cortex. A striking feature, finally, of these segmentation processes is that they are apparently triggered by any input, word or non-word, that shares the diagnostic properties (the IRP) of an inflectional affix in English (Tyler *et al.* 2002*b*).

The specific features of this decompositional grammatical processing model, both neural and functional, have been inferred from the results of research into the damaged system. In a series of experiments with intact young adults, we have started to examine the predictions of this model for performance in the normal brain, primarily using neuroimaging techniques.

5. MODULATION OF FRONTO-TEMPORAL INTERACTIONS BY MORPHO-PHONOLOGICAL CUES

The key claims of the neurocognitive model concern the interplay of stem access and affixal decomposition, modulated by the IRP, across left temporal and inferior frontal cortex. We probed these, in the normal brain, by running a version of the same–different experiment (Tyler *et al.* 2002*b*) in an event-related functional MRI (fMRI) paradigm (Tyler *et al.* 2005*b*). The stimulus set for this study (table 1), although restricted in scope by the constraints of the neuroimaging environment, allowed us to evaluate a range of neurocognitive effects. To do so, we used both standard subtractive analyses, and a functional connectivity analysis of the dependencies between different processing regions (Stamatakis *et al.* 2005).

The same–different task, as noted earlier, requires the listener to construct a stable representation of the first member of each pair, so that this can be held in memory for comparison with the incoming information about the second target word. Further, as the earlier experiment with the patients demonstrated, this process is dependent on an intact LH fronto-temporal system for pairs, where the first member of the pair ends with the English IRP. This implies that the stimulus types that caused the most severe problems to the patients should be those that generate the strongest fronto-temporal activation in normals. The first contrast in the current study, therefore, is between the (+IRP) sets—the real regulars and pseudo-

Table 1. Stimulus conditions for the speeded same–different judgement task.

conditions		real word	non-word
1 regular past	(+IRP)	played/play	crade/crey
2 pseudo-regular	(+IRP)	trade/tray	drade/drey
3 irregular past	(−IRP)	taught/teach	hort/heach
4 pseudo-irregular	(−IRP)	port/peach	gort/geach
5 additional phoneme	(−IRP)	claim/clay	blain/blay

regulars, with their matched non-word counterparts—and the (−IRP) sets, consisting of real irregulars, pseudo-irregulars and additional phoneme pairs, also with non-word counterparts (table 1). For the (+IRP) sets, the model predicts stronger LIFG activation, since the presence of the IRP should trigger decompositional activity for which LIFG involvement is required. It may also generate increased temporal lobe activity, especially for real regulars, where the presence of the IRP is claimed to lead to a reanalysis of forms like *played* into *play*+-*ed*, allowing *play* to access its stem representation.

The second broad contrast is in lexicality, with a comparison between real word and non-word pairs across all five conditions. Since none of the non-word pairs (like *snade/snay*) correspond to stored lexical representation, this should lead to reduced temporal lobe activity relative to the real words. The latter should engage lexical access mechanisms much more strongly, especially when they have an embedded competitor (as in *trade/tray* or *claim/clay*). Lexicality, however, should not interact with IRP, which should trigger LIFG activity irrespective of the status of the stem.

The third contrast, finally, allows us to compare whole word and decompositional access for pairs matched for semantic and syntactic complexity—namely the regular/irregular contrast, including pseudo-regular/irregular and non-word conditions. Both the real regulars and the real irregulars are inflectionally marked for the past tense, and seem to be fully equivalent in terms of their syntactic implications. To the extent that LIFG activation associated with regular past tense inflection is driven by the syntactic interpretation of these markers, the regular and irregular forms would generate equivalent levels of activation. If, however, as the patient data suggest, LIFG activity is primarily driven by the processing demands associated with morpho-phonological decomposition, then LIFG activation should be stronger for the regulars.

