Chapter 10

The Lexicon, Grammar, and the Past Tense: Dissociation Revisited

William D. Marslen-Wilson
MRC Cognition and Brain Sciences Unit, Cambridge, UK

Lorraine K. Tyler
Centre for Speech and Language, University of Cambridge, UK

In 1997 Liz Bates and Judith Goodman published an important paper entitled "*On the inseparability of grammar and the lexicon.*" This paper, which pulls together decades of work on normal and abnormal development, argues eloquently and persuasively for an "emergentist" view of language. Bates and Goodman argue against the autonomy of grammar, and, more generally, against the view that language learning depends on innate abilities that are specific to language. Instead, they put forward a unified lexicalist approach, whereby language is acquired through processes and learning mechanisms which are not grammar- or language-specific, and where lexical and grammatical development are so strongly interdependent that a modular approach to the acquisition of grammar is simply untenable.

A key part of Bates and Goodman's argument—and the focus of their discussion of language breakdown in brain-injured adults—is the claim that not only does the developmental evidence point towards a non-modular, emergentist approach to language acquisition, but also that there is no compelling evidence for modularity in the adult system (see also Dick, Bates, Wulfeck, Utman, Dronkers, & Gernsbacher, 2001). The facts of language breakdown, they argue, do not demonstrate a convincing dissociation between grammar and the lexicon, leading them to reject the view that these functions are mediated in the adult by separate, dedicated, domain-specific neural systems (Bates & Goodman, 1999, p. 71). Our goal in writing this chapter is to consider the implications of some new evidence for neural dissociations between aspects of linguistic function that also seem to separate grammatical and lexical aspects of the language system.

This evidence comes from a psycholinguistic domain which has also seen very robust debates about the issue of whether there are independent functional and neural levels of grammatical representation which are distinct from other forms of linguistic knowledge, in particular stored lexical representations. This is the continuing set of controversies surrounding the English regular and irregular past tense—its acquisition during language development, and the characterization of its representation in the adult system. Although Bates and Goodman do not discuss this controversy in their 1997 and 1999 papers, and although the rhetoric of the dispute has been somewhat different in emphasis, it shares the same fundamental contrast between domain-general processes required to learn the basic lexicon of the language—involving storage of sound/meaning relationships—and the potentially domain-specific processes required to handle regular inflectional morphology, which are argued to require algorithmic procedures manipulating syntactically organized symbols (for a recent overview see Pinker 1999). The views of Pinker and his colleagues, like the Chomskian accounts under attack by Bates and Goodman, have in common a conception of the specialness of language, where its critical features are indeed domain-specific and almost certainly innate (see also Pinker 1991; 1994). We will start with a brief summary of how the past-tense debate has evolved over the last few decades.

THE PAST-TENSE DEBATE

The English past tense has been center-stage almost from the beginnings of modern cognitivist approaches to language, going back nearly 40 years. The principal reason for this is the clarity of the contrast that it offers between a highly rule-like process—the formation of the regular past tense by adding the affix /-d/ to the verb stem (as in *jump-jumped; sigh-sighed*)—and the unpredictable and idiosyncratic processes of irregular formation (as in *think-thought; make-made*), applying to a small minority of English verbs, where each case seemingly has to be learned and represented separately. This contrast is frequently characterized—most prominently in Pinker's 1999 book—as a contrast between the domain of words (the lexicon) and the domain of rules (the grammar).

During the cognitivist upheavals of the 1960's, the acquisition of these contrasting linguistic components of the English past tense played an important role in establishing the view of mental computation as rule-based manipulation of symbol systems. Children learning English seemed to move from an early stage of rote-learning of individual past tense forms to the induction of rule-based representations, as reflected in over-regularizations such as *goed* and *bringed*. These followed an initial period when *went* and *brought* were used appropriately, and *goed* and *bringed* did not occur. It was argued that these anomalous forms could not be explained in terms of non-cognitive accounts of the acquisition process—for example, through imitation, or through Skinnerian reinforcement procedures—since the child would never be exposed to these forms in the environment. Their occurrence seemed instead to reflect the child's induction of a linguistic rule—in this case, governing the formation of the regular past tense—with the subsequent misapplication of this rule to verbs which had irregular past tenses, and where, crucially, the child had previously used these irregular and highly frequent forms correctly.

This widely accepted argument from acquisition was thrown into doubt by Rumelhart and McClelland's demonstration that a simple connectionist network could apparently simulate the crucial characteristics of the learning sequence attributed to human children (Rumelhart & McClelland, 1986). The network moved from an early period of correct generation of irregular past tense forms to a phase of over-regularization, where these irregular forms were regularized in ways analogous to the child's errors. The network could in no way be said to have learnt a symbolically stated rule. The fact that it could, nonetheless, exhibit seemingly rule-governed behavior, including apparent over-extension of these "rules," proved enormously influential in subsequent attempts to argue for (or against) a view of mental computation as rule-based and symbolic. It has also triggered an extensive and forceful debate.

