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TECHNICAL REPORT

Effects of Broca's Aphasia and LIPC Damage on the Use of Contextual Information in Sentence Comprehension

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Effects of Broca's Aphasia and LIPC Damage on the Use of Contextual Information in Sentence Comprehension

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Abstract

Although widely explored, the nature of the lexical-semantic deficit observed in Broca's aphasia and its relation to the brain region of the same name has remained elusive. The present study coupled a case study approach with an auditory sentence-priming task to test hypothesized deficits in activation, selection, and integration mechanisms. Lexical decision latency and accuracy for three types of "Broca's" aphasic (one with damage to Broca's area and with a diagnosis of Broca's aphasia, one with damage to Broca's area but without Broca's aphasia, and one without damage to Broca's area but with Broca's aphasia) were compared to the performance of an aphasic patient with neither damage to Broca's area nor symptoms of Broca's aphasia. Results, however, did not clearly conform to predictions of any account, nor fall along traditional diagnostic or lesion criteria. Rather, the data indicated deviant patterns of controlled processing in all patients. It is argued that these discrepancies highlight certain common, but problematic, methodological practices in patient research, and alternative approaches are suggested.

Introduction

Since Paul Broca's landmark case study of an aphasic patient suffering from a lesion damaging the left inferior prefrontal cortex (LIPC), this region has been considered a key neural area subserving language (Broca, 1861). A century and a half later, and the precise role of "Broca's" area[1] in language processing remains a source of much debate and active research. In initial conceptions of LIPC function, this region was attributed a primary role in the production of speech, and aphasia following damage to this area was accordingly described as motor aphasia. In contrast with the fluent, jargon-laden speech of patients with posterior-temporal lesions and poor comprehension (i.e. Wernicke's or sensory aphasics), these patients exhibit halting, effortful speech but relatively intact comprehension abilities. The neural proximity of Broca's region to motor cortex and Wernicke's area to primary and secondary auditory cortex bolstered this breakdown of syndromes along expressive and receptive dimensions of language (Caplan, 1987).

Although the nature of the distinction between Broca's and Wernicke's aphasia has changed with time, from this earliest classification scheme emerged a long tradition of dichotomous interpretation of the linguistic deficits associated with anterior and posterior lesions. Evidence that Broca's aphasics actually do show impaired grammatical comprehension prompted the overturn of the production/comprehension model, in favor of one contrasting the grammatical knowledge of anterior-frontal and posterior-temporal patients. Specifically, the finding that Broca's patients have difficulty understanding the same kinds of complex grammatical structures that they fail to produce (e.g. passives) was taken as evidence that LIPC is fundamentally important in representing syntactic knowledge, and the meaningless but grammatically fluent speech of Wernicke's patients was taken as evidence of the importance of posterior-temporal areas in representing semantic knowledge (Caplan, 1987). In recent years, this same fundamental syntax/semantics distinction between aphasic syndromes, and their presumed neural bases, is reflected in several prominent modular accounts of language processing (e.g. Grodzinksy, 1995; Ullman, 2001; Pinker & Ullman, 2002) and has fuelled the theoretical emphasis placed on double-dissociations.

Nonetheless, several lines of evidence contradict the differentiation of aphasic syndromes along linguistic

[1] The exact boundaries circumscribing Broca's area vary, but for the most part, this label refers to pars triangularis and pars opercularis of the left inferior frontal gyrus, and often also the more ventral area, pars orbitalis (Amunts et al., 1999).

dimensions (for reviews see Bates & Goodman, 1997; Dick et al., 2001). Foremost, impairments in grammatical knowledge are not specific to patients suffering from Broca's aphasia (or anterior-frontal lesions). A pattern of *omission* or agrammatism (whereby grammatical function words are not generally produced) characterizes the speech of these patients; however, an equally deviant pattern of *substitution* or paragrammatism (whereby extraneous or inappropriate function words are produced) characterizes Wernicke's aphasia. Further, Broca's patients score above chance on offline measures of syntactic knowledge, such as judgments of grammatical well-formedness, suggesting that they have not lost their grammatical knowledge so much as have difficulty using it in real-time (Linebarger, Schwartz, & Saffran, 1983) More recently, a study by Saygin & Wilson (2004) indicated that damage to LIPC or a diagnosis of Broca's aphasia was not associated with impaired grammaticality judgments, although lesions compromising posterior *temporal* regions were. The selectivity of lexical-semantic deficits has similarly been called into question. For instance, the observation of intact semantic priming in Wernicke's aphasics, despite their impairment on explicit measures of semantic knowledge, argues against an explanation of their semantic deficits in terms of loss of representations (Blumstein, Milberg, & Shrier, 1982; Milberg, Blumstein, & Dworetzky, 1988) Likewise, the ubiquity of anomia (word-finding difficulty) with left-hemisphere lesions undermines claims that impaired lexical-semantic processing reflects damage to any one neural region (Bates & Goodman, 1997).

Taken together, these results have provided evidence for the inseparability of grammatical and lexical processing at a neural level, a conclusion difficult to reconcile with domain-specific, localizationist accounts of language (Bates & Goodman, 1997; Dick et al., 2001). Instead, these data have contributed to a reconceptualization of aphasic syndromes in terms of deficits in how lexical and syntactic knowledge is accessed and used in the real-time demands of language comprehension and production, rather than as reflecting loss of linguistic knowledge. For example, aphasic syndromes have been reconceived in terms of several possible processing deficits: speed of processing (Prather, Zurif, Stern, & Rosen, 1992; Prather, Zurif, Love, & Brownell, 1997; Swinney, Zurif, & Nicol, 1989), automatic versus controlled processing (Milberg et al., 1995), activation versus inhibition (Blumstein & Milberg, 2000), or the validity and processing cost associated with different linguistic features (MacWhinney & Bates, 1989). With respect to language comprehension specifically, semantic priming studies suggest an interpretation of the lexical-semantic deficits in Broca's aphasia in terms of a breakdown at one of three processes in lexical access (as defined by Marslen-Wilson, 1989, and others): the *activation* of words on the basis of sensory input, the selection of words best matching the acoustic signal and context, or the *integration* of words into a larger semantic representation.

