The Neural Basis of Inhibitory Effects of Semantic and Phonological Neighbors in Spoken Word Production

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Abstract

■ Theories of word production and word recognition generally agree that multiple word candidates are activated during processing. The facilitative and inhibitory effects of these "lexical neighbors" have been studied extensively using behavioral methods and have spurred theoretical development in psycholinguistics, but relatively little is known about the neural basis of these effects and how lesions may affect them. This study used voxel-wise lesion overlap subtraction to examine semantic and phonological neighbor effects in spoken word production following left hemisphere stroke. Increased inhibitory effects of near semantic neighbors were associated with inferior frontal lobe lesions, suggesting impaired selection among strongly activated semantically related candidates. Increased inhibitory effects of phonological neighbors were associated with posterior superior temporal and inferior parietal lobe lesions. In combination with previous studies, these results suggest that such lesions cause phonological-to-lexical feedback to more strongly activate phonologically related lexical candidates. The comparison of semantic and phonological neighbor effects and how they are affected by left hemisphere lesions provides new insights into the cognitive dynamics and neural basis of phonological, semantic, and cognitive control processes in spoken word production. ■

INTRODUCTION

Theories of word production and word recognition generally agree that multiple word candidates are activated during processing and the degree of activation is based on their conceptual (semantic) and form (orthographic or phonological) similarity to the target. These similar words are typically called "lexical neighbors," and the consequences of this "parallel activation" are interestingly complex: Neighbors can have both facilitative and inhibitory effects on target processing (for a recent review, see Chen & Mirman, 2012). Chen and Mirman (2012) developed a computational model that provided a unified theory of these contrasting effects. As in other interactive activation and competition models (e.g., McClelland & Rumelhart, 1981), in the Chen and Mirman model, neighbors exert inhibitory effects through lateral inhibitory connections and facilitative effects through recurrent excitatory connections to shared form or semantic units. Their novel development was that strongly active neighbors have net inhibitory effects and weakly active neighbors have net facilitative effects; that is, neighbors' facilitative effects are larger than their inhibitory effects when neighbor activation is low, but the inhibitory effect outweighs the facilitative effect when neighbor activation is high. Simulations of this model captured the qualitative pattern of neighbor effects across a wide range of neighbor types and tasks: (1) facilitative effects of orthographic neighbors on visual word recognition, (2) inhibitory effects of higher frequency neighbors on visual word recognition, (3) inhibitory effects of phonological neighbors on spoken word recognition, (4) facilitative effects of phonological neighbors on word production, (5) inhibitory effects of near semantic neighbors (words that share many semantic features) on word recognition and word production, and (6) facilitative effects of distant semantic neighbors (words that share a few semantic features) on word recognition and word production. All of these results stemmed from the same core principle: strongly active neighbors have a net inhibitory effect and weakly active neighbors have a net facilitative effect. Although lexical neighbor effects have been studied extensively using behavioral methods and have spurred much theoretical development in psycholinguistics, relatively little is known about the neural basis of these effects and how lesions in particular brain areas may affect neighbor effects.

To our knowledge, only one study has examined the neural correlates of phonological neighbor effects in spoken word production (Peramunage, Blumstein, Myers, Goldrick, & Baese-Berk, 2011). This study used fMRI and found reduced activation for words with a minimal pair neighbor (e.g., *cape*, which has the onset minimal pair neighbor *gape*) compared with words without such a neighbor (e.g., *cake*, which has no such neighbor) in posterior superior temporal gyrus (pSTG), supramarginal gyrus (SMG), and inferior frontal gyrus (IFG). Studies that examined phonological neighbors in spoken word recognition have similarly implicated SMG and pSTG

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(Righi, Blumstein, Mertus, & Worden, 2009; Okada & Hickok, 2006; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006), along with IFG (Zhuang, Randall, Stamatakis, Marslen-Wilson, & Tyler, 2011; Righi et al., 2009).

In a study of semantic neighbor effects on word production in 62 participants with aphasia, Mirman (2011) reported an inhibitory effect of near semantic neighbors and, in a secondary analysis, that the size of this inhibitory effect was positively correlated with percent damage in IFG. More generally, semantic processing involves a distributed network of cortical regions (e.g., Binder & Desai, 2011; Patterson, Nestor, & Rogers, 2007) with the anterior temporal lobes (e.g., Schwartz et al., 2009; Patterson et al., 2007) and possibly temporo-parietal cortex (Mirman & Graziano, 2012; Binder & Desai, 2011) playing key integration or "hub" roles.

Lexical neighborhood effects have generally been considered specifically in the framework of language processing, but cognitive control is likely to be an important factor as well. Specifically, lexical neighbor effects in word recognition and word production arise because multiple lexical candidates are activated and, in most tasks (such as naming, word-to-picture matching, etc.), a single word must be selected from these activated candidates. The IFG has been identified as critical to selecting among competing alternatives, particularly in lexical processing tasks (e.g., Nozari, Schwartz, & Coslett, 2012; Schnur et al., 2009; Snyder, Feigenson, & Thompson-Schill, 2007).

Predictions

In summary, the available evidence suggests that lexical neighbor effects involve some combination of a network of regions including phonological (pSTG, SMG) and semantic (ATL) processing and competitive selection (IFG). Greater insight into the particular nature of that combination can inform cognitive theories of lexical processing as well as our understanding of the neural systems that support lexical processing. This study used voxel-wise lesion analyses to examine semantic (Experiment 1) and phonological (Experiment 2) neighbor effects in spoken word production following left hemisphere stroke. Previous studies have used lesion analysis methods to examine semantic and phonological errors in picture naming to investigate the neural basis of semantic and phonological aspects of spoken word production. Here, we take a complementary approach of examining the neural correlates of different effects of semantic and phonological neighborhoods on picture naming accuracy. That is, previous studies have examined differences in output (errors), we examine differences in target properties (neighborhood density). By taking this complementary approach, we aim to provide new insights into the cognitive and neural processes involved in spoken word production.

Near semantic neighbors have been shown to exert inhibitory effects on spoken word production (Mirman, 2011; and visual word recognition: Mirman & Magnuson, 2008), which, according to Chen and Mirman (2012), is because of such neighbors being strongly activated and competing with the target word. Neuroanatomically, the activation of semantic neighbors should be most strongly associated with ATL and selection among lexical candidates should be most strongly associated with IFG. Thus, if IFG lesions are associated with increased inhibitory effects of semantic neighbors that would indicate an effect of difficulty resolving lexical competition. If ATL lesions are associated with increased inhibitory effects of semantic neighbors that would indicate that such lesions caused greater activation of semantic neighbors. In contrast, ATL lesions could be associated with facilitative effects of semantic neighbors (or reduced inhibitory effects), which would indicate that such lesions reduced activation of semantic neighbors.