Without discussing in detail the contents of this debate, it is fair to say that the controversy between connectionist and symbolic accounts of the acquisition process for the English past tense has effectively reached stalemate as far as the observable properties of the process are concerned. Early criticisms of the Rumelhart and McClelland model did pinpoint important flaws in the model, but subsequent work—for example by Plunkett & Marchman (1993)—went a long way to meeting these criticisms. Arguably, both connectionist learning models and accounts in terms of symbolic mechanisms each seem able to account for the qualitative and quantitative properties of the acquisition of the past tense by the human child.

To distinguish the two types of account it became necessary to look, in addition, at other aspects of the mental representation of English regular and irregular past tenses. Attention shifted, accordingly, to the properties of the "end state"—the manner in which regular and irregular forms are mentally represented by the adult native speaker of English. Current views of this have converged on the contrast between a *single mechanism* approach, arguing for a complete account of mental computation in terms of current multi-layer connectionist networks, and a *dual mechanism* approach, arguing that while connectionist accounts may be appropriate for the learning and representation of the irregular forms, a symbolic, rule-based system is required to explain the properties of the regular past tense, and, by extension, the properties of language and cognition in general.

In spirit, at least, these two camps map closely onto the opposing views contrasted by Bates and Goodman. The single mechanism approach shares the crucial assumptions about language function being built out of domain-general processes, the rejection of domain specific modules with specialist processing capacities, and the claim that lexical and syntactic functions are acquired together as expressions of the same general computational process. The converse of these views of course characterizes dual mechanism approaches, where the emphasis on the special computational mechanisms required for rule-based behavior is closely linked to claims about genetic specialization underlying human language (e.g., Pinker, 1994).

DISSOCIATIONS IN PAST-TENSE PERFORMANCE

The relevance of the past-tense debate to the issues discussed by Bates and Goodman is heightened by the strongly neuropsychological turn that the debate has taken over the past five years, with several results pointing to a dissociation of the underlying neural systems required for the production and perception of regular and irregular inflected forms. Patients who typically have damage involving the temporal lobe tend to show poorer performance on the irregulars compared to the regulars in elicitation and reading tasks, while deficits for the regulars are associated with damage to left inferior frontal cortex (LIFG) and underlying structures (Marslen-Wilson & Tyler, 1997; 1998; Miozzo, 2003; Patterson, Lambon Ralph, Hodges & McClelland, 2001; Tyler, de Mornay Davies, Anokhina, Longworth, Randall & Marslen-Wilson, 2002; Ullman, Corkin, Coppola, Hickok, Growdon, Koroshetz & Pinker, 1997). This has been shown in a variety of neuropsychological studies probing the comprehension and production of the regular and irregular past tense (Marslen-Wilson & Tyler, 1997; Ullman et al, 1997; Tyler et al, 2002a).

Studies of production show that patients with damage to the LIFG have difficulty in producing regularly inflected words in elicitation tasks (Ullman et al., 1997), while their performance on irregularly inflected forms is relatively normal. Studies of comprehension of the past tense have used a priming paradigm to compare the processing of regularly and irregularly inflected verbs. Patients with damage to the LIFG do not show the normal pattern of morphological priming for the regulars, in prime-target pairs like *jumped/jump*, even though the irregulars, as in pairs like *gave/give*, prime normally (Marslen-Wilson & Tyler, 1997; 1998; Tyler et al., 2002a).

Lexical access from regularly inflected forms seems generally disrupted for these patients. Pairs like *jumped/leap* fail to elicit significant semantic priming effects, even though the uninflected stems (*jump/leap*) prime normally (Longworth, Marslen-Wilson & Tyler, 2001).

These neuropsychological dissociations have been interpreted in two different ways, which again link directly to the concerns of Bates and her colleagues. Given the key assumption of single mechanism accounts, that both types of past tense forms are processed by a uniform system where different morphological types are handled by the same underlying process, the existence of plausible and replicable evidence for dissociation seems to present a serious challenge. Like Bates and Goodman (1997; 1999), single mechanism theorists in the past-tense domain regard separability of linguistic function over different neural regions as potentially damaging evidence against their theoretical position. Not surprisingly, dual mechanism theorists regard evidence for dissociation as confirmation that distinct underlying systems are engaged by regular and irregular forms (e.g., Pinker & Ullman, 2002; Ullman, 2001).

In an influential response to this challenge, Joanisse & Seidenberg (1999) have proposed a single mechanism model capable of exhibiting dissociative behavior for regular and irregular English morphology (see also McClelland & Patterson, 2002). Dissociations in past tense performance following damage to the brain are explained in terms of the differential reliance of regulars and irregulars on the contributions, respectively, of phonology and of semantics. Selective deficits for the irregulars occur as a by-product of damage to the semantic system, while selective deficits for the regulars are caused by an impairment to the phonological system.

The value of the kind of account put forward by Joannisse and Seidenberg is not only that it reminds us that differences in behavioral outcome do not necessarily reflect corresponding underlying differences in the structure of the system, but also that it puts the theoretical cards of connectionist single system accounts very firmly on the empirical table. The way in which the model explains regular/irregular dissociations makes strong empirical predictions. As we will argue below, these predictions seem to fail, with wider ramifications for the kind of approach exemplified by this type of model.

