Supplement Article

Voxel-Based Lesion Symptom Mapping of Coarse Coding and Suppression Deficits in Patients With Right Hemisphere Damage

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Purpose: This study examined right hemisphere (RH) neuroanatomical correlates of lexical–semantic deficits that predict narrative comprehension in adults with RH brain damage. Coarse semantic coding and suppression deficits were related to lesions by voxel-based lesion symptom mapping.

Method: Participants were 20 adults with RH cerebrovascular accidents. Measures of coarse coding and suppression deficits were computed from lexical decision reaction times at short (175 ms) and long (1000 ms) prime-target intervals. Lesions were drawn on magnetic resonance imaging images and through normalization were registered on an age-matched brain template. Voxel-based lesion symptom mapping analysis was applied to build a general linear model at each voxel. Z score maps were generated for

each deficit, and results were interpreted using automated anatomical labeling procedures.

Results: A deficit in coarse semantic activation was associated with lesions to the RH posterior middle temporal gyrus, dorsolateral prefrontal cortex, and lenticular nuclei. A maintenance deficit for coarsely coded representations involved the RH temporal pole and dorsolateral prefrontal cortex more medially. Ineffective suppression implicated lesions to the RH inferior frontal gyrus and subcortical regions, as hypothesized, along with the rostral temporal pole.

Conclusion: Beyond their scientific implications, these lesion–deficit correspondences may help inform the clinical diagnosis and enhance decisions about candidacy for deficit-focused treatment to improve narrative comprehension in individuals with RH damage.

Adults with right-hemisphere brain damage (RHD) often have difficulties with aspects of discourse comprehension, nonliteral language interpretation, inferencing, and reanalysis of conflicting information (Blake, 2014; Tompkins, Klepousniotou, & Gibbs Scott, 2012; Tompkins, Lei, & Zezinka, 2015). These high-level comprehension impairments can be related to the construction of mental representations of the language input. A number of dynamic processes shape the mental representation of a final interpretation. This study focuses on the right hemisphere

(RH) substrates of deficits in three of these processes previously demonstrated to be impaired in some adults with RHD (e.g., Klepousniotou & Baum, 2005; Tompkins, Baumgaertner, Lehman, & Fassbinder, 2000; Tompkins, Fassbinder, Scharp, & Meigh, 2008). Of particular interest are RH lesions associated with deficits in (a) early semantic activation, which triggers semantic features and concepts that initiate a mental foundation (Gernsbacher, 1990, p. 289); (b) the maintenance of this original activation as the comprehender processes subsequent input and maps it onto the foundation in a cohesive way; and (c) the suppression of activation for features and concepts that become contextually incompatible or irrelevant as interpretation unfolds (Gernsbacher, 1990).

Compared with left hemisphere (LH) semantic processing, early semantic activation and maintenance in the intact RH have been characterized as involving coarse coding (CC; Beeman, 1993, 1998; Jung-Beeman, 2005); that is, the RH activates and subsequently operates on more diffusely activated, broader semantic fields (Jung-Beeman, 2005, p. 514). The RH, then, activates and retains activation

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of more distantly related semantic features and meanings compared with the LH.

In this view, a CC deficit is assumed to disrupt this type of processing. Some empirical work with patients, however, suggests that RHD impairs early activation and maintenance only for information that is especially semantically remote or atypical. For example, Tompkins, Fassbinder, et al. (2008) based a study of 38 patients with RHD on Atchley, Burgess, and Keeney's (1999) investigation of hemispheric processing of semantic features of unambiguous nouns. Compared with control participants without brain damage, adults with RHD had no difficulty activating or maintaining activation for weakly related features compatible with the dominant mental images of those nouns (i.e., dominant compatible; e.g., "crunchy" as a feature of *apple*). However, the same patients were less accurate than the control group in responding to equally weakly related features that are incompatible with those typical mental images (i.e., dominant incompatible; e.g., "rotten" as a feature of *apple*). Per a large database of semantic distance norms (Maki, McKinley, & Thompson, 2004), the dominant-incompatible features were more semantically distant from their core concept (Tompkins, Scharp, Meigh, & Fassbinder, 2008). Thus, Tompkins, Fassbinder, and colleagues (Blake, Tompkins, Scharp, Meigh, & Wambaugh, 2015; Tompkins, Blake, Scharp, Meigh, & Wambaugh, 2013; Tompkins, Fassbinder, et al., 2008; Tompkins, Scharp, Meigh, Blake, & Wambaugh, 2012) refined the concept of RHD CC deficit and operationalized it in terms of a difficulty activating or maintaining activation for particularly remote or atypical information, such as dominant-incompatible semantic features. It is in that sense that the term *CC deficit* is used in this article.

Further evidence indicates that a deficit in this coarsely coded semantic activation and maintenance may be critical for predicting discourse-level language impairments in adults with RHD. The degree of RHD deficit in sustained activation for dominant-incompatible features has been related to the degree of comprehension impairment for implied information from narratives (Tompkins, Scharp, et al., 2008).

Suppression (SUP) is another critical mechanism in normal language comprehension (Gernsbacher, 1990, 1995). SUP is an attention-driven process (Tompkins, Lehman-Blake, Baumgaertner, & Fassbinder, 2002) that acts on various language levels and dimensions to prune the evolving mental representation. It does this by dampening semantic activation that becomes incompatible with the surrounding context. For example, the "river" meaning of the word *bank*, when initially activated, is subsequently suppressed for the sentence "He entered the bank." Thus, SUP assists in selecting from among competing concepts.¹

¹One might expect that SUP would preclude the maintenance of remote or unusual aspects of meaning that RH CC processes support. Pertinent studies of CC and CC deficit, however, use stimuli that are devoid of semantic biasing context, and SUP by definition acts on that which is contextually incompatible (Gernsbacher, 1990).