To appreciate the arguments in favor of these process-based accounts of Broca's aphasia, it is necessary to consider the semantic priming paradigm in some detail. In brief, these tasks consider how recognition of a word is affected by its immediately preceding semantic context. Typically, target words are preceded by primes that are either semantically related or unrelated, and participants' responses to targets are faster and more accurate, or facilitated, when primes and targets are related (e.g. CAT-DOG) than when they are unrelated (e.g. BOOK-DOG). When a semantically neutral prime is included as a baseline (e.g. the world BLANK or a string of X's), responses in the unrelated condition are slower and less accurate, or inhibited, relative to this condition. Further, facilitatory and inhibitory priming effects are differentially sensitive to various task manipulations (e.g., stimulus onset asynchrony, the proportion of related to unrelated trials, instruction-induced manipulations of strategy, perceptual and attentional stress). Based on this evidence, researchers have argued that facilitation largely reflects automatic processes, as it occurs rapidly, is non-conscious, and requires little in the way of attentional and/or processing resources. Inhibition, on the other hand, is argued to reflect more controlled processing, as it develops more slowly, is under conscious control, and is sensitive to manipulation of strategy and attentional load (Aydelott & Bates, 2004; McNamara, 2005; Neely, 1991). Thus, it appears facilitation and inhibition reflect fundamentally different kinds of lexical-semantic processing: facilitatory priming effects are posited to reflect processes associated with the activation of words, whereas inhibitory priming effects are believed to reflect selection and integration mechanisms in word recognition (Aydelott & Bates, 2004).

One prominent, but disputed, interpretation of aphasic deficits stems from evidence that patients with Broca's aphasia appear to demonstrate reduced facilitation effects in semantic priming paradigms (Aydelott Utman, Blumstein, & Sullivan, 2001; Blumstein et al., 2000; Milberg et al., 1988; Milberg, Blumstein, & Dworetzky, 1987). Specifically, Broca's aphasics show weak facilitation effects in paired (word-word) priming studies (Blumstein et al., 2000), and fail to show facilitation when there is no predictable relationship between primes and targets, as in listand triplet priming paradigms (Milberg & Blumstein, 1981; Milberg et al., 1987). In addition, unlike neurologically intact individuals, Broca's aphasics fail to show priming when there is only partial overlap between an acoustic input and a semantically related prime, e.g. GAT – DOG (Milberg et al., 1988, cf. Aydelott Utman et al., 2001).

This pattern of performance is in contrast to that observed in other aphasic patient groups. Wernicke's aphasics, for example, show robust or larger than normal facilitatory semantic priming, suggesting an impairment in the inhibition of inappropriate words (Janse, 2006; Milberg et al., 1988; Milberg & Blumstein, 1981; Milberg et al., 1987). Thus, impaired semantic facilitation appears to be specific to Broca's aphasia. Further, in contrast to Wernicke's aphasics, Broca's aphasics are unimpaired in their ability to make explicit judgments of semantic relatedness when presented with related and unrelated word pairs (Blumstein et al., 1982, see also Price et al, 1999), and appear to be overly dependent on strategies in priming paradigms (Milberg et al., 1995).

In sum, these studies have been taken as evidence by Blumstein, Millberg and colleagues that Broca's aphasics show spared explicit semantic judgments and expectancy-based priming, but impaired implicit facilitation, whereas Wernicke's aphasics show the reverse pattern, suggesting that there are separate mechanisms for automatic and controlled processing of lexical-semantic information (cf. Blumstein, 1997). Hence, they have argued that the deviant patterns of semantic facilitation observed in Broca's aphasia reflect reduced activation levels within the lexicon, implicating LIPC in the automatic activation of word meaning in normal processing (Milberg, Blumstein, Giovanello, & Misiurski, 2003; Milberg et al., 1995).

However, a number of researchers have challenged this characterization of lexical processing in Broca's aphasia, and have argued that automatic semantic activation is intact in these patients. Ostrin and Tyler (1993) and Hagoort (1997) observe that semantic facilitation in priming paradigms reflects the operation of both automatic and controlled processes (cf. McNamara, 2005; cf. Neely, 1991), and that disturbances in facilitation do not rule out the possibility of a controlled processing impairment. Further, several studies have found normal patterns of facilitatory priming in Broca's aphasics, even showing semantic facilitation at brief stimulus onset asynchronies (SOAs), when priming is generally associated with the operation of automatic spreading activation mechanisms (Blumstein, Milberg, & Shrier, 1982; Hagoort, 1993; Hagoort, 1997; Katz, 1988; Milberg et al., 1995; Ostrin & Tyler, 1993). In contrast, Hagoort (1993) notes that patients generally fail to show facilitation only at longer SOAs, where priming is more closely associated with controlled processes such as expectancy and semantic matching strategies.

Consequently, Hagoort (1993) argues that the deficit associated with Broca's aphasia is attributable to impaired controlled, rather than automatic, processing mechanisms (see also Bushell, 1996). Specifically, he proposes that Broca's aphasics suffer from an impairment in the postlexical integration of lexical-semantic information. According to this view, Broca's aphasics are delayed in the integration of meaning associated with a target word and the preceding semantic context. In support of this perspective, an electrophysiological index of lexical-semantic integration, the N400, is delayed and reduced in Broca's aphasics when listening to sentences (Swaab, Brown, & Hagoort, 1997). Event-related potentials also indicate that they are slower than normal subjects to select appropriate meanings of homographs, a result the authors attribute to a delay in constructing a representation of the preceding context (Swaab, Brown, & Hagoort, 1998).

Further, support for a control-based interpretation of LIPC function is not limited to semantic priming studies. The poor performance of frontal-lobe patients on tasks that require inhibiting a currently active representation in order to make an appropriate verbal response also suggests a deficit in controlled semantic processing with anterior lesions. For instance, patients with frontal lobe lesions are particularly impaired in verbal fluency tasks (which require the suppression of previously generated responses; Perret, 1974), on Stroop tasks (which require the suppression of the automatic reading of a printed word; Perret, 1974), and on the Hayling test (which requires the suppression of a highly predictable sentence completion in order to generate an unlikely one; Burgess & Shallice, 1996). Additionally, frontal-lobe patients are less adept than healthy adults or posterior-lesion patients in their use of strategies to accomplish such tasks, also suggesting a controlled processing deficit. In a similar vein, patients with left prefrontal lesions including the LIPC perform worse than patients with prefrontal lesions that selectively spare the LIPC when asked to generate semantically related verbs for common nouns (Thompson-Schill et al., 1998). This differential impairment is restricted, however, to trials that have many possible, appropriate responses, suggesting the importance of the LIPC in selecting among competing (semantic) representations.

Taken together, these non-priming studies also suggest a deficit in controlled semantic processing with damage to LIPC, although not of an integrative nature. Rather, these findings suggest that the nature of the controlled processing deficit may be in the ability to flexibly select a response/representation in the presence of competition. This interpretation is consistent with the finding that Broca's aphasics are delayed in their selection of the appropriate meaning of ambiguous words (Swaab et al., 1997), and more sensitive to the presence of lexical competitors (Aydelott Utman et al., 2001; Misiurski, Blumstein, Rissman, & Berman, 2005).