Phonological neighbors have been shown to exert facilitative effects in spoken word production (e.g., Kittredge, Dell, Verkuilen, & Schwartz, 2008; Vitevitch & Sommers, 2003; Gordon, 2002), which, according to Chen and Mirman (2012), arises because the excitatory resonance between shared phonological representations and phonological neighbors outweighs their weak competition with the target word. On this view, the effect of phonological neighbors would be expected to become inhibitory if the neighbors become more strongly activated and their competition with the target begins to outweigh their facilitative effect. This pattern may arise if lesions in pSTG and SMG, which are associated with lexical-phonological deficits (e.g., Baldo, Katseff, & Dronkers, 2012; Schwartz, Faseyitan, Kim, & Coslett, 2012; Fridriksson et al., 2010; Wilson, Isenberg, & Hickok, 2009; Graves, Grabowski, Mehta, & Gupta, 2008), cause phonological neighbors to become more strongly activated. As for the semantic neighbors, IFG lesions may also cause increased inhibitory effect of phonological neighbors, but this is not as likely because phonological neighbors are only weakly activated and IFG is most important for selecting among strongly active competitors (e.g., Snyder et al., 2007). Finally, on the Chen and Mirman view, increased facilitative effects of phonological neighbors should be difficult to detect because increased activation of phonological neighbors would make their effect inhibitory and reduced activation of phonological neighbors would reduce their effects. Although it is possible that this balance can be shifted to maximize their facilitative effect, it is not clear what kind of lesion would do this.

Analysis Strategy

Lesion analysis is a foundational method in cognitive neuroscience, although the specific techniques have evolved with the advancement of available participant recruitment, neuroimaging, and statistical methods (for historical summary, see, e.g., Rorden & Karnath, 2004). One standard method is voxel-based lesion symptom

mapping (VLSM), in which a *t* test is conducted at each voxel comparing the size of a behavioral effect ("symptom") in participants with versus without a lesion in that voxel. The many repeated *t* tests inflate the probability of false positives, so it is customary to correct for the multiple comparisons (e.g., Bennett, Wolford, & Miller, 2009). This approach has been used successfully to study many aspects of cognition, including spoken word production (e.g., Baldo, Arévalo, Patterson, & Dronkers, 2013; Schwartz et al., 2009, 2011, 2012; Walker et al., 2011; Cloutman et al., 2009). However, because of the nonrandom distribution and inherent spatial coherence of lesions, the power of a statistically rigorous VLSM analysis can be severely limited (e.g., Kimberg, Coslett, & Schwartz, 2007). That is, successful detection of effects requires that the effects be large relative to the size of the sample and detecting smaller or more subtle effects requires unrealistically large samples of participants with brain lesions.

One alternative to VLSM is lesion overlap (or overlay) analysis, in which lesions of individual participants who show a particular symptom are superimposed to find the location(s) that are most strongly associated with the symptom. This approach has a long history in cognitive neuroscience (e.g., Kertesz, Harlock, & Coates, 1979; Hayward, Naeser, & Zatz, 1977) and has continued to be used more recently (e.g., Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Buchsbaum et al., 2011; Shomstein, Lee, & Behrmann, 2010; Badre, Hoffman, Cooney, & D'Esposito, 2009; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Dronkers, 1996). The more recent applications of this method typically involve two important refinements. The first is use of a lesion control group: A particular lesion site may be frequently lesioned in participants with a particular symptom simply because it is more vulnerable for cerebrovascular reasons rather because of a functional link between that site and the behavior. Comparing relative frequency of lesions in a particular site between groups of participants who do versus do not exhibit the symptom is critical for evaluating that site's functional significance. The second is use of a principled difference threshold to define what it means for a lesion site to be more frequently lesioned in one group than the other.

In this report, we take a convergent approach using both uncorrected VLSM and voxel-wise lesion overlap subtraction. The uncorrected VLSM included the full set of participants and was meant as a preliminary, all-inclusive analysis to identify lesion locations that may be functionally relevant. For the lesion overlap subtraction, we adapted the approach described by Kemmerer et al. (2012): We divided participants into two groups based on effect size and computed voxel-wise lesion probability difference maps. These maps show, at each voxel, the difference between (a) the proportion of participants with a large effect size who had a lesion in that voxel and (b) the proportion of participants with a small effect size who had a lesion in that voxel. The maps were then thresholded at 40% to identify voxels that showed the largest group differences; that is, we considered only those voxels where at least 40% more participants in one group had a lesion than participants in the other group did. For the group sizes in this study, this threshold corresponds to a χ^2 test statistically significant at the .01 level. This threshold also imposes a minimum number of lesions that must be present in a voxel for it to be included in the analysis: At least 40% of one group must have lesions in a voxel for it to be included in the analysis. Given approximately equal group sizes, the analysis only included voxels where at least 20% of the overall sample (both groups combined) had a lesion. This lower limit is important for producing stable results, much like "effective coverage maps" (Kemmerer et al., 2012). In addition, the lesion overlap subtraction method has the advantage that the groups can be matched on various control variables, thus controlling for effects such as severity in a way that is more direct and effective than is possible in VLSM.[1]

Finally, defining "high" versus "low" effect size groups for the lesion overlap subtraction requires setting arbitrary boundaries. In general, this creates a trade-off between statistical power (higher power requires larger groups) and effect size (larger differences in effect sizes require more extreme boundaries, which produces smaller groups). We used a quantile approach and compared (approximately) the top and bottom one third of participants—that is, the participants who showed the largest neighborhood facilitation effects with those that showed the largest neighborhood inhibition effects. Dividing the sample into thirds and excluding the middle group represents a reasonable compromise between strength of the manipulation (focus on participants with the strongest facilitation or inhibition effects) and statistical power (maximize the number of participants in the analysis). To verify that the results were not due to peculiarities of that particular group definition, we repeated the analysis using a more extreme comparison: the one tenth with the largest facilitation effects versus the one tenth with the largest inhibition effects and using a stricter probability difference threshold (60%).

EXPERIMENT 1: SEMANTIC NEIGHBORS

Methods

Materials

The spoken word production data were drawn from the 175-item Philadelphia Picture Naming Test (PNT; Roach, Schwartz, Martin, Grewal, & Brecher, 1996). Standard administration and scoring procedures were used.[2] As in Mirman (2011), near semantic neighbors were defined as having greater than 0.4 cosine similarity between semantic feature vectors based on the McRae, Cree, Seidenberg, and McNorgan (2005) semantic feature generation norms. The semantic feature norms were available for 95 of the 175 items in the PNT, so the analyses were restricted to

Table 1. Mean (*SD*) Target Word Properties for Near Semantic Neighborhood Manipulation

	Few	*Many*	*t*	*p*
No. of words	36	36	–	–
No. of semantic neighbors	0 (0)	3.3 (3.9)	5.14	<.0001
No. of features	14.4 (2.3)	14.9 (2.4)	0.95	*ns*
HAL word frequency	8.7 (1.3)	8.8 (1.4)	0.23	*ns*
ANC word frequency	1.0 (0.5)	1.1 (0.5)	0.86	*ns*
No. of phonemes	4.2 (1.2)	4.2 (1.4)	0.0	*ns*
Phonological neighborhood density	13.3 (13.2)	12.7 (13.8)	0.18	*ns*
Cohort density	50.4 (42.6)	43.1 (40.8)	0.74	*ns*

these 95 items. From this set of 95 target words, two groups of words were selected such that they maximally differed in number of near semantic neighbors and were matched in log-transformed word frequency (based on the HAL frequency norms [Lund & Burgess, 1996; see also Balota et al., 2007] and the spoken portion of the American National Corpus [ANC; Ide & Suderman, 2004]), word length (number of phonemes), number of semantic features (e.g., Pexman, Holyk, & Monfils, 2003; see also Mirman & Magnuson, 2008), and number of phonological neighbors based on the one-phoneme rule (i.e., number of words that can be formed by the addition, deletion, or substitution of a single phoneme; Luce & Pisoni, 1998; Luce, 1986; phonological neighborhoods were evaluated using the spoken portion of the ANC). There were 36 words in each set; the properties of the two sets of words are summarized in Table 1 and the full list of target words is provided in Appendix A.