In relatively large samples of adults with RHD, the effectiveness of SUP for lexical semantic (Tompkins et al., 2000) and inferential (Tompkins, Fassbinder, Blake, Baumgaertner, & Jayaram, 2004; Tompkins, Lehman-Blake, Baumgaertner, & Fassbinder, 2001) ambiguities predicts general narrative comprehension performance after controlling for vocabulary knowledge, age, and working memory capacity for language. An SUP deficit may also underlie difficulties switching to a future timeframe in narrative comprehension in some adults with RHD (Scharp & Tompkins, 2013).

In light of this work with patients and hypotheses that are based on the functioning of normal brains (see, e.g., Jung-Beeman, 2005), SUP and early CC-related processes have become the focus of major accounts of narrative comprehension in adults with RHD (e.g., Blake, 2014; Tompkins et al., 2000; Tompkins, Klepousniotou, et al., 2012). To date, however, nothing is known about the anatomical damage that corresponds with the deficits of patients with RHD in these fundamental processes. The current study began to address this gap by decomposing comprehension difficulties of patients with RHD into critical lexical semantic processes and investigating the anatomical correlates of each. Thus, this study aimed to reveal RH regions that contribute to the basic processes themselves and, by extension, to higher level comprehension performance in adults with RHD.

Deficits in coarse semantic activation and maintenance of particularly remote information were assessed with a semantic feature priming task replicated from Tompkins, Fassbinder, et al. (2008). An impairment in early coarse semantic activation would be evidenced by lack of priming for dominant-incompatible targets (e.g., "rotten" as a feature of *apple*) shortly after their corresponding nouns in the absence of bias from prior context (Atchley et al., 1999; Tompkins, Fassbinder, et al., 2008). Lack of priming for these targets at a later postnoun interval would be consistent with a deficit in the intact RH's maintenance function for coarse semantic activation.

SUP was assessed in a meaning-priming task. SUP effectiveness—the measure of interest in prior patient studies (Tompkins et al., 2000, 2001, 2004)—quantifies abnormally sustained priming of contextually incompatible targets. In the current study, the contextually incompatible targets represented the dominant meanings of subordinate-biased homophones. Early activation of contextually incompatible targets is normally suppressed at a relatively longer postnoun interval (Faust & Gernsbacher, 1996; Gernsbacher, 1990; Tompkins et al., 2000, 2001, 2004).

To relate impairments in these basic comprehension processes to RH lesions, we used a voxel-based lesion symptom mapping (VLSM) procedure (Bates et al., 2003; Gläscher et al., 2009). VLSM implements a massive univariate regression model that relates behavioral performance of a group of patients to the presence and absence of lesions at each given voxel. After controlling for multiple comparisons, VLSM analysis can indicate which lesions reliably influence the patients' behaviors.

Hypotheses about the RH structures of interest were derived from proposals of the bilateral activation, integration, and selection framework of language processing (BAIS; Jung-Beeman, 2005) and results of other neuroimaging and lesion studies. BAIS elaborates on Beeman's (1993, 1998) early description of complementary, computationally different RH versus LH processing styles for lexical semantic activation and ascribes these computational styles to semantic integration and selection processes. Integrating a range of neuroimaging and lesion studies, Jung-Beeman (2005) suggested that coarse semantic activation involves regions surrounding the RH Wernicke's homologue, especially the posterior middle and superior temporal gyri (MTG and STG, respectively; see also Stowe et al., 2001). He hypothesized further that RH semantic integration engages the anterior STG and superior temporal sulcus, extending into the MTG and perhaps the temporal pole. Because our measure of early CC is related to the BAIS semantic activation component and our measure of maintenance of CC is related to activation and perhaps to integration in BAIS, we hypothesized that RHD deficits in these processes would co-occur with lesions in these regions.

Our SUP process, in which one of several competing mental activations is dampened and selected against, shares some features with the attention-driven semantic selection process of the BAIS framework. As described by Jung-Beeman (2005, p. 516), "selection modulates word-level semantic activation and message-level semantic integration" via an "interactive process by which competing activated concepts are sorted out, inhibiting competing concepts while selecting one." Selection is strongly associated with the LH inferior frontal gyrus (IFG; Jung-Beeman, 2005; Kan & Thompson-Schill, 2004; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007), but the RH IFG is also crucial for semantic filtering and selection (Jung-Beeman, 2005; Zempleni et al., 2007), especially for information more strongly active in the RH (Seger, Desmond, Glover, & Gabrieli, 2000). For example, in a functional magnetic resonance imaging (MRI) study of young individuals without brain injury, Mason and Just (2007) reported activation in the RH IFG for processing biased lexical ambiguities and identified this region as potentially important for semantic selection of distantly related semantic information. Thus, lesions in this area were expected to be involved in SUP deficits. We also expected SUP deficits to be associated with basal ganglia lesions on the basis of evidence for a role of the basal ganglia in semantic selection (e.g., Copland, 2006; Mason & Just, 2007; Zgaljardic, Borod, Foldi, & Mattis, 2003).

Identifying damage to RH networks that underlie deficits in these processes has both basic and clinical implications. The basic research implications relate to furthering our understanding of RH contributions to language processing. In terms of clinical implications, there are currently no behavioral assessments for SUP and CC deficits, both of which are linked to problems in narrative comprehension, inferencing, and other higher level language outcomes for patients with RHD (e.g., Tompkins, Klepousniotou,

et al., 2012). Knowledge of lesion–deficit correlations will supplement and inform the diagnostic process and may help clinicians target interventions for these deficits.

Method

Participants

Participants were 20 adults with unilateral RH cerebrovascular accident who were recruited from acute-care hospitals and rehabilitation centers as part of a larger cohort. These 20 adults qualified for and underwent research MRI scanning for the current study, as described below. All participants (a) had confirmed unilateral RH lesion(s) on the basis of computerized tomography or MRI scan report, (b) were a minimum of 4 months postonset, (c) were between the ages of 40 and 85 years, and (d) had completed at least 8 years of formal education. All also met the following exclusion criteria per medical records and screening interviews: no documented bilateral brain lesions, no lesion to the brainstem or cerebellum, no seizure disorder before cerebrovascular accident, no head injury resulting in hospitalization, no drug or alcohol abuse, no other progressive cognitive conditions such as Alzheimer's or Parkinson's diseases, and/or no psychiatric conditions. All patients self-identified as right handed, monolingual, and as native speakers of American English. All were tested to characterize a variety of cognitive and language abilities (see Table 1 for demographic and clinical characteristics).