In summary, the patient literature suggests three possibilities for the role of LIPC in lexical processing: 1) that LIPC is critically important for the *automatic activation* of semantic information, 2) that this region is responsible for the *integration* of semantic information with the preceding semantic context, or 3) that this area subserves the *selection* of appropriate information from semantic memory in conditions of conflict. Importantly, the first suggestion implicates this frontal region in automatic processes during word recognition, whereas the latter two attribute its primary function to attentionally-mediated, controlled aspects of word recognition.

The purpose of the present experiment was to test between these processing-deficit accounts of Broca's aphasia using the sentence-priming task. In this task, primes consist of sentence fragments instead of single words, but the effects and associated mechanisms appear to be very similar to those found when word primes are used (McNamara, 2005; Neely, 1991). As in paired-priming studies, priming effects are determined relative to a semantically neutral condition (e.g. the context, "The next item is -"), with responses facilitated when they are semantically congruent completions of the sentence (i.e. plausible and predictable), and inhibited when they are semantically incongruent (Stanovich & West, 1983). Additionally, the degree of facilitation produced by a sentence context is graded by how strongly it leads participants to expect a particular completion. Primes with strong contextual constraint, which bias a single likely completion, elicit the fastest reaction times. Primes with weaker constraint, which allow for a number of semantically plausible completions, produce smaller facilitatory effects. Inhibitory priming, however, is not sensitive to these manipulations of constraint (Cardillo, 2005). There are two major advantages of using sentences rather than single words as primes. First, they produce larger priming effects than single words, thereby maximizing the possibility of detecting differences between patients and healthy adults. Second, impaired processing of more naturalistic stimuli may better correspond with the speech difficulties indicated by diagnostic tests than processing at the level of single words does.

To review, in semantic priming paradigms facilitation is associated with the activation of word meaning representations, and is considered to largely reflect the operation of automatic, fast acting processes, which occur without an individual's intention or awareness. In contrast, slower, strategically controlled mechanisms that do require a person's intention or conscious awareness, can both facilitate and inhibit target recognition (McNamara, 2005; Neely, 1991). Thus, the reduced activation account of Broca's aphasia predicts that these patients will show reduced facilitatory priming following congruent contexts since this priming effect relies, in part, on automatic activation processes. In contrast, the controlled nature of the deficit proposed by integration and selection accounts predicts deviant inhibitory priming following incongruent contexts. On the one hand, if Broca's aphasics are especially impaired in the lexical-semantic integration of target words with sentence contexts, then they should be less sensitive to the semantic mismatch of an incongruent target. Thus, the integration account of Broca's aphasia predicts smaller than normal inhibitory priming (and, possibly, reduced facilitatory priming if patients are less adept at integrating even highly predictable, plausible completions). On the other hand, if Broca's aphasics are especially impaired in lexical/response selection in conditions of competition, then they should find it difficult to switch attention from the word(s) primed by an incongruent context to the target actually presented. Consequently, a selection account of Broca's aphasia predicts normal facilitatory priming effects but *larger* than normal inhibitory priming. Lastly, ERP data suggest that Broca's aphasics are less sensitive to the contextual constraint of sentences than healthy adults (Swaab et al., 1998), a finding that has not been explored in behavioral tasks but will be considered in this study.

A multiple case-study approach was used to test these predictions Some of the disagreement between the studies reviewed above likely reflects differences in how experimenters define Broca's patients. Most researchers have grouped patients by aphasic symptoms rather than lesion site, making accurate inferences about LIPC function difficult, at best. A diagnosis of Broca's aphasia does not reliably predict a lesion in Broca's area, nor does an anterior/Broca's area lesion necessarily result in Broca's aphasia (Dronkers, Shapiro, Redfern, & Knight, 1992). Estimates of the reliability of lesion-deficit mapping are surprisingly low: in a review of more than 100 patients, only 85% of patients with Broca's aphasia had lesions affecting Broca's area. Further, only 50-60% of patients with damage to Broca's area exhibited language abilities consistent with a diagnosis of Broca's aphasia. Lesions extending beyond the typical neuroanatomical borders of Broca's area were more likely to result in their classical behavioral expression (Dronkers, Redfern, & Knight, 2000). This high degree of individual variation recommends the case study approach, as group averaging on the basis of diagnostic criteria may lead to inappropriate inferences about the neural bases of deficits (Caplan, 1995).

Thus, in order to clarify the relation of the behavioral deficit in Broca's aphasia to damage to Broca's area, three types of "Broca's" aphasics[2] were considered: 1) a patient with both a diagnosis of Broca's aphasia and damage to LIPC, 2) a patient with a diagnosis of Broca's aphasia without damage to LIPC, and 3) a patient without a diagnosis of Broca's aphasia, but with damage to LIPC. Further, in order to distinguish behavioral deficits associated with Broca's aphasia/damage from the more general deficits associated with brain lesions, the priming behavior of these patients was compared with that of a left hemisphere damaged patient without Broca's aphasia or a lesion affecting LIPC.

To summarize, the activation deficit hypothesis predicts reductions in facilitatory priming, the selection deficit hypothesis predicts larger than normal inhibitory priming, and the integration deficit hypothesis predicts smaller than normal inhibitory (and perhaps facilitatory) priming. The activation and integration deficit hypotheses are largely based on data from behaviorally-defined patients, whereas, evidence from patients with prefrontal lesions has generally supported the selection deficit account. Thus, while all three Broca's patients may perform similarly to each other, the discrepancies in the literature suggest that the performances of the behaviorally-defined and lesion-defined Broca's patients may accord with different hypotheses.

Methods

Participants

Thirty-five right-handed, native British-English speaking older adults served as the control population. Older controls had an average age of 64.6 (SD = 11.6), with each participant's age within 2 SDs of the mean age of the patient group (mean = 58.5, SD = 12.3). Although the comparison of an individual patient's priming behavior with that of a large age-matched control group is common in the priming case study literature (e.g. Kensinger, Siri, Cappa, & Corking, 2003; e.g. Ostrin & Tyler, 1993; Prather et al., 1992; Prather et al., 1997, but see Marslen-Wilson & Tyler, 1997), this practice risks attributing differences to aphasic deficits when they may simply reflect the weaker power in the analysis of a single subject's data. To check for this possibility, reaction time (RT) and accuracy analyses of variance (ANOVAs) were also calculated for a subset of the main control group. For each patient, an age-matched individual tested on the same experimental list was selected, and data from these four participants was pooled to form a smaller control group.