Joannisse and Seidenberg (1999) propose a multi-level connectionist learning model in which the representation and processing of regular and irregular English inflected forms is modeled in terms of their speech input, speech output, and semantics. The critical property of this model, from the perspective of explaining dissociation, is the differential reliance of the regulars and irregulars on the contribution of phonology and semantics in the learning process. The representation in the network of the mapping between stems and their regular past tense forms (e.g. *open—opened*) is primarily driven by the phonological relationship between them, since this relationship is entirely predictable. The equivalent mapping for the irregulars (e.g. *think-thought*) is more dependent on the semantic relationship between the stem and its past tense form, since the phonological relationship between them is much less uniform and predictable. This leads to the prediction that relatively selective deficits for the regulars will be caused by a phonological impairment, whereas deficits for the irregulars should be a by-product of damage to the semantic system.

To test these predictions, Joanisse & Seidenberg (1999) trained the model on simulations of speaking, hearing, repeating and generating the past tense, where all these input/output mappings pass through the same set of hidden units. They then lesioned the network in specific ways to determine whether this would have differential effects on the regulars or irregulars. When the speech output layer was lesioned, modeling an acquired phonological deficit, this affected past tense generation performance on nonwords and—at very severe levels of lesioning—on the regular past tense verbs. Lesioning the semantic layer modeled a semantic deficit, after which the model performed most poorly at generating irregular past tenses. By the same token, although this was not explicitly discussed in the 1999 paper, lesioning the speech input layer should allow the system to model deficits in speech comprehension, on the same phonological basis. Whether viewed from the perspective of comprehension or of production, in neither case is there any explicit morphological differentiation between regular and irregular forms; the differences between them reflect the relative balance between semantic and phonological factors during the acquisition phase of the network. Since the same mechanism is claimed to underlie the processing of regular and irregular verb morphology, this type of model is consistent with the broader Bates and Goodman claim that grammatical and lexical phenomena share the same substrate.

Leaving aside the question of how well the specific performance of the Joannisse & Seidenberg model actually matches observed patient performance, this type of model makes strong predictions about the basis of deficits for the regulars and irregulars in brain-damaged populations. Turning first to the predictions concerning the regulars, the model claims (a) that patients who have problems with the regular past tense will have an accompanying phonological deficit, and (b) patients who have a phonological deficit will also have problems with the regular past tense. Two studies that we have recently reported seem to conflict with both of these claims, as well as the corollary claims that the model makes about the role of phonological complexity in explaining poor performance on the regulars.

We find that patients with LIFG damage and difficulties with regular inflection do not have equivalent problems with uninflected words that are phonologically matched to regular past tense forms (Tyler et al., 2002b). In this latter study, patients were significantly impaired on same/different judgements to pairs of words containing regular past tense forms (as in *played/play*). These problems with the regulars could not be attributed to purely phonological factors, since the patients performed significantly better on pseudo-regular word-pairs (*trade/tray*) that were phonologically matched to the regular past tense pairs but were not themselves inflected forms. Furthermore, degree of impairment on the regular inflected forms, whether in this phonological judgement task or in priming tasks (Longworth et al., 2001; Marslen-Wilson & Tyler, 1997; 1998; Tyler et al., 2002b), does not seem to be correlated with degree of phonological impairment. Patients who are almost normal in standard tests of phonological performance can exhibit equivalent deficits in processing regular inflection to patients with very poor performance on these tests (Tyler et al., 2002b).

Turning now towards the claims made by single mechanism accounts for the basis of deficits for the irregulars, the critical association predicted by the Joannisse and Seidenberg model is that neuropsychological patients who have semantic deficits will necessarily have disproportionate problems with the irregulars. While it is true that many patients with semantic deficits have accompanying problems with the irregulars (Marslen-Wilson & Tyler, 1997; 1998; Tyler et al., 2002; Patterson et al., 2001), there are also patients who do not show this dissociation (Tyler et al., 2003). Using both priming tasks and elicitation tasks, we have recently shown that some semantic dementia patients (who have progressive temporal lobe damage resulting in semantic deficits) show normal priming for the irregular past tense and do not have a disproportionate problem with the irregulars in an elicitation task (Tyler et al., 2003). This is despite the fact that these are patients who have profound semantic deficits, as reflected in all standard tests of semantic function. The predicted other side of the association—that patients who have problems with the irregulars should also have a semantic deficit—appears to be disconfirmed by recent data from a patient who has a clear deficit for the irregulars, as measured by poor performance on a variety of different tests, but who has no detectable semantic deficit (Miozzo, 2003). Taken together, these sets of results demonstrate that semantic deficits do not necessarily go hand-in-hand with difficulties in producing or comprehending irregularly inflected past tense forms.

In summary, closer examination of the patient populations that exhibit regular/irregular dissociations does not come up with the critical set of linked deficits predicted by current single mechanism accounts of the source of these dissociations. Problems with the regular morphology can be dissociated from phonological impairment and phonological complexity, while there does not seem to be an obligatory causal link between semantic competency and performance with irregular past tense forms. This, in turn, suggests that the observed regular/irregular dissociations do reflect underlying differences in the functional specializations of different areas of the brain. To assess the implications of this, however, for the Bates and Goodman emergentist and lexicalist project, we need first to consider what these data are telling us about the likely structure of the cortical language system.