All participants also passed a hearing screening. Pure-tone screening was conducted at 500, 1000, and 2000 Hz, with a passing criterion of 35 dB HL for each frequency (a value within 0.5 *SD* of means for ambulatory older men who were not institutionalized; Harford & Dodds, 1982). Patients who failed pure-tone screening in one ear all passed an additional behavioral screen by correctly repeating 12 words that were loaded with fricative consonants in order to tax high-frequency hearing.

Stimuli

Stimuli for both the CC-related and SUP behavioral measures consisted of sentences that ended with specific kinds of nouns followed by targets that either were real words related to the sentence-final nouns in specific ways or were nonwords. In experimental stimuli, the sentence-final nouns served as primes; that is, they were expected to speed the processing of a subsequent real-word target. Stimuli were iteratively validated, revised, and revalidated. Each validation step was completed by at least eight different responders without brain damage who were socio-demographically similar to our typical stroke patient samples. The experimental stimuli for CC and SUP are listed in Appendix A.

CC Items

Sentence-final noun primes were 16 one- to two-syllable common unambiguous nouns (e.g., *apple*) from

Table 1. Demographic and clinical characteristics of study participants.

Characteristic	Value
Age (years)	
<i>M</i> (<i>SD</i>)	65.2 (11.3)
Range	42 to 78
Sex (<i>n</i>)	
Female	12
Male	8
Education (years)	
<i>M</i> (<i>SD</i>)	13.5 (2.4)
Range	10 to 20
Months postonset	
<i>M</i> (<i>SD</i>)	52.5 (54.7)
Range	4 to 167
Peabody Picture Vocabulary Test–Revised ^a (maximum = 175)	
<i>M</i> (<i>SD</i>)	156.7 (11.2)
Range	134 to 170
Behavioural Inattention Test ^b (maximum = 146; neglect cutoff = 129)	
<i>M</i> (<i>SD</i>)	137.3 (9.4)
Range	104 to 146
Auditory Working Memory for Language ^c word recall errors (maximum = 42)	
<i>M</i> (<i>SD</i>)	14.0 (7.0)
Range	1 to 27
Judgment of Line Orientation ^d (age- and gender-corrected maximum = 35)	
<i>M</i> (<i>SD</i>)	19.8 (5.5)
Range	4 to 28
Visual Form Discrimination ^d (maximum = 32; cutoff = 23)	
<i>M</i> (<i>SD</i>)	27.5 (3.5)
Range	23 to 32
ABCD ^e story retell (maximum = 17)	
Immediate	
<i>M</i> (<i>SD</i>)	13.4 (2.4)
Range	7 to 17
Delayed	
<i>M</i> (<i>SD</i>)	12.8 (3.0)
Range	5 to 17

^aDunn & Dunn (1981). ^bWilson, Cockburn, & Halligan (1987).

^cTompkins, Bloise, Timko, & Baumgaertner (1994). ^dBenton, Sivan, Hamsher, Varney, & Spreen (1983). ^eBayles & Tomoeda (1993).

Atchley et al. (1999).² These nouns were embedded in semantically neutral, simple subject–verb–object sentences (e.g., “He has an apple”). Each sentence was then paired with three types of real-word targets. Two of these, the CC-relevant targets and comparison targets, came from Atchley et al. (1999). The CC-relevant targets reflected weakly related semantic features that are incompatible with

the dominant mental representation of the noun (dominant-incompatible condition; e.g., *rotten*). Comparison targets reflected weakly related features of the dominant or prototypical mental representation (dominant-compatible condition; e.g., *crunchy*). Unrelated target words (e.g., *mermaid*), generated³ and validated for Tompkins, Fassbinder, et al. (2008), were not expected to be primed by the sentence-final nouns. The three categories of targets were matched for lexical properties, including log frequency, prosodic features, abstractness, and mean baseline reaction time, per data from the Washington University English Lexicon Project (e-lexicon; Balota et al., 2007; see Appendix B).

To validate the neutral sentence contexts, each was presented in written form as the first portion of a longer sentence that was physically separated from three or four possible extensions (e.g., “He has an apple ... that is crunchy/rotten/empty”). Respondents judged how much sense the extension made as a sentence ending (0 = *doesn't make sense*, 3 = *makes a lot of sense*). Average ratings for the dominant-incompatible and dominant-compatible targets were 2.58 and 2.64, respectively, with no rating below 2. In a relatedness rating task (0 = *not at all related*, 3 = *very strongly related*), both of these types of targets were judged to be strongly related to the isolated sentence-final noun (dominant incompatible, *M* = 2.47; dominant compatible, *M* = 2.52; no ratings below 2) and unrelated targets were rated as clearly unrelated (*M* = 0.02; no ratings above 1). Targets were not associated with sentence-final nouns (per norms from Nelson, McEvoy, & Schreiber, 1998).

SUP Items

Twelve experimental sentences were used to assess SUP function. Each ended in a polarized ambiguous noun (e.g., *bank*) that has one clearly dominant meaning and at least one secondary meaning. These nouns were identified from Clark's homophone norms (<http://www.uwinnipeg.ca/~clark/cog/norms/homall.out>) and a homophone dictionary (<http://www.earlham.edu/~peters/writing/homofone.htm>). The sentences were weakly semantically biased toward the dominant meaning of the sentence-final noun (e.g., “He entered the bank”).⁴ Each sentence was then paired with three types of real-word targets. SUP targets (e.g., *river*) were related to the subordinate meaning of the sentence-final noun primes and thus, being contextually incompatible, were candidates for SUP. Other targets words reflected the nouns' contextually compatible dominant meanings (e.g., *cash*) or were unrelated (e.g., *tiger*). The three types of target words were matched for psycholinguistic properties per data from e-lexicon (Balota et al., 2007; see Appendix B). As determined by a relatedness rating procedure (0 = *not at all related*, 3 = *very strongly related*), the dominant targets

²These items remained after culling the Atchley et al. (1999) list of nouns that (a) were homophonous or ambiguous, (b) formed a compound or undesirable reference with Atchley et al. target items (e.g., *carrot cake*, *electric chair*), or, (c) as judged by three independent raters in our lab, had dominant-compatible and dominant-incompatible “mental images” that were too similar to one another. They also remained after subjecting the remaining noun stimuli to the neutral sentence validation, described in the next paragraph.