The results of the large and small control groups were compared with the individual data from four aphasic patients. The aphasia diagnosis for each patient was determined using the Western Aphasia Battery (WAB, Kertesz & Hooper, 1982) and lesion descriptions were based on MRI structural scans. Patients' aphasic syndromes were classified as Broca's (2), Conduction (1), or Anomic (1). All patients had become aphasic as a result of a single cerebral vascular incident in the left hemisphere and were tested a minimum of six months post-onset. A summary of patient characteristics and clinical information is presented in Table 1.

Stimuli

The stimuli consisted of 60 target words, 60 nonwords, a neutral sentence context, and 240 semantically biased sentence contexts (120 to be

[2] Throughout the rest of the article "Broca's" will be used to refer to patients with either lesions to Broca's area and/or a clinical classification of Broca's aphasia.

paired with targets and 120 to be paired with nonwords).

Stimuli were controlled along a number of dimensions known to affect lexical processing. Targets consisted of one-syllable words containing 3-5 phonemes (mean = 3.27, SD = 0.64) and 0.8 seconds in duration (mean = 0.78, SD = .12), with a mean Kucera-Francis print frequency of 139 (SD = 99) (Kucera and Francis, 1967), a mean London-Lund spoken frequency of 14 (SD = 81) (Brown, 1984), and a mean concreteness rating of 546 (SD = 81) as specified in the MRC Psycholinguistic Database (Coltheart, 1981). To avoid possible morphological and morpho-phonological constraints of determiners (a/an, the), mass nouns (e.g., blood, dust) were excluded, and all targets were consonant-initial. The nonword distracter targets consisted of phonologically permissible one-syllable nonsense items that did not differ significantly from the targets in terms of number of phonemes (mean = 3.33, SD = 0.61) or duration (mean = .78, SD = 12).

The sentence contexts matched with the word targets were approximately ten syllables in length (mean = 9.47, SD = 2.66) and 2 seconds in duration (mean = 2.11, SD = .50), containing a maximum of six content words (mean = 3.37, SD = 1.07), and a maximum of three words semantically related to the congruent target (mean = 1.13, SD = 0.51). Further, contexts varied in their contextual constraint and the cloze probability of their target completions. Half of the sentence contexts were strong constraint, with a mean cloze probability of .94 (SD = 07), while the other half were weak constraint, with a mean cloze probability of .28 (SD = .19). Cloze probability refers to the proportion of people who complete a given context with a particular word (Taylor, 1953), and is often used to operationalize contextual constraint, or the extent to which the semantics and syntax of a context suggests a specific final word. In the strongest instance, the contextual constraint of a sentence biases a single appropriate completion, whose cloze probability is 1.00 (e.g. “One day the prince will become the - KING”). In contrast, weak contextual constraint allows for a variety of plausible endings (e.g. “One of the important pieces in chess is the - KING”). The cloze probability of congruent targets was determined by pilot testing with 22 British English speaking volunteers. In all cases, the congruent target word was the most frequently given completion (i.e. the highest cloze response) for its matching context. There was no significant difference in length, duration, or number of content words between strong and weak constraint contexts, or between contexts paired with word targets and contexts paired with nonwords. Strong and weak contexts did differ significantly ($t = 2.131$, df = 118, $p < .001$), however, in the number of content words semantically or associatively related to their targets (strong contexts: mean = 1.17, SD = .71; weak contexts: mean = .96, SD = .86).

Manipulation of contextual constraint and semantic congruity of primes with their target completions resulted in five trial types: congruent-strong, congruent-weak, neutral, incongruent-weak, or incongruent-strong. In the congruent-strong condition, word targets were matched with highly constraining semantically appropriate sentence contexts that biased the listener to anticipate a single possible completion. In the congruent-weak condition, targets were matched with a less semantically constraining context that could plausibly be completed by one of several words. In the incongruent-strong and incongruent-weak conditions, word targets were matched with a strongly or weakly biasing sentence context appropriate to another target in the stimulus set. Therefore, in either incongruent context a target’s cloze probability was zero, making it both unpredictable and semantically anomalous. A sentence context providing no semantic cues with regard to the target (“The next item is -”) served as the neutral baseline condition. Thus, targets also had a zero cloze probability in this context, however, unlike incongruent targets, they did not render the sentence nonsensical. In order to ensure target presentation in each context condition but avoid inadvertent repetition priming, five experimental lists were generated. Each list contained 120 trials, 60 corresponding to word targets and 60 corresponding to nonwords. Thus, in each list, 12 word targets appeared in each context condition. Each patient received one of these five lists.

Stimuli were produced by native speakers of British English who were naïve to the purpose of the experiment. To distinguish each target clearly from the preceding context, words and nonwords were produced by a male speaker, and sentence contexts were produced by a female speaker. The stimuli were recorded onto digital audio tape in an Industrial Acoustics 403-A audiometric chamber with a Tascam DA-P1 Digital Audio Tape recorder and a Sennheiser ME65/K6 supercardioid microphone and pre-amp at gain levels between -6 and -12 dB. The recorded stimuli were then digitised via digital-to-digital sampling onto a Macintosh G4 computer via a Digidesign audio card using ProTools LE software at a sampling rate of 44.1 kHz with 16-bit quantization. The waveform of each sentence, target, and nonword was then spliced from the master file at the points visually indicating its onset and offset, and saved in its own System 7 mono audio file.

Procedure

Patients were tested individually on two occasions at least two weeks apart. On the first session, lasting approximately 45 minutes, the spoken language skills of the patient were assessed using the WAB. On the second session, lasting approximately 20 minutes, patients were tested on the sentence-priming task. Participants were seated in front of a 2-key response box that was placed between two satellite speakers (Harman Kardon SoundSticks). Trials were presented auditorily on a Macintosh G4 computer using SuperLab 1.5 software and with reaction times (RTs) and accuracy recorded from a Cedrus RB-610 response box. Participants were instructed to make a lexical decision ("Is it a real word?") to the final word of the sentence, and to respond as quickly and accurately as possible using the index finger of their preferred hand (in some cases the nondominant hand). To minimise inadvertent bias, subjects were told to rest their finger between the colored response keys (green for YES, red for NO) while listening to each sentence.

In order to familiarize patients with the task and to adjust volume to a comfortable level, unlimited practice was offered with five prime-target pairs that did not appear in the subsequent test. No patient requested more than two sets of practice trials. In order to allow for self-pacing and minimal fatigue, trials were followed by a pause that required a key press (by the experimenter) to begin the next trial. Additionally, all patients were encouraged to take breaks if they felt fatigued at any point during the task. The task was identical for the older control group with three exceptions: stimuli were presented over Sennheiser HD 25-1 headphones via a Sirocco VideoLogics amplifier, the pause between trials was replaced with a 1500ms inter-trial interval, and practice was not offered.