FRONTO-TEMPORAL INTERACTIONS IN HUMAN LANGUAGE FUNCTION

The classic dual mechanism account, as developed by Pinker, Ullman and colleagues (Pinker, 1991; Prasada & Pinker, 1993; Ullman et al., 1997; Pinker & Ullman, 2002; Ullman, 2001), claimed that a specific rule-based system processes the regulars by adding and stripping away inflectional affixes from their stems. The irregulars, in contrast, are learned individually by rote and stored in a separate knowledge store. On this view, past tense dissociations are explained in terms of selective damage to either the rule-based system or to the store of lexical representations. In these terms, evidence for neural dissociation is clearly inconsistent both with single mechanism accounts of the English past tense and with the Bates & Goodman arguments against specialized sub-systems supporting grammatical function.

We have recently proposed a modified version of a dual route account which places less emphasis on the regularity/irregularity distinction *per se*—and its associated theoretical baggage—and more emphasis on the role of morphophonological parsing processes which allow the segmentation and identification of stems and affixes (Marslen-Wilson & Tyler, 1998; 2003; Tyler et al., 2002a; Tyler, Randall & Marslen-Wilson, 2002b). These processes, associated with LIFG, are required for the analysis of regularly inflected forms in English, with their stem + affix structure, but do not apply to English irregular past tense forms. These have no overt morphophonological structure and must be accessed as whole forms. On this account, deficits for the regulars arise when there is disruption of morphophonological parsing processes, associated with damage to the LIFG, whereas deficits for the irregulars stem from damage to temporal lobe structures supporting access from phonological input to representations of stored lexical form.

These proposals can be linked more generally to claims about the overall neural and functional architecture of the human language system, almost all of which have in common an emphasis on language-relevant processing structures in superior temporal and inferior frontal areas, and their linkage into a fronto-temporal network. The origins of these claims lie in the 19th century Broca-Wernicke-Lichtheim framework, where disorders of comprehension were associated with superior temporal lobe damage ("Wernicke's area"), while problems in language production—so-called telegraphic speech, for example—were associated with damage to Broca's area in frontal cortex. More subtle aphasic deficits were analyzed in terms of damage to connections between these areas, thought to be primarily mediated by the arcuate fasciculus, running posterior from Wernicke's area and looping round to connect to inferior frontal structures.

More recently, these types of account have been restated in a more anatomically and neurophysiologically explicit framework, deriving from work on the primate auditory system (e.g., Rauschecker & Tian, 2000). Rauschecker and colleagues have proposed an analysis of the functional organization of primate audition in terms of the dorsal/ventral distinction already established for primate vision, with a "ventral" system running anteriorly down the temporal lobe from primary auditory cortex to connect to inferior frontal areas, and a "dorsal" system running posteriorly into the temporo-parietal junction and then forward to connect to a different set of frontal lobe structures. A number of proposals have begun to emerge for the interpretation of human speech and language systems in this general framework (e.g., Hickok & Poeppel, 2000; Scott & Johnsrude, 2003). These have in common the assumption that ventral pathways in the left temporal lobe are involved in the mapping from phonology onto semantics, but put forward divergent views of the nature and function of the dorsal pathways.

In recent publications (Tyler et al., 2002a; 2002b) we have proposed a possible relationship between the global dorsal/ventral distinction and the evidence for processing and neurological dissociations involving the English regular and irregular past tenses. The ventral system, on this account, involves temporal lobe structures that mediate access (both phonological and orthographic) to stored lexical representations. The dorsal pathway links *via* the arcuate fasciculus to systems in L inferior frontal areas important for the analysis and production of complex morphophonological sequences. The language-specific properties of the English past tense would therefore map differentially onto these two systems, with irregular forms linking into ventral systems optimized for access to stored whole forms, while regular forms require in addition the involvement of frontal systems supporting processes of phonological assembly and disassembly.

In recent research we have taken forward this emerging account of the human speech and language system, using event related fMRI in the intact brain to investigate more directly the neural systems underlying the processing of regular and irregular morphology. To do this we use the same-different judgement task whose sensitivity to critical inflectional variables was previously demonstrated in research on patients with LIFG damage (Tyler et al., 2002b). The pattern of performance shown by these patients indicated that the processing of regular past tense pairs depended on brain regions that were damaged in this patient population. By running the same task on normal participants in an fMRI study, we were able to activate the full range of neural regions engaged in the processing of regular past tense inflection in the intact system, as well as illuminating their relationship to the language system as a whole.

The results confirmed, first, that regular and irregular past tenses in English differentially activate the cortical language system in the intact brain, and that these differences cannot straightforwardly be reduced to lower-level phonological factors (Tyler, Stamatakis, Post, Randall & Marslen-Wilson, 2003). The critical factor seems to be the presence of an overt inflectional affix, attached to a real-word verb stem. Second, the results make it clear that we are dealing with an extended fronto-temporal network, and that the additional demands made by regular inflected forms extend not only to LIFG structures, but also to the superior temporal lobes, and to mid-line regions in the anterior cingulate. This connected system of sites is clearly related to the classical Broca-Wernicke system in traditional neuropsychology, and to the dorsal route in more recent accounts. We now turn to a consideration of the possible functional interpretation of this fronto-temporal network, and why processes involving the regular past tense should be differentially affected when the LIFG is damaged.