³Two of the 16 unrelated targets were dominant-incompatible targets for other items in Atchley et al. (1999).

⁴As determined by pre-experimental cloze judgment of 12 responders who were sociodemographically similar to typical stroke patient samples. A weaker bias was implemented to minimize the chance of selective activation of the dominant meaning.

were highly related to the experimental sentences ($M = 2.87$), but the subordinate ($M = 0.43$) and unrelated ($M = 0.06$) targets were not. In additional validation, with a 175-ms interval between the sentence and the target, only the dominant targets were primed by the stimulus sentences. That is, lexical decision responses to dominant targets were quicker (by 91 ms) than those to unrelated targets.

Filler Stimuli

Filler stimuli ($N = 84$) were designed to minimize expectancies related to the structure and repetition of experimental sentences, each of which occurred three times in the experimental task, and to provide lexical decision trials that had nonword targets. Because the experimental sentences paired unambiguous final nouns with neutral verbs (CC) or ambiguous nouns with specific biasing verbs (SUP), filler sentences paired (different) unambiguous nouns with (different) specific verbs (e.g., “He built the house”) or (different) ambiguous nouns with neutral verbs (e.g., “She saw the pipe”). Two thirds ($N = 56$) of the filler sentences were lengthier and more syntactically diverse than the experimental sentences (e.g., “She listened intently to the speakers”). Three strategies were used to reduce expectancies about stimulus repetition. First, two thirds of filler sentences began with the same few words as experimental items but ended differently (e.g., “He ate a banana”). Second, portions of each filler sentence recurred, but no filler sentence was repeated verbatim. Variations in filler sentences were achieved by changing the sentence-final word, the lexical decision target, or both. Third, each nonword target occurred three times, each time with a different filler sentence. A total of 66 filler sentences were paired with nonword targets, and the remaining sentences were paired with real-word targets (subordinate-related, dominant-related, unrelated). Nonword targets were derived from real-word targets by changing one or two phonemes of single-syllable or multisyllable target words, respectively. All changes were made in the final third of the phoneme string, and the resulting nonwords were phonotactically plausible in the English language.

Tasks

Experimental Lexical Decision Task

An auditory lexical decision task was used to assess priming of target semantic features (for CC) and of alternative meanings (for SUP) of sentence-final nouns. For this 168-item task (CC = 48, SUP = 36, fillers = 84), participants indicated as quickly as possible whether or not a target phoneme string was a real word. About 40% of the targets were nonwords. Across all stimuli, the relatedness proportion (related targets/all real-word targets) was .59 and the nonword ratio (nonwords/unrelated plus nonword targets) was .55. Sentence offset and target onset were separated by both short (175 ms) and longer (1000 ms) interstimulus intervals. Accuracy and response times (RTs) were recorded.

For CC items, the two intervals were included to assess both early activation and maintenance of activation for dominant-(in)compatible semantic features. SUP effectiveness, as noted previously, is quantified by relative priming of contextually incompatible targets at the long versus short interval.

Word Monitoring Task

A secondary auditory word monitoring task was incorporated to keep participants attending until the end of each stimulus sentence. The words to be monitored were common nouns or verbs that were one to three syllables in length (e.g., *animal*, *gave*).

Experimental Task Construction

The stimulus recording procedure was reported in Tompkins, Fassbinder, et al. (2008). One detail worth repeating here is that sentence stimuli were recorded by a woman and the lexical decision targets were recorded by a man to assist participants with perceptual segmentation.

E-Prime software (Schneider, Eschman, & Zuccolotto, 2002) was used to assemble the stimuli. Each item consisted of a trial number, a 500-ms pause, the sentence, a silent interval (175 or 1000 ms), and the spoken target. Stimuli were pseudorandomly arranged into 14 blocks of 23 or 24 trials each. Within each block, there were no verbatim sentence repetitions, no more than three sequential word or nonword targets, and no more than three of each type of filler sentence. Any recurring experimental sentence was separated across blocks by a minimum of nine trials. At least two filler trials began each block, and each block ended with at least one filler.

Experimental Apparatus and Procedures

The lexical decision task was delivered via a Dell (Round Rock, TX) Inspiron 5150 notebook computer. Participants listened at individually selected, comfortable loudness levels (via Quick Mixer version 1.7.2, Softpedia Mirror, <http://www.softpedia.com>) through high-quality supra-aural earphones (DT150, Beyerdynamic, Heilbronn, Germany). Participants were asked to respond to each target as quickly and accurately as possible by pressing one of two buttons labeled either *yes* or *no* on a manual response box. E-Prime software recorded both accuracy and millisecond RT values.

Before each block of lexical decision trials, an index card was presented for the word monitoring task. The word to be monitored was printed in 0.5-in. block letters. The examiner read the word aloud and set the card on the response box. At the end of each block of trials, the examiner asked participants whether they had heard the word. The word in question occurred in eight blocks of trials and did not occur in the other six blocks. Each word that did occur appeared only once per block in a filler sentence in the last third of the block.

General Procedures

The order of presentation of stimulus blocks was counterbalanced for each participant within and across sessions. The tasks for this study were interspersed with screening measures, clinical descriptive tasks, and tasks for other experiments, with the result that behavioral testing was completed in four to five sessions of 60 to 90 min each over a period of 3 to 7 weeks.