These three contrasts interact in an illuminating manner to support and extend the model. Across the board, we see stronger activations in temporal cortex bilaterally for (+IRP) conditions, coupled with significant LIFG effects. These effects are modulated by lexicality and decompositionality. We consider first the regular/irregular comparison, which compares decomposable and non-decomposable forms while holding syntactic properties constant. Overall, there is stronger superior/middle temporal gyrus (STG/MTG) activation bilaterally for all regulars (real, pseudo- and non-word) when compared with all irregulars, coupled with significantly greater LIFG activation (and no

effects in the reverse direction). In addition, as shown in figure 6, the real regular/irregular contrast shows a further focus of activation in the left anterior cingulate (with some RH involvement). This activation, reflected in an interaction between past tense type (regular/irregular) and word type (real past/pseudo-past), seems specific to the real regulars (*played*/*play*)—namely, those stimuli which are genuinely segmentable into a stem and an inflectional affix, as opposed to pseudo-affixed pairs like *trade*/*tray*.

The appearance of this anterior cingulate activation is significant, since it potentially relates to control processes that regulate the proposed processing relationship between left frontal and temporal regions. Several lines of evidence suggest that the integration of information between superior temporal and left frontal areas may be modulated by anterior midline structures including the anterior cingulate. Work with non-human primates shows that the anterior cingulate projects to or receives connections from most regions of frontal cortex (Barbas & Pandya 1989) and superior temporal cortex (Pandya *et al.* 1981). Recent neuroimaging data not only implicate the anterior cingulate in the modulation of fronto-temporal integration (Fletcher *et al.* 1999), but also show it to be active in situations requiring the monitoring of interactions between different information processing pathways (Braver *et al.* 2001).

In this view, the increased activation of the anterior cingulate by real regular inflected forms (figure 6) may reflect the greater demands made on this monitoring function when complex forms such as *jumped* need to be parsed into a stem + affix, with the bare stem then able to act as a well-formed input to temporal lobe lexical access processes. The properties of this potential anterior cingulate contribution were examined in more detail in a subsequent functional connectivity analysis (Stamatakis *et al.* 2005) carried out on the same data, using the PPI (psycho-physiological interaction) approach developed by Friston *et al.* (1997). This allowed us to address more directly the functional relationship between regions in the fronto-temporal language system.

The resulting connectivity analysis shows that the LH regions in the LIFG and anterior cingulate identified by the subtractive analyses (figure 6*a*,*c*) covary with activity in the left posterior MTG more for regularly inflected forms compared with irregularly inflected forms (*played* versus *taught*). This fronto-temporal interaction was reduced when the words were phonologically similar to the regular and irregular past tense but were not themselves morphologically complex (e.g. for contrasts like *trade* versus *port*). This suggests that the modulatory effects we found for the regulars reflect the stronger dependency between components of the fronto-temporal language system required for processes of morpho-phonological decomposition and analysis, rather than being attributable to the phonetic differences between the regular and irregular pairs.[9] The greater activation for real as opposed to pseudo-regulars means that a form like *played* triggers more activity than *trade*, both in terms of its consequences for the lexical access process, with the assignment of the stem morpheme (*play*) and the grammatical morpheme (*-ed*) to different processing destinations, and in terms of morpho-syntactic analysis

processes. These latter processes will presumably be engaged more strongly when the evidence suggests that a grammatical morpheme is indeed present.

These results, showing connectivity between inferior frontal and middle temporal regions, are consistent with anatomical connectivity dorsally via the arcuate fasciculus between frontal and temporal regions, but also between orbito-frontal and anterior temporal regions via ventral connections (Petrides & Pandya 1988; Morris *et al.* 1999). They are also consistent with recent *in vivo* analyses of anatomical connections in the human brain, using diffusion tensor imaging to visualize white matter tracts connecting different brain areas (Catani *et al.* 2005; Parker *et al.* 2005). One indication that the connectivity implied by our analyses was via dorsal rather than ventral connections is that the LIFG seed for these analyses was the more superior of the two activation foci seen in the subtractive analyses, being located in BA 44 pars opercularis (figure 6*a*). Studies on humans and macaques suggest that neurons in the dorsal stream project to regions of superior LIFG which overlap with area BA 44 and its macaque homologue (Kaas & Hackett 1999; Scott & Johnsrude 2003).