Both neuropsychological and neuroimaging data associate superior temporal regions, especially on the left, with the access of lexical form and meaning from the phonological input (e.g., Kertesz, Lau & Polk, 1993). In the neuropsychological literature, the focus has been specifically on the role of 'Wernicke's area'—the posterior regions of the superior temporal gyrus (STG)—in spoken language comprehension. This region has been claimed to store 'the memory images of speech sounds' (Wernicke, 1874), with connections between Wernicke's area and other cortical regions (temporal and frontal) enabling access to both meaning and speech production Lichtheim (1885). In support of the view that this region is specifically involved in the processing of speech, neuroanatomical studies have shown that posterior STG is larger in the left hemisphere, suggesting a major role in speech processing (Geschwind & Levitsky, 1968), and patients with LH damage in this region typically have spoken language comprehension deficits (e.g., Kertesz, 1981; Damasio, 1992). It is important to note, however, as Saygin, Dick, Wilson, Dronkers, & Bates (2003) have recently reminded us, that the critical role of these structures in speech processing does not mean that they are uniquely dedicated to language functions. They also play an important role in processing and interpreting nonverbal auditory information, such as environmental sounds.

Neuroimaging studies typically find that speech processing activates broad regions of bilateral STG (Crinion et al, 2003; Davis & Johnsrude, 2003; Scott et al, 2000). In our own imaging study we found that speech (words and non-words) activates the same extensive region of STG, extending both anteriorly and posteriorly from Heschl's gyrus, as has been reported in previous studies (e.g., Scott et al, 2000; Binder et al, 2000). Within this region, the regularly inflected verbs produce significantly enhanced activation in bilateral STG compared to the irregulars. In the left hemisphere, the greater activation for the regulars compared to the irregulars is centered on Wernicke's area, with the peak activations close to those reported in other imaging studies which have explored the neural underpinnings of speech processing (e.g., Wise at al, 2001; Binder et al, 2000).

These results show that, while the exact function of the posterior STG in speech processing and spoken language comprehension is unresolved, it is clear that it plays an important role in the mapping of speech inputs onto stored representations of word meaning, and that it is particularly active during the processing of regular inflected forms. This is the basis for the first component of our analysis, which assumes that the primary process of lexical access—of mapping from acoustic-phonetic input to lexical semantic representations—is mediated by superior temporal lobe systems, possibly bilaterally, linking to other areas of the temporal lobe.

The second component of our analysis is the claim that regular inflected forms, such as *jumped*, are not well-formed inputs to this mapping process, and that the intervention of inferior frontal systems is required for the access process to flow smoothly. Although *jump*, or any other stem form, can map straightforwardly onto lexical representations, the presence of the affix (t) makes it transiently a "non-word"—in the same way, perhaps, that the addition of a (t) to the form *clan* would produce the sequence *clant* which is not a well-formed input to the access process.

To interpret *jumped* correctly, and to allow the process of lexical access to proceed normally, the past tense affix needs to be recognized, and reassigned to a different linguistic function. This process requires an intact LIFG, and intact links to left superior temporal cortex. Note that irregular past tense forms, which are never realized as an unchanged stem plus an affix, are not subject to the same additional processing requirement. They are assumed to be accessed as whole forms, exploiting the same temporal lobe systems as uninflected stems.

The clearest evidence for this functional interpretation comes from the priming results recently reported by Longworth et al (2001), showing that patients with LIFG damage, and difficulties with regular inflectional morphology, show deficits not only in morphological priming (i.e., between *jumped* and *jump*; Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a) but also in semantic priming when the primes are regularly inflected forms, as in pairs like *jumped/ leap*. At the same time, critically, they show normal performance both for pairs with stems as primes, as in *jump/leap*, and for pairs where the prime is an irregular past tense form, as in *slept/doze*.

Normal semantic priming performance in these auditory-auditory paired priming tasks, where a spoken prime (e.g., *jump*) is immediately followed by a spoken target (e.g., *leap*), requires rapid access to lexical semantic representations in the processing of both prime and target. The patients' preserved performance for stem and irregular spoken primes shows that the systems supporting fast access of meaning from speech are still intact for these types of input—either through remaining functionality in left temporal lobes, or through right temporal processes. This means that, to explain the decrement in performance on the regular inflected forms, we have to attribute different properties to these inflected forms than to stem or irregular forms, and look for damage elsewhere in the brain that could be the source of these difficulties.

This brings us to the role of left inferior frontal areas, which are strongly associated with the processing of grammatical morphemes, and with syntactic function more generally (Zurif, 1995; Caplan, Alpert, & Waters, 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996). Neuropsychological studies associate damage to inferior frontal regions, especially BA 44 and 45 (Broca's area) with both syntactic and morphological deficits (Miceli & Caramazza, 1988; Marslen-Wilson & Tyler, 1997, 1998; Tyler, 1992). A number of neuroimaging studies investigating spoken sentence comprehension have reported significant activations in BA 44 for syntactic processing, which overlap with the activations that we find in the current study for the regulars compared to the irregulars (e.g., Embick et al., 2000; Friederici, Opitz, & von Cramon, 2000). There is also evidence from a number of sources for LIFG involvement in processes of phonological segmentation (e.g., Burton et al., 2000; Zatorre et al., 1992).