Participants

The full sample of participants consisted of 106 individuals who had been diagnosed acutely with aphasia secondary to left hemisphere stroke, were at least 3 months post onset and who had completed the PNT and CT or MRI imaging. Data from this sample have been reported in VLSM analyses of phonological (Schwartz et al., 2012) errors in picture naming. Participants had no major psychiatric or neurological comorbidities; were premorbidly right handed; had English as their primary language, adequate vision, and hearing (with or without correction); and had some ability to name pictures (at least one correct response of 175 PNT trials). For each of the participants, the near semantic neighbor effect size was computed as the picture naming accuracy difference between the items with few near semantic neighbors and the items with many near semantic neighbors. The distribution of near semantic neighbor effect sizes is shown in Figure 1A.

To define groups for the lesion overlap subtraction analysis, first, 11 participants with unusually large lesions (>2*SD* above the mean lesion size) or unusually severe aphasia (>2*SD* below the mean Western Aphasia Battery Aphasia Quotient [WAB AQ; Kertesz, 1982]) were excluded from analyses. Then, the top and bottom 30 participants based on near semantic neighbor effect size were selected

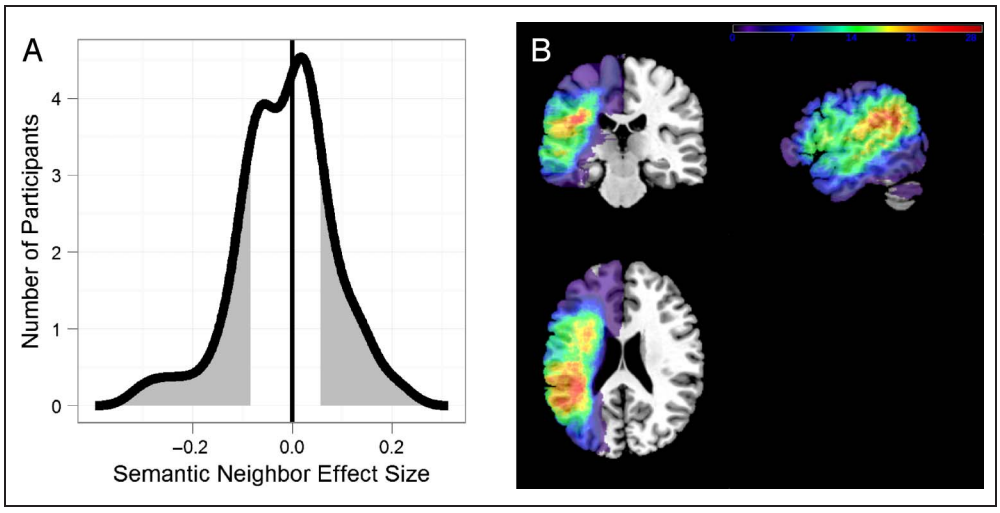

Figure 1. (A) Distribution of semantic neighbor effect sizes in proportion correct picture naming (i.e., negative values correspond to inhibitory effect of neighbors). Shaded regions correspond to participants selected for lesion overlap subtraction analysis. (B) Coverage map for semantic neighbor lesion overlap subtraction at $x = -52, y = 7, z = 4$.

(i.e., approximately the top and bottom one third of the overall group). Finally, participants were removed to maximize the effect size difference between groups and match the groups on lesion size and aphasia severity as measured by WAB AQ (both $t < 1, p > .5$). The groups also did not differ on overall picture naming accuracy or on the proportion of semantic, formal, or nonword errors (all $p > .25$). See Appendix B for group means and standard deviations. The group formation was done while blinded to lesion location so this information could not bias which participants were removed. The selected groups are represented by the shaded regions in Figure 1A. The resulting Inhibition group ($n = 25$) had higher accuracy on words with few near semantic neighbors than words with many near semantic neighbors ($M_{DIFF} = 13.1\%$, $SD_{DIFF} = 6.7\%$; i.e., near semantic neighbors inhibited performance in this group) whereas the Facilitation group ($n = 22$) showed the reverse effect: higher accuracy on words with many near semantic neighbors than words with few near semantic neighbors ($M_{DIFF} = 10.4\%$, $SD_{DIFF} = 4.9\%$; i.e., near semantic neighbors facilitated performance in this group). This group difference was highly statistically significant ($t = 13.81, p < .0001$).

Lesion Analysis

Image acquisition, lesion segmentation, and template registration methods followed the procedures established in previous work by our research group (Schwartz et al., 2009, 2011, 2012; Schnur et al., 2009), and detailed descriptions are available there (particularly Schwartz et al., 2012, who reported data from the same sample). Briefly, lesion location was assessed based on MRI ($n = 60$) or CT ($n = 46$) brain scans. Lesions imaged with MRI were manually segmented on each participant's T1-weighted structural image by a trained technician blinded to the behavioral data and registered to the Montreal Neurological Institute space Colin27 template by an automated process (Avants, Schoenemann, & Gee, 2006). Lesions imaged with CT were drawn by an experienced neurologist directly onto the Colin27 template after rotating it (pitch only) to match the approximate slice plane of the participant's scan. Lesion volume was calculated by using the digital Brodmann atlas available with MRIcron and using tools available in the VoxBo software package. The VLSM analysis consisted of a t test at every voxel comparing the semantic neighbor effect size of participants with vs. without a lesion in that voxel.

Voxel-wise Lesion Overlap Subtraction

Figure 1B shows the coverage map (number of lesions in each voxel) for the 47 participants in the lesion overlap subtraction analysis (25 in the Inhibition group and 22 in the Facilitation group). The lesions covered essentially the entire left hemisphere, with particular concentration in the peri-sylvian region. Note, however, that coverage was comparatively poor in the anterior temporal lobe, indicating that there was limited power to evaluate the predictions regarding ATL involvement in semantic neighborhood effects. As described above, for each voxel, we computed the difference between the proportion of the Facilitation group participants who had a lesion in that particular voxel compared with the proportion of the Inhibition group participants who had a lesion in that particular voxel (and vice versa). To focus on just the voxels where this proportion difference was large, we only consider voxels where this difference was at least 40% of group size (i.e., 9 participants for the Facilitation group, 10 participants for the Inhibition group). To further reduce the likelihood of interpreting possibly spurious findings and to take into consideration the fact that the inherent spatial coherence of lesions emphasizes contiguous effects, we focus our discussion on brain regions where at least 10% of the voxels in the region met the 40% difference threshold. Brain regions were defined by the Automated Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002).