Testing occurred in a quiet room in participants' homes or in the second author's laboratory. Five thoroughly trained examiners performed the testing, though only one examiner worked with each participant. Extensive orientation, instruction, and practice were provided. During practice, participants became skilled at indicating their lexical decision with a single finger of the right hand and at returning that finger between trials to a home base that was equidistant from the response buttons. Training and practice continued until RTs stabilized. The same response buttons were used for the word monitoring task.

To remind participants to continue responding quickly throughout the task, a response deadline signal (standard Windows bell) was incorporated on 50% of the filler trials. This signal occurred after the target at an interval individually determined for each participant, which was calculated by averaging RTs for correct responses to the final set of practice trials.

Behavioral Outcome Measures

As in our prior work (e.g., Tompkins et al., 2000; Tompkins, Fassbinder, et al., 2008), the primary dependent measures for the behavioral data were RT ratios, which were calculated for accurate responses. For both prime–target intervals, the CC-relevant ratios focus on RTs for dominant-incompatible features in relation to RTs for unrelated semantic features. These ratios, denoted *dominant-incompatible ratios*, are calculated as $RT_{\text{Incompatible}}/RT_{\text{Unrelated}}$. For comparison purposes, RT ratios were also computed for dominant-compatible features compared with unrelated features ($RT_{\text{Compatible}}/RT_{\text{Unrelated}}$) and are denoted as *dominant-compatible ratios*. Ratios smaller than 1 indicate that an unambiguous noun, such as *apple*, activates weakly related semantic features, and ratios larger than 1 indicate a deficit (i.e., for the dominant-incompatible ratio, impaired priming of remote semantic features).

For SUP, the index of interest is the SUP effectiveness ratio. This ratio is computed in two steps. First, RT ratios of subordinate targets to unrelated targets ($RT_{\text{Subordinate}}/RT_{\text{Unrelated}}$) are calculated for both short and long intervals. The former indicates the degree of activation for the contextually incompatible target at an early time point, whereas the latter indicates how much of this activation remains after it is typically suppressed by comprehenders without brain damage (Tompkins et al., 2000). Values smaller than 1 for these ratios indicate activation of contextually incompatible targets. The second step in calculating SUP effectiveness is to subtract the ratio for the long

interval from the ratio for the short interval. Adequate SUP thus yields a negative value for the SUP effectiveness index: An RT ratio that is smaller at the short interval than at the long interval reflects temporary activation of contextually incompatible meanings that is later suppressed.

MRI Acquisition and Preprocessing

MRIs were obtained contemporaneously with behavioral testing using a GE Healthcare (Barrington, IL) Signa 1.5T scanner. The coronal high-resolution volumetric spoiled gradient recalled acquisition sequence was the basis for analysis. Using MRIcron (Rorden, 2007), the acquired files were converted from DICOM to NifTi format and scalp stripped. Lesions were independently demarcated directly on coronal slices (refined on axial and sagittal slices) by multiple drawers blind to participants' symptoms. Reliability was assessed in VoxBo, a Linux-based package (Kimberg & Aguirre, 2001). The criterion for interrater reliability was less than 8% discrepant voxels (greater than or equal to two voxels away in three-dimensional space; Fiez, Damasio, & Grabowski, 2000). Discrepant voxels were defined per Fiez et al. (2000) as two voxels away from overlapping voxels. An experienced stroke neurologist, also blinded, assessed and validated 25% of the lesion drawings.

Using the display tool of SPM8 (Ashburner et al., 2012), these drawings were globally oriented to within 5° of an age-matched brain template (Rorden, Bonilha, Fridriksson, Bender, & Karnath, 2012; Rorden, Fridriksson, & Karnath, 2009). Then, cost-function masking was used to delineate the lesion boundaries when calculating transformation parameters (Bates et al., 2003; Brett, Leff, Rorden, & Ashburner, 2001). Segmentation and normalization functions were then performed to register each patient's scan onto the template using the clinical toolbox (Rorden et al., 2012). The same transformation matrix was applied to the patient's lesion drawing. The results are transformed lesion areas of all the patients into the template space, which allow for comparisons of lesions across participants.

Voxel-Lesion Symptom Mapping Procedures

The normalized lesion files, masked occipitally, were entered with the behavioral RT ratios into NPM to construct design matrices (Rorden, 2007). For each matrix, we ran a separate VLSM analysis, which generates a general linear model for each voxel using the behavioral scores as continuous predictors (Rorden, 2007; Rorden et al., 2009). Each VLSM analysis yielded a Brunner–Munzel z score map (Brunner & Munzel, 2000; Gläscher et al., 2009; Tsuchida & Fellows, 2009), which was parceled and labeled by automated anatomical labeling (AAL; Tzourio-Mazoyer et al., 2002). Regions of labeled anatomical structures, Montreal Neurological Institute coordinates, voxel sizes, and Brodmann area labels were generated. The resulting regions were considered significant only if (a) the q values of all the voxels (false discovery rate controlled for multiple

comparisons) were smaller than 0.05 and (b) the cluster was larger than 15 voxels.

Results

Preliminary Analyses of Behavioral Data

Raw accuracy and RT data are provided in Appendix C. Mean lexical decision accuracy was 94.8% for all CC stimuli and 90.2% for all SUP items.⁵ Between-groups *t* tests were used to assess accuracy and RT data for sex differences in each condition. None of these analyses were significant; all $t(18) < |1.65|$, $p > .12$. Speed–accuracy trade-offs were ruled out by Pearson correlation of accuracy and raw RT data in each condition; all $r(18) < |.22|$, all $p > .11$. RT values at least 3 *SD* away from their condition means were coded as errors and excluded from the RT analysis. These outliers represented 7.5% of all trials.

Descriptive and Main Analyses of Behavioral Data

Table 2 summarizes the descriptive statistics for the behavioral RT ratios. As in our prior work, Pearson correlations indicated that none of these ratios were associated with age, all $r(18) < .23$, all $p > .32$, or with estimated working memory capacity for language (Tompkins et al., 1994), all $r(18) < .42$, all $p > .067$. In addition, per between-groups *t* tests, there were no sex differences in the ratio measures; all $t(18) < |1.23|$, all $p > .23$.