Returning to the original subtractive analyses of the same–different task, the second main contrast was between the regulars and the additional phoneme conditions. The results here, under conditions where the two sets could be closely matched in their phonetic properties, are also consistent with the view that LH fronto-temporal interactions in speech processing are modulated by morpho-phonological cues to potential inflectional affixes. As shown in figure 7, we again see increased temporal activation bilaterally together with increased LIFG activation for the real regulars and non-word regulars, compared to the additional phoneme sets (*claim*/*clay*, *blane*/*blay*). This difference seems to depend on the presence of the IRP contrast between the regular and additional phoneme conditions. When the irregulars are compared with the additional phoneme condition, where neither set carries the IRP, there is no sign of the left fronto-temporal pattern seen for comparisons involving the regulars.

Finally, and reinforcing the view that the IRP triggers decompositional activity blindly and obligatorily, irrespective of the lexical status of the stem to which it is attached, we see significant LIFG activity, but no differential temporal lobe activity (figure 8) in a specific comparison between regular non-words (*snade*/*snay*) and additional phoneme non-words (*blain*/*blay*). Here, there are no real stems, either embedded or inflected, so that there is no basis for substantial differences in stem-based access processes in either type of material. Nonetheless, the IRP is still present for the regular non-words, and this is still effective as a cue to potential decomposition, engaging similar LIFG regions to the real regulars.

In summary, this experiment is consistent with our basic hypotheses for an underlying grammatically driven neurocognitive system, instantiated in a left lateralized fronto-temporal network linking temporal and inferior frontal areas, which prioritizes the identification and interpretation of inflectional morphemes. Functional connectivity analyses point to the

dynamic modulatory relationships across this network, consistent with the view that the functional properties of such a network emerge from cooperation between anatomically distant areas.

Additional evidence for dynamic fronto-temporal interactions, operating on millisecond time-scales, comes from studies using electroencephalography (EEG) and magnetoencephalography (MEG) techniques, which allow us to track brain events with high temporal resolution. Research across a variety of languages shows additional left fronto-temporal activity associated with the presence of grammatical morphemes. This holds for contrasts between isolated function and content words (e.g. Pulvermüller & Mohr 1996), and for several EEG studies examining the effects of morphological violations involving regular and irregular inflected forms, typically as they occur in sentence contexts (e.g. Münte *et al.* 1999; Rodriguez-Fornells *et al.* 2001; Lück *et al.* 2006), using both written and spoken materials.

Recent MEG experiments using the mismatch negativity (MMN) paradigm demonstrate with spatial as well as temporal precision the dynamic properties of the fronto-temporal links underpinning inflectional processes. Pulvermüller *et al.* (2006), using modern source localization techniques, are able to discriminate a left superior/middle temporal burst of activation, triggered by successful word recognition, from a second burst of activity in left inferior temporal regions that follows within approximately 20 ms. This is for inflected verbal forms in Finnish, where a stem like {tuo-} is accompanied by the inflectional suffix {-t}, giving the surface form tuot, 'you bring'. Other MEG research using the MMN paradigm indicates that this left frontal activation reflects the status of the final phoneme as an inflectional affix (e.g. Shtyrov & Pulvermüller 2002; Shtyrov *et al.* 2005). This is consistent with the fMRI research described previously (Tyler *et al.* 2005*b*), where a marked increase in left inferior frontal activation is stimulated by the presence of an inflectional affix.

Running through all the research discussed so far is the theme that identifying inflectional morphemes is a major priority for the language processing system. Evidence is now emerging that this is a truly general property of language interpretation, and that the other major class of grammatical affixes—derivational morphemes—are also prioritized by the system for early blind identification. In §7 of the paper, we examine this novel and complementary evidence for the salience of grammatical information in the early stages of language comprehension.