Both inferior frontal and superior temporal areas will be involved in the analysis of forms like *played*, which require the simultaneous access of the lexical content associated with the stem *play* (primarily mediated by temporal lobe systems), and of the grammatical implications of the {-d} morpheme (primarily mediated by inferior frontal systems). Unless these different components of the word-form are assigned to their appropriate processing destinations, effective on-line processing of such forms is disrupted, as demonstrated in the priming studies mentioned earlier (Longworth et al., 2001; Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a). In contrast, for irregular forms like *gave* or *bought*, no such on-line differentiation is either required or possible. Patients with LIFG damage do not have problems with the irregulars, suggesting that their processing does not necessitate the involvement of this region (Tyler et al., 2002a,b). Access for words like *gave* is mediated, as a whole form, through temporal lobe systems, and does not require segmentation into phonologically separate stem and affix components (Marslen-Wilson & Tyler, 1998). Thus, although irregular past tense forms will activate LIFG to some extent—for example, because of the syntactic implications of their grammatical properties—immediate access to lexical meaning does not obligatorily require LIFG phonological parsing functions in the same way as regular past tense forms.

On this emerging account, the increased activation for regulars in temporal and inferior frontal areas reflects, on the one hand, the specialized LIFG processes involved in analyzing grammatical morphemes, and on the other the continuing STG activity involved in accessing lexical representations from the stems of regular inflected forms. Although the exact nature of LIFG function is still unclear (and may be quite diverse), the area seems to be critically involved in supporting both morphophonological parsing—the segmentation of complex forms into stems and affixes—and the syntactic processes triggered by the presence of grammatical morphemes such as the past tense marker.

In a further refinement of this emerging model, we suggest that the processing relationship between L frontal and temporal regions is modulated by anterior midline structures including the anterior cingulate, which both neuroanatomical and functional neuro-imaging evidence suggest is well suited for this role. The anterior cingulate projects to or receives connections from most regions of frontal cortex (Barbas, 1995) and from superior temporal cortex (Petrides & Pandya, 1981), while recent neuro-imaging data implicate the ACC in the modulation of fronto-temporal integration (e.g., Fletcher, McKenna, Friston, Frith, & Dolan, 1999).

IMPLICATIONS

To summarize these proposals, we argue that the fronto-temporal neural system involved in language processing is critically involved in the on-line process of separating the speech input into complementary processing streams, on the one hand extracting information about meaning, conveyed by uninflected nouns and verb stems, such as *house* or *stay*, and on the other information about grammatical structure, conveyed in part by inflectional morphemes such as the past tense {-d}. These proposals point to a more specific and dynamic account of how aspects of language function are organized in the human brain, and provide a functional framework within which to interpret behavioral and neuropsychological differences in the processing of English regular and irregular past tense forms.

The core issue raised by these claims, in the current context, is the strong position they take on the differentiation of language function across different neural areas. We interpret evidence for dissociation as indeed being evidence that different areas of the brain can make different types of contribution to the functioning of the language system, and that these contributions can have a specifically linguistic character that is not reducible simply to phonological or semantic processes and their interaction. This is clearly contrary to the claims of the predominant single mechanism account in the past tense debate. However, it does not necessarily provide strong support to the converse view—the classical dual mechanism approach as stated by Pinker, Ullman, and others. The results we report, and our interpretation of them, are arguably neutral with respect to many of the most prominent theoretical issues in this domain, especially those concerning specific differences in types of mental computation, the modularity and domain-specificity of the different systems involved, and the extent to which these differences are directly genetically specified. Some or all of these may, conceivably, turn out be true of the fronto-temporal contributors to language processing, but there is little in the current data that directly addresses these issues. For example, to claim, as we and many others have done, that there is a critical role for superior temporal areas in the mapping of phonological inputs onto lexical representations, is not to exclude the possibility that these same regions also serve other cognitive functions (c.f., Saygin et al, 2003, as discussed earlier). In other words, to assign a function to a given area is not necessarily to claim domain specificity for that area.

In terms of the Bates and Goodman (1997, 1999) proposals, our analysis does seem to be inconsistent with their view that processing difficulties in aphasic patients with receptive agrammatism (Broca's aphasics) do not have any specific localization implications. Aphasic patients' deficits, for example, in the processing of grammatical morphemes, are argued not to reflect damage to specific neural subsystems, but rather the sensitivity of these morphological operations to any source of degradation in the global functioning of the relevant brain areas (Dick et al., 2001). Neurologically intact normal populations, including both elderly controls and college students, can be shown to exhibit patterns of deficit comparable to aphasic patients when required to process spoken utterances under conditions of perceptual and cognitive stress (e.g., low-pass filtering of the speech accompanied by a digit memory task). This is argued to support a distributive model of language in the brain, where language functions are distributed over several cooperating areas, rather than having any specific locus.