Before reporting the group results, it is important to note that the CC-related indices and SUP are all individual difference variables, such that individual participants within a group have these deficits even when there is no impairment evident in group average results. Group average RT ratios for the CC-related stimuli were all significantly larger than 1, as indicated by one-sample *t* test on log-transformed data⁶; dominant-incompatible short interval: $t(19) = 5.76$, $p < .001$; dominant-incompatible long interval: $t(19) = 4.62$, $p < .001$; dominant-compatible short interval: $t(19) = 6.33$, $p < .001$; dominant-compatible long interval: $t(19) = 4.72$, $p < .001$. In addition, strong effects were obtained for all tests; dominant-incompatible short interval: Cohen's $d = 2.64$, effect size $r = .80$; dominant-incompatible long interval: Cohen's $d = 2.12$, $r = .73$; dominant-compatible short interval: Cohen's $d = 2.90$, effect size $r = .82$; dominant-compatible long interval: Cohen's $d = 2.16$, $r = .73$. The two types of ratios did not differ statistically at either interval, as indicated by paired-samples *t* test; short interval: $t(19) = 0.683$, $p = .503$; long interval: $t(19) = -0.663$, $p = .515$. Further, the two types of ratios were significantly correlated with each other at both prime–target intervals; short interval: $r(18) = 0.468$, $p = .037$; long interval: $r(18) = 0.601$, $p = .005$. Together, these results indicate that this sample of participants with RHD on average had difficulty activating and

Table 2. Descriptive statistics for behavioral response time ratios.

Variable	<i>M</i> (<i>SD</i>)	Range
Coarse coding		
Dominant incompatible		
Short interval	1.23 (0.22)	0.97 to 2.05
Long interval	1.39 (0.57)	1.00 to 3.68
Dominant compatible		
Short interval	1.20 (0.19)	0.89 to 1.61
Long interval	1.32 (0.24)	0.92 to 1.80
Suppression		
Subordinate/unrelated		
Short interval	1.04 (0.16)	0.79 to 1.32
Long interval	1.11 (0.15)	0.88 to 1.39
Suppression effectiveness	−0.07 (0.15)	−0.58 to 0.08

Note. Dominant-incompatible index = response times for dominant-incompatible representations/response times for unrelated trials. Dominant-compatible index = response times for dominant-compatible representations/response times for unrelated trials. Subordinate/unrelated = response times for subordinate meaning trials/response times for unrelated trials. Suppression effectiveness = index of suppression function = (short interval subordinate/unrelated) − (long interval subordinate/unrelated).

maintaining activation of both types of weakly related semantic features.

Turning to the SUP data, the group subordinate/unrelated RT ratio was not significantly different from 1 at the short interval by one-sample *t* test on the log-transformed data, $t(19) = 0.924$, $p = .367$, indicating that the contextually incompatible subordinate target was not reliably activated by the group as a whole. At the long interval, this ratio was significantly larger than 1, $t(19) = 3.299$, $p = .004$, indicating that the contextually incompatible target also was not active on average at this point in time. For the primary SUP outcome of interest, the negative value of the SUP effectiveness index, which was marginally significantly different from zero, $t(19) = -2.084$, $p = .051$, suggests a trend toward effective SUP in this particular group of RHD participants. A medium effect size was obtained for this test (Cohen's $d = 0.96$, effect size $r = .43$).

VLSM Results

Coarse Semantic Activation and Maintenance

Figure 1 represents the VLSM results for the CC-related (dominant incompatible) and comparison (dominant compatible) ratios. Results for both of these indices are described in Table 3. At the short interval, poor activation of dominant-incompatible features was associated uniquely⁷ with RH lesions in the MTG (Brodmann area [BA] 21, 39). Also implicated were lesions in a dorsolateral portion

⁵All participants were 100% accurate on the word monitoring task.

⁶The log transformation was conducted to achieve data distributions that were roughly normal and centered around zero. This was done to conform to the assumptions of the *t* test.

⁷When a significant voxel cluster was identified for both RT indices in the same AAL-defined anatomical area (e.g., portions of the inferior frontal gyrus; see Table 3), the lesion–behavior relationship was considered unique to one of these indices if the AAL-quantified voxel count for the other index was less than 10% of the total voxels in that anatomical area.

Figure 1. Clusters of significant lesion voxels in the right hemisphere related to coarse coding deficit in voxel-based lesion symptom mapping models, registered on an older brain template. From top to bottom: coronal view, axial view, and sagittal view. Red: dominant-incompatible index for short interval; blue: dominant-incompatible index for long interval; pink: overlap.

of the posterior middle frontal gyrus in BA 46 and in the lenticular nuclei. At the long interval, the dominant-incompatible index reflects the maintenance of activation of particularly remote semantic features. Poor maintenance

was related to lesions in the anterior STG/temporal pole (BA 38) as well as dorsolateral prefrontal lesions (BA 9, 46) extending into the medial superior frontal gyrus in BA 10, including white matter (superior corona radiata).

Table 3. Right hemisphere anatomical areas significant for coarse coding reaction time (RT) indices for short and long intervals.