6. EARLY SEGMENTATION OF DERIVATIONAL MORPHEMES

Derivational affixes—forms in English like {-ness}, {-er} and {-ize}—function primarily to create new lexical items, combining with existing free or bound content morphemes to create words like *darkness*, *builder* and *radicalize*. These derived forms are generally treated in the language as new words, with different meanings from their stems and very often with different syntactic categories—*builder*, for example, is a noun,

formed from the verb stem *build*. Compelling evidence is now emerging that all potential derivationally complex words undergo an initial obligatory process of segmentation into their morphemic components, irrespective of whether the words actually are morphologically complex—paralleling the kind of obligatory early decomposition we have seen for inflectionally complex forms. Although this obligatory early decomposition was initially proposed over 30 years ago (Taft & Forster 1975), the recent wider acceptance of this view reflects new experiments, across a range of languages, using the visual masked priming technique (for a recent review, see Marslen-Wilson in press)—and contrasting, therefore, with the primarily auditory focus of the research on inflectional morphology described previously.

Masked priming is an experimental situation where a visual prime word (preceded by a pattern mask and followed by a visual target) is presented so briefly that the reader is not aware that the prime is present and simply makes a lexical decision to the target (Forster & Davis 1984). Several experiments using this task provide converging evidence cross-linguistically for the dominance of morphological factors in the early analysis of derivational complex forms (e.g. Frost *et al.* 1997; Forster & Azuma 2000; Boudelaa & Marslen-Wilson 2004). This dominant role for morphology is underlined by a further series of experiments which show that this early segmentation is conducted independently of the stored lexical properties of the forms in question. Several studies in English (Rastle *et al.* 2000, 2005; Marslen-Wilson *et al.* in press) show strong masked priming not only between transparent pairs like *bravely/brave*, which are genuinely morphologically related, but also between pairs like *hardly/hard*, which are not transparently morphologically related in modern English, and even for pseudo-derived pairs like *corner/corn*, where *corner* clearly has no morphological interpretation as {*corn+-er*}. The process underlying these effects is nonetheless morphologically sensitive, since pairs like *harpoon/harp*, where '-oon' is not a derivational affix in English, do not show priming.

Similar patterns are reported for French by Longtin and colleagues, who not only replicate the results of Rastle *et al.* (2000), but also go on to show that non-word primes (such as *rapidifier*) can prime their real word pseudo-stem (*rapide*, 'rapid') just as well as transparent real-word primes (*rapidement*, 'rapidly'), but only if the pseudo-stem co-occurs with an existing French suffix (Longtin *et al.* 2003; Longtin & Meunier 2005). Thus *rapiduit*, where -*uit* is not a possible suffix in French, does not prime *rapide*. These results not only support a lexically blind early segmentation account of masked morphological priming (non-words, by definition, cannot have a stored lexical representation), but also confirm that this early segmentation is sensitive to morphological factors. Only if the potential stem is paired with an actual suffix in the language do we see priming.

In summary, these masked priming results point to an early phase of the visual lexical access process, where all morphologically decomposable surface forms are segmented into potential stems and affixes by a process which is blind to higher-order lexical structure (cf.
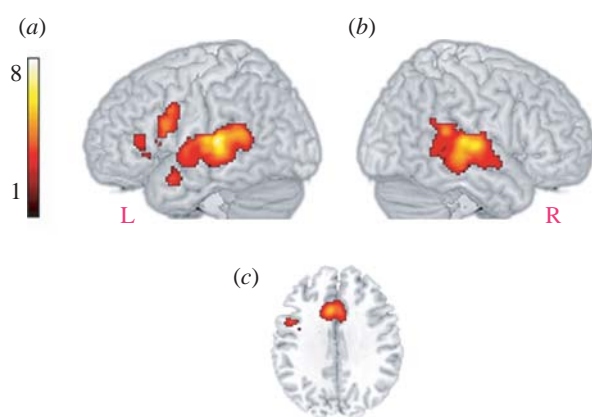
(a) *(b)*

(c)

Figure 6. fMRI data: significant activations for the contrast of real regulars minus real irregulars. Significant clusters were found in the right superior temporal gyrus (RSTG), left superior temporal gyrus (LSTG), left anterior cingulate cortex (LACC), and left inferior frontal gyrus (LIFG) (data redrawn from Tyler *et al.* 2005*b*).