Our proposals, however, suggest that this view should not be taken too far. Of course language is instantiated in the brain as a distributed system, but this does not mean that specific functions may not depend on specific areas, and on the links between them, so that damage to a given subnetwork can lead to specific functional deficits. The possibility of simulating aspects of these deficits by degrading performance in unimpaired populations does not in itself, in our view, permit the inference that therefore there is no specific substrate to the performance of the linguistic processing function at issue.

More broadly, however, we see no inconsistency between our proposals here and the general emergentist and lexicalist approach to language in the brain proposed by Bates and her colleagues. As we understand current statements of this approach, it in no way excludes—and indeed seems to predict—an adult brain with highly differentiated assignments of processing functions to particular dynamic combinations of brain areas (e.g., Bates, 1999; Elman, Bates, Johnson, Karmiloff-Smith, Parisi, and Plunkett, 1996). As these authors have convincingly argued, our current understanding of the biology of neural maturation points to a process whereby cortical function differentiates during development as the result of a subtle interplay between phylogeny and ontogeny. The basic sensorimotor wiring of the brain may be genetically specified, but the way in which complex cognitive functions are recruited to different brain systems will reflect an interaction between the demands of particular kinds of processing operations and the properties of the areas being projected to.

The critical challenge for a future cognitive neuroscience of language will be to flesh out this vision of the functional and neural properties of the human language system, and of its developmental trajectory. To do this we will need to specify in detail, at multiple levels of description, what the specific functional characteristics of the system are, how they give rise to the particular, detailed properties of speech comprehension and production, and how these functional characteristics themselves flow from the properties of the neural systems underlying them. In this context, evidence for differentiation of function in the adult brain is in no way evidence *per se* against an emergentist view. Rather, it is part of the process of moving from very general questions about human language systems—modular/nonmodular, domain general/domain specific, and so forth—to a specific program of investigation of the underlying scientific facts of the matter. One of the beacons that will help to guide us in this enterprise will undoubtedly be the pioneering work of Liz Bates and her colleagues.

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REFERENCES

Barbas, H. (1995). Anatomic basis of cognitive-emotional interactions in the primate prefrontal cortex. *Neuroscience and Biobehavioral Reviews, 19*(3), 499–510.

Bates, E. (1999). Plasticity, localization and language development. In S. H. Broman & J. M. Fletcher (Eds.), *The changing nervous system: Neurobehavioral consequences of early brain disorders* (pp. 214–253). New York: Oxford University Press.

Bates, E., & Goodman, J. (1997). On the inseparability of grammar and the lexicon: Evidence from acquisition, aphasia and real-time processing. *Language and Cognitive Processes, 12*(5–6), 507–584.

Bates, E., & Goodman, J. (1999). On the emergence of grammar from the lexicon. In B. MacWhinney (Ed.) *The emergence of language.* Mahwah, NJ: Lawrence Erlbaum Associates.

Binder, J. R., Frost, T. A., Hammeke, P. S. F., Bellgowan, P. S. F., Springer, J. A., Kaufman J. N., & Possing, E. T. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex, 10,* 512–528.

Burton, M., Small, S., & Blumstein, S. (2000). The role of segmentation in phonological processing: An fMRI Investigation. *J Cognitive Neuroscience, 12,* 679–90.

Caplan, D., Alpert, N., & Waters, G. (1998). Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *J Cognitive Neuroscience, 10,* 541–552.

Crinion, J., Lambon-Ralph, M. A., Warburton, E., Howard, D., & Wise, R. (2003). Temporal lobe regions engaged during normal speech comprehension. *Brain, 126,* 1193–1201.

Damasio, A. (1992) Aphasia. *New England Journal of Medicine, 326,* 531–539.

Davis, M., & Johnsrude, I. (2003). Hierarchical processing in spoken language comprehension. *J. Neuroscience, 23*(8), 3431–3423.

Dick, F., Bates, E., Wulfeck, B., Utman, J. A., Dronkers, N., & Gernsbacher, M. A. (2001). Language deficits, localization, and grammar. *Psychological Review, 108,* 759–788.

Dronkers, N., Redfern, B., & Knight, R. (2000). The neural architecture of language disorders. In MS Gazzaniga (Ed.) *The New Cognitive Neurosciences,* MIT Press.

Elman, J. L., Bates, E., Johnson, M. H., Karmiloff-Smith, A., Parisi, D., & Plunkett, K. (1996). *Rethinking innateness: A connectionist perspective on development.* Cambridge, MA: MIT Press.

Embick, D., Marantz, A., Miyashita, Y., O'Neill, W., & Sakai, K. (2000). A syntactic specialization for Broca's area. *Proceedings of the National Academy of Sciences, 97*(11), 6150–6154.

Fletcher, P. J., McKenna, K. J., Friston, C. D., Frith, & Dolan, R. J. (1999). Abnormal cingulate modulation of fronto-temporal connectivity in schizophrenia. *Neuroimage, 9*(3), 337–342.

Friederici, A., Opitz, B., & von Cramon, Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cerebral Cortex, 10,* 698–705.

Geschwind. N., & Levitsky, W (1968). Human brain: Left-right asymmetries in temporal speech region. *Science, 16*1, 186–187

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4*(4), 131–138.