Coarse coding–related variables	Main significant anatomical areas (per AAL)	(MNI coordinates); BA
Dominant-incompatible ratio: dominant-incompatible RT/unrelated RT Short interval	Posterior middle temporal gyrus Inferior frontal gyrus (pars triangularis and opercularis) Inferior (pars opercularis) and posterior middle frontal gyrus Anterior lateral and medial putamen Lateral globus pallidus Superior temporal gyrus	(36, -63, 16); BA 21 (43, 24, 19); BA 44, 45, 46 (43, 6, 27); BA 44, 46 (26, 2, 12) (24, -14, -2) (49, -31, 5); BA 22, 41, 42
Dominant-compatible ratio: dominant-compatible RT/unrelated RT Short interval	Inferior frontal gyrus (pars triangularis, orbitalis, and opercularis) Anterior lateral caudate Anterior medial insula	(27, 19, 22); (31, 23, -22); BA 11, 44, 45, 47 (22, -9, 15) (27, -19, 22); BA 13, 14
Dominant-incompatible ratio: dominant-incompatible RT/unrelated RT Long interval	Temporal pole, anterior superior temporal gyrus (most rostral part) Inferior frontal gyrus (pars triangularis) Dorsolateral prefrontal area and medial superior frontal gyrus	(34, 3, -19); BA 38 (38, 17, 22); BA 45 (26, 4, 25); BA 9, 10, 46
Dominant-compatible ratio: dominant-compatible RT/unrelated RT Long interval	Inferior frontal gyrus (pars triangularis) Putamen	(38, 17, 22); BA 45 (25, 4, 25); (30, -3, 10)

Note. AAL = automated anatomical labeling; MNI = Montreal Neurological Institute; BA = Brodmann area.

SUP Effectiveness

Figure 2 and Table 4 present VLSM results for SUP effectiveness. The extent to which early activation of a contextually incompatible meaning was dampened over time was related to large RH lesion clusters in corticostriatal circuits, including parts of the IFG (BA 45, 47), STG/temporal pole (BA 22, 38) and its underlying white matter, insula (BA 13, 14), and caudate, putamen, and globus pallidus.

Discussion

This study uniquely relates neural anatomical areas in the RH to language processing deficits in the patient population. Unlike neuroimaging data from the healthy population, this approach can reveal lesion–deficit relationships directly and may help map clinical assessment and management. The results were largely consistent with predictions set forth in the introduction as well as with past RHD behavioral studies and other neuroimaging studies conducted with the population without brain damage.

Coarse Semantic Activation and Maintenance

Early activation of particularly remote features of lexical–semantic representations uniquely depends on the posterior RH MTG, as hypothesized, but also on the RH dorsolateral prefrontal cortex (DLPFC). Longer term maintenance of this activation is related to more medial, posterior, and inferior DLPFC. DLPFC involvement may

suggest a greater need for RH postactivation and post-retrieval refreshing, monitoring, or evaluation (Hayama & Rugg, 2009; Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006) of semantic features that are particularly remote from a dominant representation than for less remote features. The DLPFC is connected to CC-relevant posterior temporal and parietal regions as well. Lesions extending into the RH temporal pole also impair maintenance of remote-feature activation, perhaps due to its representation-inconsistent nature (Ferstl, Rinck, & Cramon, 2005) or to disruption of multimodal semantic memory representations (Binder & Desai, 2011). The lenticular nuclei involvement was not predicted and is addressed below. Although not explicitly predicted, the white matter contribution to CC deficit is not surprising. The implicated region, the superior corona radiata, connects different parts of the DLPFC. As such, it may contribute to the DLPFC's postactivation and post-retrieval monitoring functions.

SUP Effectiveness

As hypothesized, effective SUP of contextually incompatible meanings implicates RH corticostriatal circuits (Copland, 2006; Mason & Just, 2007; Zempleni et al., 2007) important for resolving lexical ambiguity (Mason & Just, 2007). The nature of the basal ganglia contribution is considered further below. Beyond the IFG and basal ganglia, though, the integrity of the RH anterior STG and underlying white matter is important, perhaps due to a role in processing representation-incompatible material (Ferstl

Figure 2. Clusters of significant lesion voxels related to suppression effectiveness deficit in the right hemisphere, registered on an older brain template. From top to bottom: coronal view, axial view, and sagittal view.

Table 4. Right hemisphere anatomical areas significant for suppression effectiveness.

Suppression effectiveness RT ratio	Main significant anatomical areas (per AAL)	(MNI coordinates); BA
Subordinate RT/unrelated RT (short interval) – subordinate RT /unrelated RT (long interval)	White matter, superior frontal gyrus	(24, –3, 41)
	Posterior middle frontal gyrus	(29, 10, 33)
	Anterior part of superior temporal and middle temporal gyri and insula	(39, 8, –27)
		BA 22, 21, 13, 14
	White matter, anterior angular gyrus	(34, –52, 20)
	Lenticular nucleus, putamen	(23, –8, 23)
		(21, –3, 15)

Note. RT = reaction time; AAL = automated anatomical labeling; MNI = Montreal Neurological Institute; BA = Brodmann area.

et al., 2005). If information is not registered as context inconsistent, SUP would not be triggered. Again, although not predicted, the white matter involvement in SUP deficit is not unexpected. The main contributing white matter connects the STG and basal ganglia. Effective communication between these cortical and subcortical areas might be critical for achieving the routing of lexical alternatives.

Basal Ganglia

All of the behavioral indices reported here are related to at least part of the basal ganglia complex, defined as the caudate, putamen, and globus pallidus. Numerous recent studies have confirmed a role for the basal ganglia in cognitive functions, including language (e.g., Prat & Just, 2011; Prat, Keller, & Just, 2007; Ullman et al., 1997) and lexical–semantic processing in particular (e.g., Whelan et al., 2004). Stocco, Lebiere, and Anderson (2010) proposed that the basal ganglia serve a general-purpose “routing operation,” directing information to appropriate cortical areas (p. 548). An example of how such signal routing is important for language can be seen in the basal ganglia’s critical role in language switching for bilingual speakers (for review, see Buchweitz & Prat, 2013; Stocco, Yamasaki, Natalenko, & Prat, 2014). Therefore, the relationship of basal ganglia to each of our indices may reflect the flexible routing of task-relevant information to the prefrontal cortex for processing.

Clinical Implications

The results of this work have potential implications for assessment and treatment of patients with RHD. Armed with knowledge of an individual patient’s lesion and the lesion patterns associated with deficits in early CC, maintenance of CC, and SUP, clinicians will have an important supplement to behavioral diagnostic assessments. Identification of these deficits has implications beyond the lexical level to the domain of narrative comprehension (e.g., Tompkins et al., 2000; Tompkins, Scharp, et al., 2008) and possibly to other processes that may involve CC and SUP (e.g., Blake et al., 2015; Tompkins et al., 2013). Better diagnosis of these difficulties should help clinicians shape behavioral intervention choices as well. Recent evidence, for example,

substantiates the promise of a novel theoretically and empirically based contextual constraint treatment (Blake et al., 2015; Tompkins et al., 2013; Tompkins, Scharp, et al., 2012) that targets these deficits. Early work suggests that this treatment approach, with separate versions for CC or SUP processes, yields generalized improvement to narrative comprehension in adults with RHD.