Shallice & Saffran 1986; McKinnnon *et al.* 2003). Given the ample evidence for masked priming between inflectionally related pairs (e.g. Forster *et al.* 1987; Drews & Zwitserlood 1995; Pastizzo & Feldman 2002), this undoubtedly extends to inflectionally complex forms as well. In terms of the neural substrate for these early segmentation processes, a strong candidate is the left fusiform gyrus—a LH brain region known as the visual word form area (cf. Cohen *et al.* 2002; McCandliss *et al.* 2003), which plays an important role in the early interpretation of orthographic inputs.

Consistent with this, a recent paper by Devlin *et al.* (2004) reports masked priming effects in exactly this area, using an event-related fMRI approach, for a mixture of semantically opaque and pseudo-derived stimuli (such as *department/depart*, *hardly/hard* and *slipper/slip*). The behavioural priming effect for these materials was identical in size to the effect for morphologically transparent pairs like *teacher/teach*, consistent with the masked priming literature. The neural priming effect, however, was stronger in the visual word form area for the opaque and pseudo-stem pairs than for the transparent pairs, consistent with the view that activation at this level primarily reflects pre-lexical segmentation processes.[10]

Neuroimaging data from a different study (Bozic *et al.* in press) indicate that the effects of these early analyses propagate more widely than the Devlin *et al.* (2004) data would suggest. Using delayed repetition priming in an event-related fMRI paradigm, Bozic compared effects for transparent and opaque morphologically decomposable pairs (*bravely/brave*, *archer/arch*) with appropriate form and meaning controls (*harpoon/harp*, *accuse/blame*). Second presentations of morphologically related words produced significantly reduced activation in left inferior frontal regions, whether the pairs were semantically transparent or opaque. No effects were observed for the form and meaning control conditions. The appearance of these frontal morphologically driven effects at long repetition delays, for opaque as well as for transparent pairs, suggests that potential morphemic segmentations are widely evaluated in the neural language system.

7. IMPLICATIONS AND SPECULATIONS

The research discussed here provides a preliminary glimpse of the processing networks underlying human language comprehension, framed in the broader context of how linguistic inputs convey meaning through the sequential packaging of syntactic and semantic morphemes, and constrained by a general neurobiological processing architecture. The empirical picture that has emerged for inflectional and derivational morphology, though still quite fragmentary, underlines the importance of morpheme-level analysis across the language comprehension process. It seems to be one of the highest priorities of the system, as soon as orthographic or phonological information starts to accumulate, to identify possible stems and possible grammatical morphemes.

In the case of inflectional morphology, where the neurocognitive picture is better established, the basic process of lexical access for stems interacts with morpho-phonological parsing processes which identify the presence of potential grammatical morphemes. Regular inflected forms do not seem to participate in language comprehension as whole forms, but rather as bearers of inflectional morphemes relevant to basic phrasal and sentential interpretation, and of stem morphemes conveying further semantic and syntactic information.[11]

The neuropsychological nature of the evidence for this underlyingly decompositional system points strongly to the separability of these processes, tied to core LH language networks, from more broadly based and robust systems for whole form lexical access and interpretation. Patients who are unable to access lexical semantic information from regular inflected stems can still do so with essentially normal efficiency from equivalent non-inflected stems, even in cases where there is substantial damage to much of the LH perisylvian language system. Although the evidence here is not fully developed, this robustness must in large part reflect the bilateral lexical representation of content words and bilateral mechanisms for accessing these representations (e.g. Mohr *et al.* 1994). Our same–different study on normal young adults, for example, showed strong lexically related RH as well as LH temporal activation in contrasts between different types of real word stimuli (figures 6 and 7).