Joanisse, M., & Seidenberg, M. (1999). Impairments in verb morphology after brain injury. *Proceedings of the National Academy of Sciences, 96,* 7592–7.

Just, M., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, R. (1996). Brain Activation Modulated by Sentence Comprehension. *Science, 274,* 114–116.

Kertesz, A. (1981) Anatomy of jargon. In J. Brown (Ed.). *Jargonaphasia.* New York: Academic Press.

Kertesz, A., Lau, W. K. & Polk, M. (1993). The structural determinants of recovery in Wernicke's aphasia. *Brain & Language, 44,* 153–164.

Longworth, C. E., Randall, B., Tyler, L. K. & Marslen-Wilson, W. D. (2001). Activating Verb Semantics from the Regular and Irregular Past Tense. In J. Moore (Ed.), *Proceedings of the 23rd Annual Conference of the Cognitive Science Society* (pp. 570–575). Mahwah, NJ: Lawrence Erlbaum Associates.

Marslen-Wilson, W. D., & Tyler, L. K. (1997). Dissociating types of mental computation. *Nature, 387,* 592–594.

Marslen-Wilson, W. D., & Tyler, L. K. (1998). Rules, representations, and the English past tense. *Trends in Cognitive Science, 2,* 428–435.

McClelland, J., & Patterson, K. (2002). Rules or connections in past-tense inflections: what does the evidence rule out? *Trends in Cognitive Sciences, 6*(11), 465–472.

Miceli, G., & Caramazza, A. (1988). Dissociation of inflectional and derivational morphology. *Brain & Language, 35,* 24–65.

Miozzo, M. (2003). On the processing of regular and irregular forms of verbs and nouns: Evidence from neuropsychology. *Cognition, 87*(2), 101–127.

Petrides, M., & Pandaya, D. E. N. (1988). Association fiber pathways to the frontal cortex from the superior temporal region in the rhesus monkey. *Journal of Comparative Neurology, 273*, 52–66,

Plunkett, K., & Marchman, V. A. (1993). From rote learning to system building: Acquiring verb morphology in children and connectionist nets. *Cognition, 48*, 21–69.

Pinker, S. (1991). Rules of language. *Science, 253*, 530–535.

Pinker, S. (1994). *The language instinct.* New York: HarperCollins.

Pinker, S. (1999). *Words and rules: the ingredients of language.* New York: HarperCollins.

Pinker, S., & Ullman, M. (2002). The past and future of the past tense. *Trends in Cognitive Sciences, 6*(11), 456–463

Prasada, S., & Pinker, S. (1993). Generalizations of regular and irregular morphological patterns. *Language and Cognitive Processes, 8*, 1–56.

Rauschecker, JP & Tian, B (2000). Mechanisms and streams for processing of 'what' and 'where' in auditory cortex. *Proc Natl Acad Sci USA, 97*, 11800–11806

Rumelhart, D. E., & McClelland, J. L. (1986). On learning the past tense of English verbs. In McClelland, J. L. & Rumelhart, D. E. (Eds.), *Parallel distributed processing* (pp. 217–270). Cambridge: MIT Press.

Saygun, A. P., Dick, F., Wilson, S. W., Dronkers, N. F., & Bates, E. (2003). Neural resources for processing language and environmental sounds. *Brain, 126*, 928–945.

Scott, S., Blank, C., Rosen, S., & Wise, R. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123*, 2400–2406.

Scott, S., & Johnsrude, I. (2003). The organization and functional organization of speech perception. *Trends in Neurosciences, 26*(2), 100–107.

Tyler, L. K. (1992). *Spoken language comprehension: An experimental approach to normal and disordered processing.* MIT Press; Cambridge, Mass. 1992

Tyler, L. K., de Mornay Davies, P., Anokhina, R., Longworth, C., Randall, B., Marslen-Wilson, W. D. (2002a). Dissociations in processing past tense morphology: Neuropathology and behavioral studies. *Journal of Cognitive Neuroscience, 14*(1), 79–95.

Tyler, L. K., Randall, B., & Marslen-Wilson, W. D. (2002b). Phonology and neuropsychology of the English past tense. *Neuropsychologia, 40*, 1154–1166.

Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. D. (2003). *Differentiation in the neural architecture for spoken language: An fMRI study of past tense processing.* Manuscript, Center for Speech and Language, University of Cambridge.

Ullman, M. T. (2001). The declarative/procedural model of lexicon and grammar. *Journal of Psycholinguistic Research, 30*, 37–69.

Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., Pinker, S. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory and that grammatical rules are processed by the procedural system. *J Cognitive Neuroscience, 9*, 266–76.

Wernicke, C. (1874). *Der Aphasische Symptomenkomplex, eine Psychologische studie auf anatomischer basis.* Cohn & Weigert, Breslau.

Wise, R., Scott, S., Blank, C., Mummery, C., Murphy, K., & Warburton, E. (2001). Separate neural systems within "Wernicke's area." *Brain, 124*, 83–95.

Zatorre, R. J., Evans, A. C., Meyer, E., Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science, 256*, 846–849.

Zurif, E. B. (1995). In L. Gleitman & M. Liberman (Eds.), *Invitation to Cognitive Science.* Cambridge, MA: MIT Press.