Results

Details of the analysis of lexical decision data for the whole group of older controls are reported elsewhere (Cardillo, 2005; Cardillo & Aydelott, in preparation) so these results will be only broadly referred to here. RT and percent accuracy data for the four patients and the smaller set of their age-matched controls were analysed separately. RTs more than 2 SD from the mean for each participant in each condition were excluded from analysis, as were RTs from incorrect trials. In order to minimize the effects of individual variability, statistical analyses were conducted on log normalized RTs averaged across conditions. These accuracy and adjusted RT values served as random effects in one-way ANOVAs conducted for each patient and for the smaller control group. Post-hoc Newman-Keul's means comparisons were conducted to test for the presence of facilitatory and inhibitory priming (each biasing context vs. neutral), and their sensitivity to contextual constraint (congruent-strong vs. congruent-weak and incongruent-strong vs. incongruent-weak).

Controls

The large control group of older adults showed similar priming behavior to young adults (Cardillo, 2005; Cardillo & Aydelott, in preparation). Responses were significantly faster following congruent contexts and significantly slower and less accurate following incongruent contexts (relative to the neutral baseline condition). Moreover, RTs following congruent contexts were graded by contextual constraint such that congruent-strong contexts elicited faster responses than congruent-weak contexts. As with young adults, inhibitory priming effects were not graded by constraint.

In the smaller-sized control group, a total of 13 responses exceeded 2 SD from the mean for any subject in a particular condition and were omitted. As in the analysis with all older controls, results of the RT ANOVA for this group revealed a significant main effect of Context ($F(4,224) = 14.22$, $p < 0005$). However, planned comparisons indicated that the priming effects were weaker in this analysis. Significant facilitation following congruent contexts was observed, but inhibition following incongruent contexts did not reach significance. Further, facilitation showed no sensitivity to contextual constraint in this smaller control group. Likewise, the main effect of Context did not reach significance in the analysis of percent accuracy values, nor did the planned comparisons indicate any significant differences in accuracy across conditions. Thus, results from the analyses with a small-sized control group suggest that comparing individual data with a large control group may be misleading. For thisreason, discussion will be limited to the comparison of patient data with this smaller control group. The RT and accuracy values for the small control group are reported in Table 2.

Table 1. Summary of patient characteristics

Patient	Age at testing	Months post-onset	AQ[1]	Fluency	Comprehension	Repetition	Naming	Aphasia type	Fluency	Damage to Broca's Area	Damage to Wernicke's Area	MRI Structural Scan
AM	68	6	78.8	7	9.6	6.9	6.9	Conduction	Fluent	No	Yes – minor	Atrophy of left posterior perisylvan areas, including temporo-parietal junction and supratemporal plane
MB	57	26	59.6	4	7.7	3.7	5.4	Broca's	Nonfluent	No	Yes – major	Left temporal lesion affecting entire temporal lobe and temporo-parietal junction; inferior parietal damage extending into precentral gyrus
MF	63	19	N/A	2	7.1	3.6	N/A	Broca's	Nonfluent	Yes – partial	Yes – minor	Left fronto-parietal lesion extending from anterior temporo-parietal junction to posterior frontal regions, including ventral premotor and pars opercularis and encroaching on supratemporal plane
PS	37	21	83.0	6	8.4	9.1	9.0	Anomia	Fluent	Yes – major	Yes – minor	Left fronto-paretial lesion affecting prefrontal cortex and encroaching on anterior temporal poles; damage extends posteriorly along sylvian fissure to anterior temporo-parietal junction

[1]All scores taken from the Western Aphasia Battery. AQ = Aphasia Quotient, a summary score based on spoken language subtests, reflecting overall severity of impairment (maximum possible score = 100, aphasia cut-off score = 93.8)

Table 2. Control reaction time ($\log^{10}$) and accuracy (percent correct) across context conditions

		CONS		CONW		NEU	INCW		INCS	
RT	Mean	3.0396	*	3.0514	*	3.1003	3.1380	~	3.1347	~
	SE	0.0122		0.0091		0.0132	0.0133		0.0127	
	95% Confidence Interval	3.0151 – 3.0641		3.0370 – 3.0697		3.0736 – 3.1270	3.1112 – 3.1647		3.1092 – 3.1603	
Accuracy	Mean	100	~	100	~	100	98.33	~	96.67	~
	SE	0.00		0.00		0.00	1.67		2.34	
	95% Confidence Interval	100 – 100		100 – 100		100 – 100	95.00 – 100		91.99 – 100	

*= significantly different from mean in Neutral condition; ~= not significantly different from mean in Neutral condition

Case Study AM: Conduction Aphasia with Sparing of Broca's Area

AM, a 68 year-old retired chartered surveyor, sustained a small posterior infarct earlier the same year. The MRI structural scan revealed minimal damage. Broca's area was entirely spared but the posterior perisylvian areas showed atrophy. Wernicke's area appeared affected along with other slightly more anterior supratemporal plane structures.

Evaluation of AM's spoken language comprehension and production using the WAB indicated a diagnosis of conduction aphasia. It is worth noting that conduction aphasia is usually defined as an isolated deficit in the sequencing of speech sounds, an impairment that severely impacts repetition abilities. Thus, the behavioral pattern associated with this form of aphasia is like fluent anomia with jargon. AM's comprehension was perfect on all measures with the exception of a single confusion on the sequential commands section of the WAB. On the other hand, although his production was fairly normal, it was marked by word-finding difficulty and frequent phonological and semantic paraphasia's. AM did not unknowingly produce jargon so much as have difficulty producing the word he had in mind. He was nearly always aware of his paraphasic errors, making successive approximations until he produced the correct word. Oftentimes, writing down what he was attempting to express facilitated this trial and error process. For example, when asked about his condition, he replied: "I was here because I got a crook, koot. Oh gosh, lost it. A skoot. Oh jeepers. Scr- skate, skoot. I can write it [STOKE]. That's it, a *skote*." AM found repeating sentences very difficult, although his repetition of single words and numbers was generally accurate.

AM's results are presented in Table 3. Three responses exceeded 2 SDs from the mean and were omitted. An analysis of variance over correct RTs revealed a significant main effect of Context ($F(4,54) = 16.76$, $p < .0005$), indicating AM was sensitive to the semantic bias of sentence contexts. Planned means comparisons indicated significant facilitation following congruent contexts and significant inhibition following incongruent contexts, but no sensitivity to contextual constraint. The main effect of Context was not significant in the corresponding ANOVA of percent accuracy values, and means comparisons revealed no significant differences. Thus, relative to the control group, AM showed more RT inhibition.