Results and Discussion

Figure 2 shows the results of the uncorrected VLSM analysis that included the entire set of participants ($n = 106$) and the continuous measure of effect size (i.e., not dividing participants into Inhibition and Facilitation groups). These results suggested that the primary inhibitory effects were in the frontal lobe (Figure 2A) and that the facilitative effects were in posterior parietal, occipital, and superior medial frontal regions (the latter two are likely to reflect artifacts of very large lesions). The lesion overlap subtraction analyses examined this more closely.

The voxel-wise lesion overlap subtraction results are shown in Figure 3. A total of 20,522 voxels met the 40% threshold for the "Inhibition > Facilitation" comparison (i.e., Inhibition group more likely to have lesion than Facilitation group; Figure 3A). The largest concentration of these voxels was in the precentral gyrus (8543 voxels, 30.3% of region) and neighboring regions, including the IFG pars opercularis (2866 voxels, 34.7% of region), the postcentral gyrus (3929 voxels, 12.7% of region), and the Rolandic operculum (1567 voxels, 19.7% of region). For the reverse contrast (Facilitation > Inhibition, Figure 3B), only 914 voxels met the 40% threshold with no clusters meeting the 10% of region threshold (the largest cluster was in the angular gyrus: 617 voxels, 6.6% of region; the arrow in Figure 3B highlights this small cluster). As an internal replication, we repeated the analysis using a more restrictive group definition (upper and lower 10% of effect size) and a higher difference threshold (60% of group size). The results showed the same qualitative pattern: increased inhibitory effects associated primarily with inferior frontal lesions and increased facilitative effects not substantively associated with any lesion location.

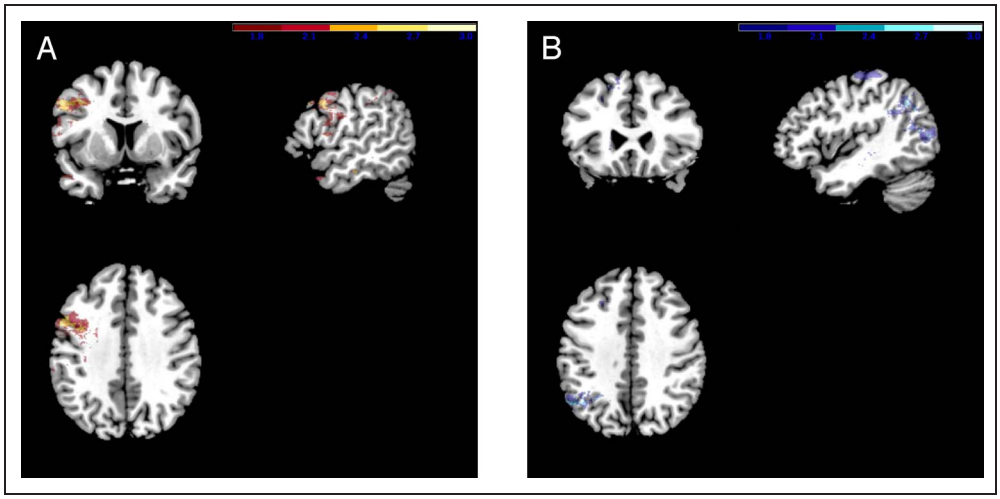

Figure 2. VLSM of near semantic neighbor effects (uncorrected t maps). Larger t values (brighter colors) correspond to larger inhibitory (A; $x = -55$, $y = -25$, $z = 17$) or facilitative (B; $x = -44$, $y = 42$, $z = 21$) effects of near semantic neighbors in participants with a lesion in that voxel than participants without a lesion in that voxel. Only $t > 1.66$ ($p < .05$) values are shown.

These results indicate that damage to inferior frontal lobe structures (and perhaps the anterior inferior parietal lobe) increases the inhibitory effect of near semantic neighbors on word production. As discussed in the Predictions section, this result suggests that the increased inhibitory effect of near semantic neighbors was because of decreased ability to select among competing alternatives resulting from IFG lesions. This result converges with the previous report of a positive correlation between inhibitory effects of near semantic neighbors and percent damage in IFG (Mirman, 2011).

We did not observe an effect of ATL lesion, but only 11 of the 47 participants had substantive lesions in ATL (i.e., including at least 10% of either the superior or middle temporal pole; see Figure 1B), and our 40% difference threshold required a group difference of at least 9–10 participants, so it was difficult to detect an ATL effect with so few ATL lesions (nearly all of the participants with ATL lesions would have had to be in one group or the other). Thus, the present data cannot rule out the possibility that ATL lesions do modulate semantic neighborhood effects, either in a facilitative or inhibitory direction, but the results can shed light on the role of IFG in word production. Related investigations of semantically related errors in picture naming (e.g., *cow–horse*) have reported that lesions in anterior and middle temporal lobe increase the likelihood of such errors (Walker et al., 2011; Schwartz et al., 2009). These studies also found weaker effects of IFG lesions that were eliminated after controlling for nonverbal semantic deficits, which they interpreted as indicating that IFG is involved in conceptualization whereas the ATL is involved in lexical-semantic access.

Our results further clarify the role of IFG in word production, namely its involvement in selecting among competing alternatives. Although the competitive selection demands of picture naming are relatively low, they are increased when naming a target with many near semantic neighbors, which is why individuals with IFG lesions show particularly large inhibitory effects of near semantic neighbors. Because selection errors will frequently—but not always—lead to semantic errors and semantic errors

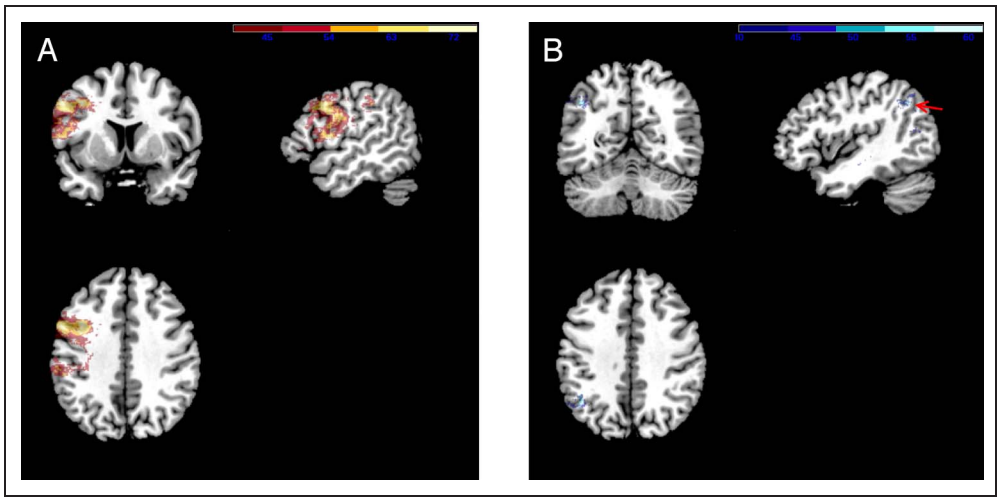

Figure 3. Voxel-wise lesion overlap subtraction maps of near semantic neighbor effects. (A) Voxels where Inhibition group had at least 40% more lesions than the Facilitation group did; at $x = -53$, $y = -25$, $z = 20$. (B) Voxels where the Facilitation group had at least 40% more lesions than the Inhibition group did (arrow highlights the small cluster of voxels meeting this threshold); at $x = -44$, $y = 42$, $z = 21$.