Limitations and Future Directions

First, one intrinsic limitation of the VLSM approach is related to the distribution of lesion sites in the participant sample. When constructing the general linear model, voxels can be modeled only when there are sufficient numbers of lesioned samples (i.e., patients who have a lesion at a particular voxel) and nonlesioned samples (i.e., patients who do not; Bates et al., 2003). This fact intrinsically limits the results for any particular patient sample. Because we did not control for lesion distribution in a broad sense and could not control it at the voxel level, some symptom-related areas may be missed. Therefore, in interpreting these results, it must be kept in mind that VLSM is a highly specific yet potentially insensitive approach.

Another technical limitation is that VLSM assumes that all voxels are independent. It does not model dependence between voxels, which is critically important for understanding the neurobiology of language. This might be improved by implementing a Bayesian framework in the future (Chen & Herskovits, 2010).

Last, the static neuroanatomic assessment that we used in this study was inherently limited in representing the nature of the interconnected brain networks that underlie processes of interest. Future work assessing structural connectivity and neural processing dynamics will yield a much deeper understanding of the neural underpinnings of the behavioral performances assessed in this study.

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Appendix A

Experimental Stimuli

Table A1. Coarse coding items.

Experimental sentence	Dominant-incompatible targets	Dominant-compatible targets	Unrelated targets
He has an <i>apple</i> .	rotten	crunchy	mermaid
He was concerned about the <i>airplane</i> .	captain	window	simple
He has a <i>cabin</i> .	cramped	chimney	teammate
He had a <i>car</i> .	hood	gas	sweet
He visited the <i>castle</i> .	royal	dungeon	powder
He drank some <i>coffee</i> .	beans	bitter	needle
I saw the <i>cotton</i> .	field	ball	wife
She used the <i>garlic</i> .	powder	bulb	lamp
He liked the <i>milkshake</i> .	calories	smooth	medicine
There is the <i>mustard</i> .	plant	spicy	prison
He moved the <i>oak</i> .	furniture	branches	calories
He ate the <i>potatoes</i> .	fluffy	skin	shiny
She didn't like the <i>rice</i> .	bland	sticky	glove
Here is a <i>shirt</i> .	wrinkled	pocket	parsley
He inspected the <i>sofa</i> .	springs	leather	rocket
She spit out the <i>milk</i> .	spoiled	warm	knife

Table A2. Suppression items.

Experimental sentence	Dominant meaning targets	Subordinate meaning targets	Unrelated targets
She greeted her <i>pupils</i> .	students	eyes	nation
She wore a cheap <i>ring</i> .	marriage	alarm	window
He told her one more <i>story</i> .	tell	building	pistol
She fed her <i>calf</i> .	baby	leg	snow
She wrote down the <i>dates</i> .	calendar	figs	hospital
She picked up the <i>ball</i> .	catcher	dance	folder
He entered the <i>bank</i> .	cash	river	tiger
His hands were sticky from the <i>lime</i> .	lemon	garden	bull
At the store he bought a <i>mint</i> .	jelly	coins	library
She reached for the <i>pen</i> .	ink	pig	car
He threw away the <i>pit</i> .	trench	stone	bag
She laughed at the lively <i>seal</i> .	circus	envelope	poster

Appendix B

Mean (SD) Lexical Properties^a of Target Words for Coarse Coding and Suppression Items

Coarse coding items	Dominant-incompatible targets	Dominant-compatible targets	Unrelated targets
Log frequency	8.5 (1.4)	8.8 (1.5)	9.0 (1.4)
Mean RT (ms)	636 (58.3)	633 (66.5)	635 (58.7)
Phoneme count	4.9 (1.1)	4.7 (1.0)	4.8 (1.2)
Syllable count	1.7 (0.7)	1.6 (0.5)	1.8 (0.5)
Concreteness	5.2 (1.2)	5.3 (1.0)	5.3 (1.0)
Suppression items	Dominant targets	Subordinate targets	Unrelated targets
Log frequency	9.3 (1.5)	9.4 (1.2)	9.6 (1.2)
Mean RT (ms)	594 (40.3)	597 (45.3)	600 (26.2)
Phoneme count	4.6 (1.5)	4.3 (1.4)	4.6 (1.4)
Syllable count	1.7 (0.6)	1.6 (0.7)	1.7 (0.7)
Concreteness	5.7 (1.0)	5.9 (0.5)	6.0 (0.8)

Note. RT = reaction time.

^aFrom Washington University English Lexicon Project (ellexicon.wustl.edu; Balota et al., 2007).

Appendix C

Descriptive Statistics for Lexical Decision Task Performance

Table C1. Mean (SD) of accuracy and response times for coarse coding items.

Coarse coding item	Accuracy (%)	Response time (ms)
Dominant incompatible		
Short interval	97 (3)	666 (278.5)
Long interval	96 (4)	712 (280.4)
Dominant compatible		
Short interval	98 (6)	664 (304.3)
Long interval	98 (4)	749 (314.4)
Unrelated		
Short interval	88 (18)	736 (308.9)
Long interval	92 (16)	691 (200.8)

Table C2. Mean (SD) of accuracy and response times for suppression items.

Suppression item	Accuracy (%)	Response time (ms)
Subordinate		
Short interval	85 (13)	707 (199.4)
Long interval	90 (12)	728 (222.3)
Dominant		
Short interval	98 (5)	697 (186.3)
Long interval	97 (10)	720 (179.8)
Unrelated		
Short interval	91 (19)	659 (213.5)
Long interval	80 (19)	653 (198.2)