Table 3. AM reaction time ($\log^{10}$) and accuracy (percent correct) across context conditions

		CONS		CONW		NEU	INCW		INCS	
RT	Mean	3.1423	*	3.1486	*	3.2532	3.3506	*	3.3476	*
	SE	0.0223		0.0117		0.1605	0.0281		0.0393	
Accuracy	Mean	91.67	~	100	~	91.67	100	~	91.67	~
	SE	8.33		0.00		8.33	0.00		8.33	

*= significantly different from mean in Neutral condition; ~= not significantly different from mean in Neutral condition

Case Study MB: Broca's Aphasia with Sparing of Broca's Area

MB, a 57 year-old entomologist, sustained a left cerebral vascular accident at age 55. The MRI structural scan revealed loss of the entire length of the left temporal lobe, including the middle and superior temporal gyri. Damage extended to inferior parietal areas, encompassing Wernicke's area, and the precentral gyrus. The frontal lobes were largely unaffected and Broca's area showed no obvious damage. This was the largest lesion among the five patients.

Evaluation of MB's spoken language comprehension and production using the WAB indicated a diagnosis of Broca's aphasia. His comprehension was relatively spared, although he appeared impaired in his comprehension of body part names. On the more difficult items of sequential commands section of the WAB he sometimes confused gestures (e.g. touching instead of pointing at an object), or indicated the wrong object. He showed similar semantic confusions when producing words. For instance, in the sentence completion task he responded with "green," after hearing "Roses are red, violets are…" His speech was nonfluent, consisting mostly of single words or short phrases. For example, when asked to describe his occupation, he replied: "Oh, it's entomology. Behavior with, and, um… teaching… and with, um, insects in the field… Crops. Farms… and that sort of thing." MB also had difficulty repeating back anything longer than a single word. He appeared to become fatigued on the naming task, producing fewer correct names on the second half than on the first. He similarly struggled on the word fluency task, producing only six animal names before the one minute deadline. Thus, MB showed many of the characteristics associated with agrammatism.

MB's results are presented in Table 4. Two responses exceeded 2 SDs from the mean and were omitted. The main effect of Context was not significant in the analysis of variance over correct RTs and planned means comparisons indicated no significant differences between conditions. However, a significant main effect of Context ($F(4,59) = 26.99$, $p < 0005$) emerged in the analysis of percent accuracy values, reflecting MB's large inhibition in incongruent contexts. Means comparisons confirmed that responses in incongruent-strong and incongruent-weak conditions were significantly less accurate than following neutral contexts. Further, this priming effect was significantly graded by constraint, reflecting the fact that MB made only one correct lexical decision following incongruent-strong contexts, but four following incongruent-weak contexts. Thus, MB's behavior deviated dramatically from normal: he showed no evidence of RT priming, but did demonstrate strong accuracy inhibition that was graded by constraint.

Table 4. MB reaction time (log^{10}) and accuracy (percent correct) across context conditions

		CONS		CONW		NEU	INCW		INCS	
RT (log)	Mean	3.2102	*	3.3054	*	3.3093	3.4327	*	3.3128	*
	SE	0.0346		0.0553		0.0223	0.1611		-	
Accuracy	Mean	91.67	*	100	*	100	33.33	~	8.33	~
	SE	7.33		0.00		0.00	14.21		8.33	

~= significantly different from mean in Neutral condition; *= not significantly different from mean in Neutral condition

Case Study MF: Broca's Aphasia with Minor Damage to Broca's Area

MF, a 63 year-old homemaker, sustained a left parietal infarct at age 61. Due to an error during scanning, the MRI structural scan for MF was of a lower resolution than for the other patients, but a large fronto-parietal lesion was clearly visible. Damage encroached on the supratemporal plane and appeared to include some of the temporal-parietal junction. Likewise, the lesion extended to anterior regions, affecting ventral premotor cortex and encroaching on posterior Broca's area (i.e. pars opercularis).

Evaluation of MF's spoken language comprehension and production using the WAB indicated a diagnosis of Broca's aphasia. Her comprehension was relatively spared, but her speech output was extremely limited and she quickly abandoned attempts to articulate her responses. For instance, although she had no difficulty with yes/no questions, she could only produce her first name, but not her last. In fact, she became so discouraged following her difficulty with object naming that the final section of the WAB was omitted (word fluency, sentence completion, and responsive speech). Her description of a picture showing a picnic scene by a lake was her most expressive during the testing session, and required pointing prompts: "A horse, horse, I don't know, I don't… I don't know, here…oh, I don't know. I don't, don't know… Yes. Eating. Reading. Reading. Book. Bottle. Yes. Horse. Yeah. Spade."

MF's results are presented in Table 5. Five responses exceeded 2 SDs from the mean and were omitted. An analysis of variance over correct RTs revealed a significant main effect of Context ($F(4,46) = 6.93$, $p < .0005$), indicating she was sensitive to the semantic bias of contexts. Further, planned means comparisons revealed significant facilitation in congruent contexts. Inhibition following incongruent contexts was not significant. The corresponding analysis of variance over percent accuracy values also revealed a main effect of Context ($F(4,59) = 4.125$, $p < 005$). In this case, means comparisons revealed significant inhibition following both incongruent contexts. Thus, like the control group, MF experienced facilitatory RT priming; but, unlike the control group, she also experienced accuracy inhibition.

Table 5. MF reaction time ($\log^{10}$) and accuracy (percent correct) across context conditions

		CONS		CONW		NEU	INCW		INCS	
RT (log)	Mean	3.2955	~	3.3196	~	3.4738	3.5120	*	3.4429	*
	SE	0.0289		0.0417		0.0372	0.0224		0.0425	
Accuracy	Mean	100	*	100	*	100	66.67	~	66.67	~
	SE	0.00		0.00		0.00	14.21		14.21	

~= significantly different from mean in Neutral condition; *= not significantly different from mean in Neutral condition

Table 6. PS reaction time ($\log^{10}$) and accuracy (percent correct) across context conditions

		CONS		CONW		NEU	INCW		INCS	
RT (log)	Mean	3.1048	*	3.1052	*	3.1403	3.2039	~	3.1977	~
	SE	0.0135		0.0136		0.0195	0.0166		0.0134	
Accuracy	Mean	100	*	100	*	100	100	*	83.33	*
	SE	0.00		0.00		0.00	0.00		11.24	

~= significantly different from mean in Neutral condition; *= not significantly different from mean in Neutral condition

Case Study PS: Anomia with Major Damage Broca's Area

PS, a 37 year-old salesman, sustained a left cerebral vascular accident at age 35. The MRI structural scan revealed a large fronto-parietal lesion, affecting most or all of Broca's area. Damage impinged on the anterior temporal pole and extended posteriorly along the sylvian fissure, including anterior portions of the temporo-parietal junction.