Consistent with this, when we analyse the fMRI activation patterns and resulting functional connectivity for a severe LH patient performing the same–different task (Tyler & Marslen-Wilson in press), we see an enhanced RH fronto-temporal pattern of connectivity, with increased activity in the anterior temporal lobes in both hemispheres. Earlier voxel-based lesion–behaviour correlation studies (Tyler *et al.* 2005*c*) show that the temporal poles, bilaterally, play a key causal role in word recognition performance. At the same time, however, although such patients' reorganized lexical processing system performs well in speeded priming tasks (Longworth *et al.* 2005), and they have good spoken language comprehension, they still exhibit a significant syntactic deficit, as well as persistent problems with regularly inflected words. These grammatical functions depend on an intact LH perisylvian system, and the homologous RH structures seem
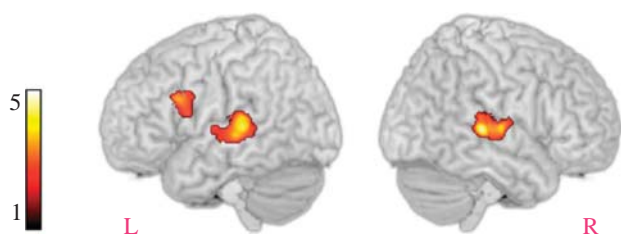
Figure 7. fMRI data: significant activations for the contrast of regulars (real, non-word) minus additional phoneme (real, non-word). Clusters were found in the RSTG, LSTG and LIFG (data redrawn from Tyler *et al.* 2005*b*).
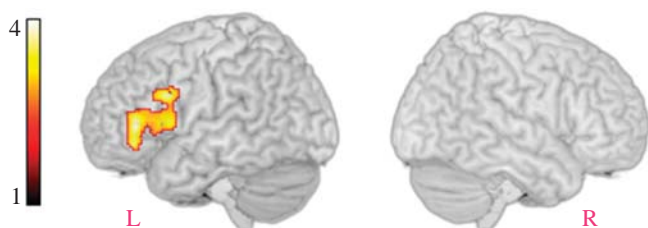

Figure 8. fMRI data: significant activations for the contrast of regular non-words minus additional phoneme non-words. Clusters were found in the LIFG (data redrawn from Tyler *et al.* 2005*b*).

unable to compensate, in this respect, for damage on the left.

This brings us back to the issues, raised at the beginning of this paper, of how to characterize the neurobiological framework for human language and whether this has special properties not found in non-human primate systems for auditory object processing and conspecific vocal communication. The fronto-temporal organization detected by Gil-da-costa *et al.* (2006) clearly holds for the human language system, although it is doubtful how informative this apparent homology is without a better understanding of both the functional properties of these connections in the human and the macaque, and the basis for the strong lateralization of core language functions in the human brain. Indeed, since the left lateralized fronto-temporal system in humans seems to handle grammatical and possibly combinatorial functions that are arguably only seen in human language, it may be that no direct precursors for these functions will be seen in the macaque. Instead, as Dehaene and others (e.g. Dehaene 2005; Dehaene *et al.* 2005) have argued for the left fusiform gyrus—that it provides a suitable processing substrate for the representation and analysis of abstract visual forms such as letters and words—it may be that the primate fronto-temporal system provides a suitable processing substrate, in ways as yet unknown, for exaptation in the process of human linguistic evolution.[12]

Finally, it is worth considering how far the notion of different processing streams is helpful in illuminating the organization of the human language system. While the evidence is not definitive, there are several hints in the data that the decompositional morphemic processes focusing on grammatical affixes are particularly dependent on dorsal pathways, linking left temporal and inferior frontal regions via the arcuate fasciculus (cf. Catani *et al.* 2005). Damage to these

pathways has also been shown to affect syntactic function (Tyler & Marslen-Wilson in press). The ventral route, in contrast, seen as resembling the classical 'what' pathway in primate vision, seems to be more engaged in processes of semantic interpretation (e.g. Scott *et al.* 2000; Davis & Johnsrude 2003), being sensitive to the intelligibility of the speech stream.