can be produced in other ways, examination of semantic errors provides a less direct window on the consequences of competitive selection deficits. Nevertheless, because of impaired competitive selection, IFG lesions should tend to increase the likelihood of semantic errors, which converges with more recent analyses of a larger group of participants in which the IFG lesion effect on semantic errors survived controlling for nonverbal semantic deficits (Schwartz et al., 2012, particularly their Figure 7).

To interpret these findings fully, it is important to examine whether inhibitory and facilitative effects of a different sort of lexical neighbors have similar or different lesion correlates. To this end, Experiment 2 used the same approach to examine phonological neighbor effects.

EXPERIMENT 2: PHONOLOGICAL NEIGHBORS

Methods

Materials

The spoken word production data were drawn from the same set of PNT data. Phonological neighborhood density was defined as the summed log frequency of the target word and all words that share the word onset (i.e., same initial two phonemes; called "cohort density"; see Magnuson, Dixon, Tanenhaus, & Aslin, 2007). This measure was selected because word onsets have particular importance in word production (e.g., Goldrick, Folk, & Rapp, 2010) and because preliminary studies suggested that this phonological neighborhood measure had the biggest impact on picture naming performance in a large group of participants with aphasia. The full set of PNT target words was divided based on a median split on cohort density and then a few words were removed to create two equal-sized ($n = 85$) groups of words that were matched on (log-transformed) word frequency, word length, and, when available, number of near semantic neighbors (using the same definition and norms as in Experiment 1). Measures of phonological neighborhood density tend to be highly correlated, so these two sets of words also differed in number of phonological neighbors as defined by the one-phoneme rule and the summed log frequency of the target word and its one-phoneme rule neighbors. In other words, the two groups of words differed based on just about any measure of phonological neighborhood and were matched on word frequency, word length, and semantic neighborhood. The properties of the two sets of words are summarized in Table 2 and the full list of items is provided in Appendix A.

Participants

The full sample of participants consisted of the same 106 individuals as Experiment 1, and groups for the lesion overlap subtraction analysis were defined using the same approach. Phonological neighbor effect size was computed as the difference between picture naming accuracy for words with many phonological neighbors and words with few phonological neighbors. The top and bottom 30 participants based on this effect size were selected, and then participants were removed to maximize the effect size difference between groups and match the groups on lesion size ($t < 1, p > .8$) and aphasia severity ($t = 1.58, p > .1$). The groups also did not differ on overall picture naming accuracy or on the proportion of semantic, formal, or nonword errors (all ps $> .1$). See Appendix B for group means and standard deviations. The groups were formed while blinded to lesion location. The overall distribution of phonological neighbor effect sizes is shown in Figure 4A, with the shaded regions corresponding to the selected groups. The resulting Inhibition group ($n = 27$) had higher accuracy on words with few phonological neighbors than words with many phonological neighbors ($M_{DIFF} = 3.5\%$, $SD_{DIFF} = 3.7\%$; i.e., phonological neighbors inhibited performance in this group) whereas the Facilitation group ($n = 30$) showed the reverse effect: higher accuracy on words with many phonological neighbors than words with few phonological neighbors ($M_{DIFF} = 8.2\%$, $SD_{DIFF} = 3.4\%$; i.e., phonological neighbors facilitated performance in this

Table 2. Mean (*SD*) Target Word Properties for Phonological Neighborhood Manipulation

	Few	*Many*	*t*	*p*
No. of words	85	85	–	–
Cohort density	14.9 (8.7)	73.2 (36.0)	14.5	<.0001
No. of phonological neighbors	10.2 (8.8)	14.1 (11.3)	2.51	<.05
Phonological neighborhood density	11.8 (12.8)	16.2 (15.2)	2.05	<.05
HAL word frequency	8.7 (1.5)	9.1 (1.6)	1.51	*ns*
ANC word frequency	1.1 (0.7)	1.2 (0.7)	0.94	*ns*
No. of phonemes	4.3 (1.7)	4.4 (1.5)	0.09	*ns*
No. of semantic neighbors	2.0 (3.7)	1.6 (3.7)	0.59	*ns*

Number of semantic neighbors data were only available for 92 of the 170 words (43 in the Few condition, 49 in the Many condition).

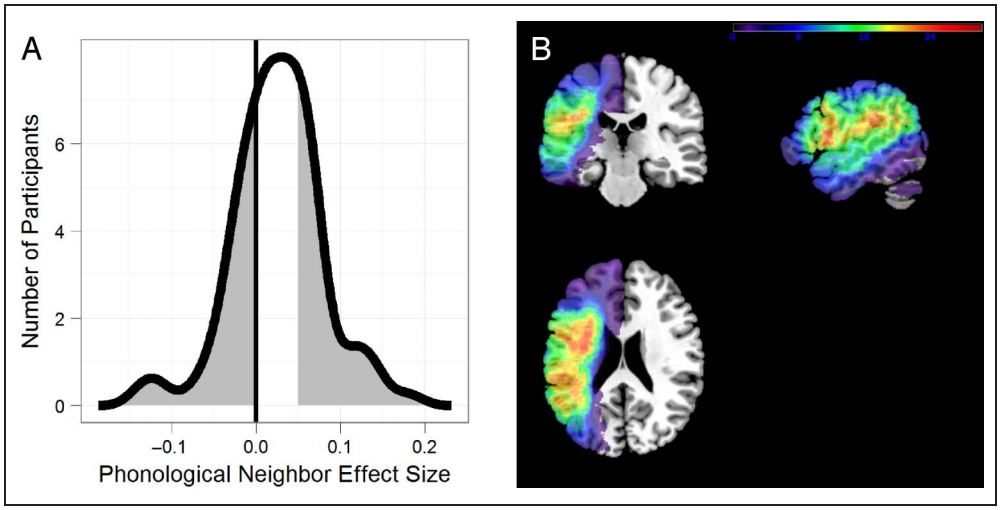

Figure 4. (A) Distribution of phonological neighbor effect sizes in proportion correct picture naming (i.e., positive values correspond to facilitative effect of neighbors). Shaded regions correspond to participants selected for lesion overlap subtraction analysis. (B) Coverage map for phonological neighbor lesion overlap subtraction at $x = -52$, $y = 7, z = 4$.

group). This difference was highly statistically significant ($t = 12.42, p < .0001$). These groups did not differ in their near semantic neighbor effect size (both groups exhibited an approximately 2% inhibition effect, $t < 1, p > .9$); nor did the groups in Experiment 1 differ in the cohort density effect size (both groups exhibited an approximately 2% facilitation effect, $t < 1, p > .9$).