Evaluation of PS's spoken language comprehension and production using the WAB indicated a diagnosis of anomia. His comprehension was relatively spared, although he showed difficulty with the some items in the sequential commands subtest. His output was slow and effortful, consisting of simple declarative sentences or short phrases. He occasionally omitted grammatical inflections but, for the most part, his speech was syntactically correct. For instance, when asked about his stroke he responded, "Fully conscious. I struggle to get words out. Two and a half years ago." Repetition was accurate on single words, numbers, and short phrases, but more impaired on the longer test items.

PS's results are presented in Table 6. Three responses exceeded 2 SDs from the mean and were omitted. An analysis of variance over correct RTs revealed a significant main effect of Context ($F(4,54) = 9.16$, $p < .0005$), indicating that PS was sensitive to the semantic bias of contexts. Planned means comparisons revealed significant inhibition following incongruent contexts, but facilitation following congruent contexts did not reach significance. The main effect of Context was not significant in the corresponding analysis of percent accuracy values, nor did means comparisons reveal any significant differences between conditions. Thus, like the control group, PS showed no accuracy priming, but unlike the controls, he showed RT inhibition, not facilitation.

RT and accuracy data for patients and controls are plotted together in Figure 1 to facilitate comparison. All patients responded considerably more slowly than the healthy controls in all conditions, a visual trend supported by the failure of any patient's mean RT in any condition to fall within the 95% confidence intervals defined by the control group. This figure also illustrates well the abnormal patterns of inhibitory priming in these patients relative to the control population. For MB, a Broca's aphasic with sparing of Broca's area, and MF, a Broca's aphasic with damage to Broca's area, incongruent contexts elicited many incorrect lexical decisions. In contrast, AM, a conduction aphasic and "control" patient, and PS, an anomic patient with damage to Broca's area, showed large inhibition effects in their response latencies but high levels of accuracy.

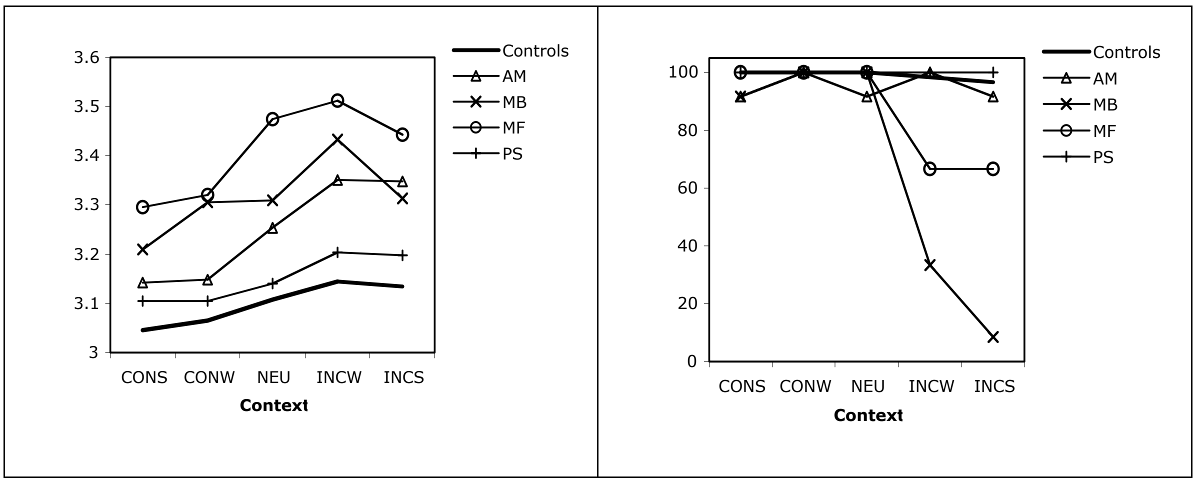

Figure 1. Mean reaction time ($\log^{10}$) and accuracy (percent correct) for each patient relative to the small control group.

Discussion

The present study aimed to test the predictions generated by the activation, selection, and integration accounts of processing deficits in Broca's patients. According to the reduced activation account, these aphasics should demonstrate smaller than normal facilitatory priming effects. In contrast, the controlled processing deficits suggested by the selection and integration accounts predict deviant inhibitory priming effects. A selection deficit would impair patients' ability to shift attention from the task-irrelevant word primed by the incongruent context to the word actually presented, resulting in larger inhibition. An integration deficit, however, would reduce patients' sensitivity to the semantic mismatch of contexts and targets, thereby reducing inhibitory priming effects.

On the basis of behavioral classification, it seems reasonable to expect the priming of MB and MF to pattern together, as both were diagnosed as Broca's aphasics of fairly similar severity. On the other hand, if the location of tissue loss is a more important determinant of processing deficits, then we might expect the priming pattern of MF and PS to look similar, as both of these patients had damage to LIPC. Further, we might expect that a pattern common to PS and MF would be stronger in PS since his lesion spared very little, if any, of Broca's area, whereas, MF sustained only minor damage. Lastly, given that AM showed neither damage to or near LIPC, nor the hallmark symptoms of Broca's aphasia, we might expect his priming behavior to look unlike either hypothesized pairing of "Broca's" aphasics, or even all three "Broca's" patients.

However, the patterns of priming observed in this study provide only mixed support for these predictions. Turning to the two behaviorally-defined Broca's aphasics (MB and MF), both showed abnormal and severe accuracy inhibition, suggesting an inability to recover from a bias to respond "No" when a semantically anomalous target is heard (cf. Neely, 1991). That this accuracy inhibition was not accompanied by RT inhibition suggests that these patients may have compromised accuracy in trying to respond quickly, thereby preventing adequate time to recover from their violated expectations. This larger than normal inhibitory priming suggests an impaired ability of Broca's aphasics to overcome a response bias, an interpretation consistent with the selection deficit hypothesis. Further, although not significant, both patients showed a trend for slower responses in incongruent-strong contexts than incongruent-weak contexts, and MB, the patient with Broca's aphasia but not Broca's damage, showed a significant difference in accuracy between these two conditions. Sensitivity to contextual constraint in incongruent contexts has not been observed in several previous sentence-priming studies (Cardillo, 2005; Cardillo & Aydelott, in preparation; Fischler & Bloom, 1985; Masson, 1986), raising the possibility that patients with Broca's aphasia process these sentences differently from healthy adults. However, MB and MF do not respond to congruent contexts similarly to one another, a de-coupling that argues against attributing their behavior to similar processing deficits. In particular, MB (the Broca's aphasic with sparing of Broca's area) shows no facilitation priming, consistent with hypothesized deficits in automatic activation. However, MF (the Broca's aphasic with damage to Broca's area) shows relatively spared facilitation priming.