This is a highly interconnected system of pathways, in both time and space, but if the role of grammatical constraints is to orchestrate and direct the interpretation of semantic and pragmatic information carried by content words and morphemes, in the general pragmatic context of speaking, then one could suggest some division of labour along these lines, between dorsal and ventral processing streams, and heavily dependent on frontal control processes. This would be consistent with the evidence for the separability of morpho-syntactic function on one hand, and semantic and pragmatic interpretation on the other, which is clearly seen in the online performance of patients with damage to the core LH system, and would point to a neurobiologically constrained basis for future research into this most complex of neurocognitive systems.

ENDNOTES

[1]This is a simplification of a neuroanatomically much more complicated story (e.g. Petrides & Pandya 1994).
[2]Ullman (2004) distinguishes a memorized 'mental lexicon' and a computational 'mental grammar', mapping onto a more basic distinction between declarative and procedural neurocognitive systems. On our view, however, the 'lexicon' is intrinsically both 'memorized' and 'computed', built around a set of fronto-temporal circuits that permanently link brain areas that Ullman primarily assigns to either procedural or declarative functions.
[3]In all of these neuropsychological studies, unless indicated otherwise, we are working with small sets of patients (typically four to five) treated both individually and as small groups.
[4]We refer here to the phonological access representation for these irregular forms. The whole form, once accessed, may well link to an abstract underlying morpheme corresponding to the stem.
[5]Extensive testing for possible phonetic differences between regular inflected forms and stem or irregular forms showed no effects of these variables on priming, tying the effects instead to the morpho-phonological properties of the regulars.
[6]Patients heard both same (played/played) and different (played/play) pairs in equal proportions. Since they only made 'different' responses (to minimize task demands), we focus here just on the different stimuli. The experiment also contained sets of irregular and pseudo-irregular pairs. Responses to these are not directly relevant to the current discussion (patients performed very well) and are not presented here. For further details, see Tyler *et al.* (2002*b*).
[7]Note that an account of these results in terms of deficits in phonetic (as opposed to morpho-phonological) processing (cf. Joanisse & Seidenberg 1999; Bird *et al.* 2003) is unlikely for two reasons. First, the regular and the additional phoneme sets were matched in terms of phonological complexity. Second, patients performed poorly on the regular sets even when they did not have deficits in phonetic processing as standardly assessed (Tyler *et al.* 2002*b*).
[8]The dorsal network may also be engaged in the morpho-syntactic interpretation of the grammatical implications of the inflectional affix.
[9]Note that, as discussed in Tyler *et al.* (2005*b*), these data on their

own do not allow us to exclude an account of the ACC involvement in terms of differences in task requirements between regular and other conditions—although RT and error data suggest that there is no major difference in difficulty between, for example, regular and pseudo-regular forms.

[10] Devlin *et al.* (2004) themselves interpret these results quite differently, since they regard their pseudo-derived/semantically opaque condition (*department/depart, hardly/hard*) as a purely orthographic control for their morphologically related condition (*teacher/teach*). This does not seem tenable to us, given the ample evidence (cited above) for the morphologically driven processing elicited by opaque and pseudo-derived pairs of exactly this type.

[11] For derivational morphology, where we also see very early identification of morphemic structure, for both transparent and opaque derived forms, it is unlikely that this leads to a disassembly of the complex form into its morphemic components for the purposes of subsequent analysis (for further discussion, see Marslen-Wilson in press).

[12] 'Exaptation' is the reutilization, during phylogenesis, of biological mechanisms for a new function different from the one for which they evolved (Gould & Vrba 1982).

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