Lesion Analysis and Voxel-wise Lesion Overlap Subtraction

Image acquisition, lesion segmentation, and template registration methods were the same as in Experiment 1, as was the voxel-wise lesion overlap subtraction method. Figure 4B shows the coverage map for the full set of 57 participants in this analysis, which was nearly identical to Experiment 1. As in Experiment 1, we only report voxels where the subtraction difference was at least 40% of group size (11 for the Inhibition group, 12 for the Facilitation group) and focus our discussion on brain regions where at least 10% of voxels met this 40% threshold.

Results and Discussion

Uncorrected VLSM analysis examining the entire set of participants ($n = 106$) and the continuous measure of effect size (i.e., not dividing participants into Inhibition and Facilitation groups) suggested that the primary inhibitory effects were in the posterior superior temporal and inferior parietal lobes (Figure 5A), and there were virtually no voxels that showed a facilitative effect difference even at the uncorrected threshold (Figure 5B).

The voxel-wise lesion overlap subtraction results for cohort density effect size are shown in Figure 6. A total of 6362 voxels met the 40% threshold for the "Inhibition > Facilitation" comparison (i.e., Inhibition group more likely to have lesion than Facilitation group; Figure 6A). Almost all (89.4%) of these voxels were in the posterior

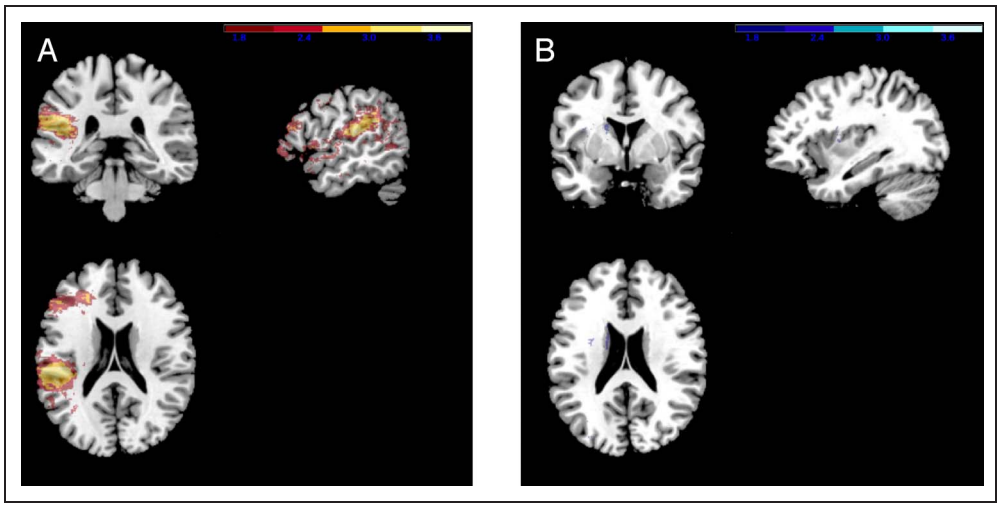

Figure 5. VLSM of near phonological neighbor effects (uncorrected t maps). Larger t values (brighter colors) correspond to larger inhibitory (A; $x = -55, y = 16, z = 1$) or facilitative (B; $x = -35, y = -18, z = 3$) effects of phonological neighbors in participants with a lesion in that voxel than in participants without a lesion in that voxel. Only $t > 1.66$ ($p < .05$) values are shown.

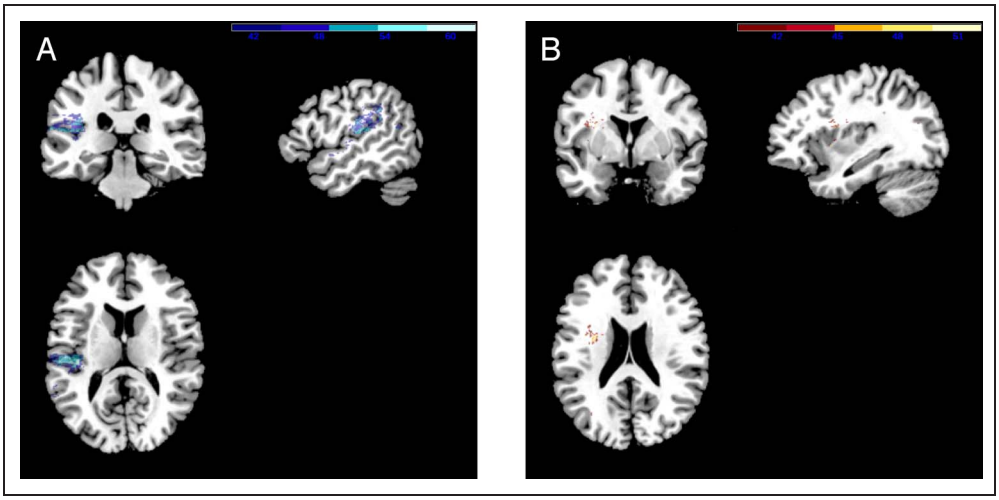

Figure 6. Voxel-wise lesion overlap subtraction maps of phonological neighbor effects. (A) Voxels where the Inhibition group had at least 40% more lesions than Facilitation group did; at $x = -50$, $y = 12$, $z = 6$. (B) Voxels where the Facilitation group had at least 40% more lesions than the Inhibition group did; at $x = -35$, $y = -18$, $z = 3$.

superior temporal and inferior parietal lobes, including the pSTG (2189 voxels, 12.0% of the region), SMG (1786 voxels, 18.0% of the region), and Heschl's gyrus (462 voxels, 25.6% of the region) and extending into the Rolandic operculum (1250 voxels, 15.8% of the region). For the reverse contrast (Facilitation > Inhibition, Figure 6B), only 82 voxels met the 40% threshold with no region substantially affected (no region had more than 0.5% of voxels that met this threshold). As in Experiment 1, this qualitative pattern was replicated using a more restrictive group definition (upper and lower 10% of effect size) and a higher difference threshold (60% of group size): Increased inhibitory effects were associated with pSTG and SMG lesions and increased facilitative effects not substantively associated with any lesion location.