Results from MF and PS, the two patients with damage to Broca's area, are similarly inconsistent. Both patients show larger than normal inhibitory priming, although for the patient who also has symptoms of Broca's aphasia (MF), this manifests itself in accuracy. For the anomic patient (PS), this effect is seen in response latencies. Nonetheless, these effects are consistent with the selection account's prediction of larger inhibitory priming effects. It may be that in less severely aphasic patients, such as PS, a selection deficit delays the ability to overcome a response bias, generating RT inhibition, but still allows for accurate performance. In contrast, for more severely aphasic patients, damage to LIPC makes it extremely difficult to override a prepotent response, resulting in accuracy inhibition. However, once again, the presence of facilitatory priming in MF (the patient with a diagnosis of Broca's aphasia as well as Broca's area damage), but not PS, suggests damage to LIPC is insufficient explanation for their lexical semantic impairments.

Foremost, the failure of all three Broca's patients to behave similarly highlights the importance of distinguishing between the clinical syndrome of Broca's aphasia and damage to Broca's area. Further, these cases also suggest a more complicated pattern of deficits than predicted by traditional classifications based on diagnostic category or lesion site. In this way, the results prevent making strong claims about the underlying deficit in Broca's aphasia, or the role of LIPC in normal lexical-semantic functions. However, the data suggest two other interesting and surprising patterns.

First, although not all patients showed a similar profile of priming following congruent contexts, all four patients showed larger than normal inhibitory priming following incongruent contexts. That is, even AM, the conduction aphasic and "control" patient, showed large reaction time inhibition relative to the control group. At the least, this common finding of enhanced inhibitory priming suggests all patients, regardless of lesion site or symptom classification, are impaired in controlled processing. This pattern is inconsistent with hypothesized deficits in semantic integration, which predict smaller than normal inhibitory priming. Rather, larger inhibition is consistent with a deficit in shifting attention away from an interfering, prepotent representation in order to select a task-relevant one. The suggestion of such a selection deficit in patients with diverse classifications and lesions may indicate that many forms of lesion affect this control capacity, or perhaps weaken controlled processing in general Alternatively, it may be that the selection deficit of these patients is of different origin depending on the site of their lesion. Effective selection on incongruent trials likely relies upon several processes (e.g. becoming aware of representational conflict, suppressing the primed word, shifting activation resources to the presented target, delaying response selection until the competition is resolved). LIPC may be especially important for coordinating these operations (cf. Novick, Trueswell, & Thompson-Schill, 2005), but the intactness of other brain regions may also be critical for the effective function of one or more of these contributing processes[3].

[3] Indeed, Blumstein & Milberg (2000) posit that patients with Wernicke's aphasia hyperactivate lexical items, implicating Wernicke's area in this deficit. As all our patients experienced at least some damage to the temporal-parietal junction, the necessity of this region for normal inhibitory priming behavior will be of particular interest in future research.

Second, notwithstanding differences in facilitatory priming, the overall patterns of behavior illustrated in Figure 1 suggest that PS, an anomic patient with damage to Broca's area, and AM, a conduction aphasic with sparing of Broca's area, performed more similarly to each other than to the other two patients, and vice versa. This unexpected grouping of behavior is not predicted in terms of diagnostic category or lesion site, but does reflect similarities in the higher and lower comprehension levels of PS/AM and MB/MF, respectively, as well as differences in severity and fluency. These trends highlight concerns about the utility of classic diagnostic criteria for predicting performance and inferring neural function. The shortcomings associated with conceiving of aphasia syndromes in terms of dichotomous categories have been raised elsewhere in the literature (e.g. Bates & Goodman, 1997; Dick et al., 2001), and are reflected by the high number of "mixed" aphasics and relatively low number of "pure" cases of Broca's (or other types of) aphasia. Discrete classifications are practical, and provide a vital conceptual framework for empirical research, but they may prove inadequate tools for mapping the relationship between brain and language in any specificity. In response to this methodological gridlock, Bates and colleagues have argued for the replacement of classic taxonomies based on arbitrary cut-offs with multivariate analyses that preserve the continuous range of information provided by behavioral assessments (Bates et al., 2005). The adoption of this approach may shed light on unanticipated clusterings of performance, as were found with the cases presented here.

In addition to suggesting two patterns warranting further investigation, this study also raises concerns about the determination of a suitable reference group for inferring language deficits in single cases. After statistical manipulations to reduce the effects of outliers and variability, data from individual patients are routinely compared to patterns of behavior produced by a group of age-matched controls (e.g. Kensinger et al., 2003; e.g. Ostrin & Tyler, 1993; Prather et al., 1992; Prather et al., 1997). As the present comparison of priming in a group of 35 age-matched controls versus 5 age-matched controls indicates, this may be a questionable practice. Differences in power between a random-effects analysis with individual data and a repeated-measures group analysis are likely to exaggerate differences between patients and controls if effect sizes are small. Using a smaller sized control group may not entirely ameliorate this problem, either. In the present experiment, when data from each age-matched control were analysed separately, only one of the age-matched controls showed the same pattern of priming as the group of five. Thus, individual variability does not just complicate comparisons between patients, but also references made to healthy, normal performance. In this case, the difficulty in establishing an appropriate healthy control population supports claims made by others in favour of group analyses (Bates, Appelbaum, & Allard, 1991).

No other brain area captures the interest of language researchers like Paul Broca's vexing namesake, but reconsideration of certain methodological practices may be necessary in order to clarify its role. As the current study illustrates, challenges inherent to the study of patients – such as unreliable lesion-symptom mapping, individual variability, assumptions about normal function from impaired behavior, and the lack of discretely localized lesions – necessarily limit the conclusions offered by a strictly behavioral approach. A coupling of functional neuroimaging with a new lesion-deficit, group analysis technique, Voxel-Based Lesion Symptom Mapping (VLSM; Bates et al, 2003), may provide the most effective means of refining brain-language relationships and is an option we are now pursuing with this task. VLSM preserves the continuous nature of behavior by comparing task performance on a voxel by voxel basis, much as in neuroimaging research, rather than by diagnostic category or lesion classification. Several imaging studies have already implicated LIPC in semantic context effects (Van Petten & Luka, 2006), including an fMRI experiment using a subset of the present stimuli (Cardillo, Aydelott, Matthews, & Devlin, 2004). However, since neuroimaging cannot determine the necessity of any brain region for normal performance, VLSM promises a critical test for interpretations of this area's function.

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