These results indicate that damage to posterior superior temporal lobe and inferior parietal lobe structures increases the inhibitory effect of phonological neighbors on word production. This finding is consistent with prior evidence that SMG and pSTG are sensitive to effects of phonological neighborhood density (Peramunage et al., 2011; Righi et al., 2009; Okada & Hickok, 2006; Prabhakaran et al., 2006) and converges with evidence that lesions in these regions correlate with phonological impairments in aphasia (e.g., Baldo et al., 2012; Schwartz et al., 2012; Fridriksson et al., 2010; Wilson et al., 2009; Graves et al., 2008). This region is also associated with mapping between phonological representations and articulatory representations in speech perception and speech production (e.g., Gow, 2012; Hickok, 2012; Hickok & Poeppel, 2007). In the framework developed by Chen and Mirman (2012), the current results suggest that posterior superior temporal and inferior parietal lesions increased activation of phonological neighbors. This increase in phonological neighbor activation caused their lateral inhibition effect to outweigh their recurrent facilitation effect, thus making their net effect on target processing inhibitory (see also Chen & Mirman, under review, for behavioral evidence of this sort of reversal in spoken word comprehension). In addition, increased activation of phonological neighbors is consistent with recent voxel-based lesion symptom mapping evidence that lesions in this region are associated with increased production of phonologically related errors in picture naming (Schwartz et al., 2012).

GENERAL DISCUSSION

Voxel-wise lesion overlap subtraction was used to examine how brain lesions impact the effects of semantic and phonological lexical neighbors on spoken word production. Starting with a large group of individuals with aphasia secondary to left hemisphere stroke, for each type of neighborhood effect, two severity-matched groups of individuals were identified: a group that exhibited maximal facilitation effects and a group that exhibited maximal inhibition effects. A lesion overlap subtraction method was then used to identify brain regions where lesions tended to produce inhibition or facilitation effects. No lesion locations convincingly corresponded to facilitation effects. Inferior frontal lobe lesions tended to increase the inhibitory effect of near semantic neighbors; posterior superior temporal and inferior parietal lobe lesions tended to increase the inhibitory effect of phonological neighbors (summarized in Figure 7). This pattern also emerged when a more restrictive group definition was used and in uncorrected VLSM analyses using a continuous measure of effect size in the full set of 106 participants. Given the convergence between all three analysis methods, the results are unlikely to be because of peculiarities of the group assignment or comparison procedure.

We interpret these results in the context of the Chen and Mirman (2012) computational model account of lexical neighbor effects. The core principle of that account is that lexical neighbors exert both inhibitory and facilitative effects, with facilitative effects dominating when neighbor activation is low and inhibitory effects dominating when neighbor activation is high. Because picture naming is a

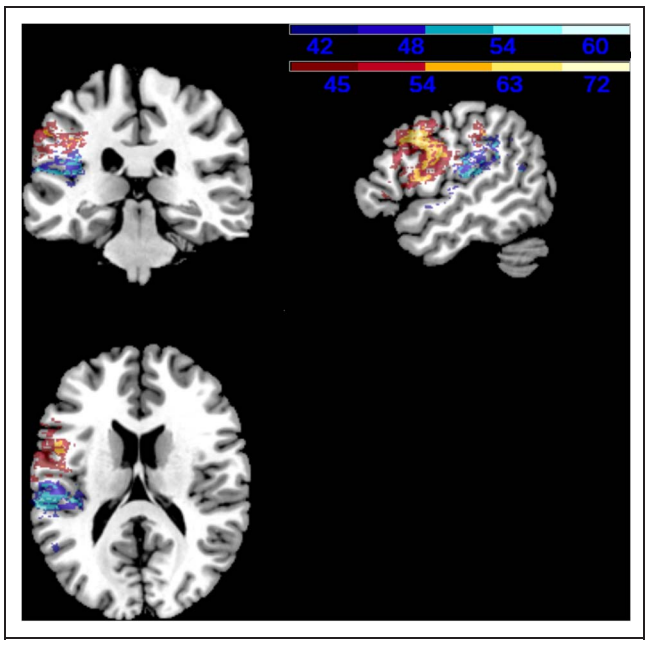

Figure 7. Voxel-wise lesion overlap subtraction proportion difference maps (at $x = -52$, $y = 12$, $z = -2$) of inhibitory effects of semantic (red–yellow) and phonological (blue–white) neighbors in spoken word production.

semantically driven task, near semantic neighbors are expected to be highly activated and already exerting a net inhibitory effect (Mirman, 2011). A large body of evidence indicates that inferior frontal damage impairs cognitive control mechanisms involved in selection among competing alternatives (e.g., Nozari et al., 2012; Schnur et al., 2009; Snyder et al., 2007); the current evidence suggests that this cognitive control impairment exacerbates the inhibitory effect of near semantic neighbors.

Several functional imaging studies have documented the involvement of posterior superior temporal and inferior parietal regions in phonological-lexical processing, including phonological neighbor effects (Peramunage et al., 2011; Righi et al., 2009; Okada & Hickok, 2006; Prabhakaran et al., 2006). Furthermore, damage to pSTG and SMG is known to cause phonological processing deficits (Baldo et al., 2012; Schwartz et al., 2012; Fridriksson et al., 2010; Wilson et al., 2009). Efforts to develop a theoretical framework for speech processing have cast this region as a "dorsal lexicon" that is involved in mapping between phonological and articulatory representations (e.g., Gow, 2012; Hickok, 2012; Hickok & Poeppel, 2007). The present finding that damage to this region increases the inhibitory effect of phonological neighbors in spoken word production is consistent with these past findings in the general sense that it reflects a phonological-lexical impairment. In the context of the theoretical and computational framework developed by Chen and Mirman (2012), the increased inhibitory effect provides additional elaboration: When these brain regions are lesioned, phonological-lexical feedback more strongly activates phonological neighbors, causing their inhibitory effect to outweigh their facilitative effect. Although the specific reason for this increased activation is not clear, one possibility is that the downstream mapping from phonological targets to articulatory motions is impaired, resulting in a build-up of phonological-lexical feedback that increases activation of phonological neighbors. This possibility is consistent with Hickok's (2012) recent proposal that this region (which he calls Spt: Sylvian fissure at the parieto-temporal boundary) is involved in mapping between phonological targets and motor syllable programs.

Unlike the inhibitory effect of semantic neighbors, IFG lesions did not appear to increase the inhibitory effects of phonological neighbors, suggesting that the inhibitory effect of phonological neighbors was not because of deficits of selection among competing alternatives. As discussed in the Introduction, in typical (neurologically intact) spoken word production, phonological neighbors are weakly activated by phonological-to-lexical feedback. This weak activation may only weakly engage competitive selection mechanisms supported by IFG, which are thought to be particularly important for resolving competition among strongly activated candidates (e.g., Snyder et al., 2007). It is possible that the conjunction of SMG/pSTG and IFG damage would cause particularly strong inhibitory effects of phonological neighbors if phonological neighbors were more strongly activated because of SMG and pSTG damage and competitive selection mechanisms were deficient because of IFG damage. However, the present subtraction methodology is not well suited to detecting such conjunctions. A multivariate or multivoxel pattern analysis method would be necessary, but such methods are only beginning to be developed for voxel-wise lesion analysis (e.g., Smith, Clithero, Rorden, & Karnath, 2013). More importantly, lesions that include both posterior temporal and inferior frontal regions would be quite large and would likely cause severe word processing deficits, so it is not clear that such a conjunction could be distinguished from an overall effect of lesion size and/or cognitive deficit severity.

We did not observe any lesion location that was convincingly associated with increased facilitative effects of either semantic or phonological neighbors. In the case of phonological neighbors, this may be because of the very narrow window for increasing their typical facilitative effect. Increasing the facilitative effect of phonological neighbors requires optimizing the balance between more neighbor activation, which would make their effect inhibitory, and less neighbor activation, which would eliminate their effect. In the present data, there is no evidence that lesions in a particular location optimize this balance. In the case of semantic neighbors, ATL—because of its association with semantic deficits—was the primary candidate for a lesion location that might reduce the activation of semantic neighbors, thus making their effect less inhibitory and more facilitative. First, it is also possible that

ATL lesions would cause the opposite result because semantic deficits may equalize the activation between the target and its semantic neighbors, thus making their effect more inhibitory. Second, there were relatively few participants in the semantic neighbor analysis with substantive lesions in ATL, so it was difficult to detect an ATL effect with so few ATL lesions.[3] Thus, the present data cannot rule out the possibility that ATL lesions do modulate semantic neighborhood effects, either in a facilitative or inhibitory direction.

Parallel activation of multiple related candidates is a core principle of lexical processing theories. The present results demonstrate the different ways that lesions can disrupt the dynamics of this process. The inhibitory effects of semantic neighbors were increased by inferior frontal lobe lesions, suggesting impaired competitive selection mechanisms. Inferior frontal lesions did not cause comparable increases in inhibitory effects of phonological neighbors because phonological neighbors are only weakly activated during spoken word production. Rather, posterior superior temporal and inferior parietal lesions caused an increase in inhibitory effects of phonological neighbors, indicating that this sort of damage allows phonological-to-lexical feedback to more strongly activate lexical items that are phonologically similar to the target. These findings further refine our understanding of the functional and neural coordination of interactive activation, competition, and response selection mechanisms in spoken word production.

APPENDIX A: COMPLETE TARGET WORD LISTS

All items are taken from the Philadelphia Naming Test (Roach et al., 1996). Test administration and scoring details, along with the complete set of pictures, are available at: www.mrri.org/philadelphia-naming-test.

Experiment 1: Semantic Neighbors

Few: anchor, balloon, bed, belt, bench, book, bread, bridge, camel, candle, carrot, clock, closet, comb, corn, crown, desk, drum, football, fork, hose, key, kite, lamp, pencil, pig, pyramid, rake, rope, ruler, skis, slippers, table, tent, tractor, whistle.

Many: apple, ball, banana, bottle, bowl, broom, bus, cake, cannon, celery, chair, church, dog, door, elephant, frog, hammer, horse, knife, necklace, octopus, owl, pear, pen, piano, pie, pillow, pumpkin, scarf, scissors spider, squirrel, train, turkey, van, wagon.

Experiment 2: Phonological Neighbors

Few: ambulance, anchor, apple, ball, binoculars, book, boot, bread, bride, bridge, broom, chair, cheerleaders, chimney, church, clock, closet, clown, cow, cowboy, cross, crown, crutches, dinosaur, dog, door, dragon, drum, ear, elephant, eskimo, eye, flashlight, flower, foot, football, frog, garage, ghost, glass, glove, goat, grapes, hair, house, iron, key, kite, knife, mountain, nail, necklace, nurse, octopus, owl, pie, pineapple, pipe, pirate, plant, queen, ruler, saw, scale, scarf, shoe, skis, skull, slippers, snake, sock, spider, spoon, squirrel, strawberries, toilet, towel, train, tree, vase, vest, volcano, wagon, whistle, zipper.

Many: baby, balloon, banana, basket, bat, beard, bed, bell, belt, bench, bone, bottle, bowl, bus, butterfly, cake, calendar, camel, camera, can, candle, cane, cannon, carrot, cat, celery, comb, corn, desk, dice, duck, fan, fireman, fireplace, fish, fork, hammer, hand, harp, hat, heart, helicopter, horse, hose, king, kitchen, lamp, leaf, letter, lion, man, map, microscope, monkey, mustache, nose, pear, pen, pencil, piano, pig, pillow, pumpkin, pyramid, rake, ring, rope, saddle, sailor, sandwich, scissors, seal, star, suit, sun, table, tent, top, tractor, turkey, typewriter, van, waterfall, well, window.

APPENDIX B: PARTICIPANT GROUP MEANS (*SD*)

	Experiment 1: Semantic Neighbors		*Experiment 2: Phonological Neighbors*	
	Inhibition	*Facilitation*	*Inhibition*	*Facilitation*
n	25	22	27	30
WAB AQ	75.4 (14.8)	76.8 (15.8)	71.8 (16.6)	78.3 (14.1)
Lesion volume (cc)	99.8 (69.5)	87.8 (59.4)	86.7 (71.5)	83.0 (62.3)
PNT				
% Correct	70.0 (20.8)	63.2 (25.5)	62.0 (28.1)	69.4 (21.6)
% Semantic errors	3.4 (2.0)	4.0 (2.5)	3.1 (2.2)	3.7 (2.8)
% Formal errors	3.4 (4.2)	5.2 (6.5)	5.6 (6.6)	3.3 (3.9)
% Nonword errors	8.5 (7.7)	9.7 (10.8)	11.7 (11.4)	8.7 (8.9)

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Notes

1. It is possible to enter control variables into VLSM, but this tends to very severely reduce power and (typically) only controls for linear effects of the control variables, whereas it is quite possible that factors like overall severity, lesion size, etc., have nonlinear effects on behavioral outcomes.

2. Full test materials and procedures are available at www.mrri.org/philadelphia-naming-test.

3. There was good coverage throughout the peri-sylvian regions, including IFG, STG, angular gyrus, and SMG, so the contrast between the IFG effect for semantic neighbors and pSTG/SMG effect for phonological neighbors cannot be due simply to power differences.

REFERENCES

Avants, B., Schoenemann, P. T., & Gee, J. C. (2006). Lagrangian frame diffeomorphic image registration: Morphometric comparison of human and chimpanzee cortex. *Medical Image Analysis, 10,* 397–412.

Badre, D., Hoffman, J., Cooney, J. W., & D'Esposito, M. (2009). Hierarchical cognitive control deficits following damage to the human frontal lobe. *Nature Neuroscience, 12,* 515–522.

Baldo, J. V., Arévalo, A., Patterson, J. P., & Dronkers, N. F. (2013). Grey and white matter correlates of picture naming: Evidence from a voxel-based lesion analysis of the Boston Naming Test. *Cortex, 49,* 658–667.

Baldo, J. V., Katseff, S., & Dronkers, N. F. (2012). Brain regions underlying repetition and auditory-verbal short-term memory deficits in aphasia: Evidence from voxel-based lesion symptom mapping. *Aphasiology, 26,* 338–354.

Balota, D. A., Yap, M. J., Cortese, M. J., Hutchison, K. A., Kessler, B., Loftis, B., et al. (2007). The English Lexicon Project. *Behavior Research Methods, 39,* 445–459.

Bennett, C. M., Wolford, G. L., & Miller, M. B. (2009). The principled control of false positives in neuroimaging. *Social Cognitive and Affective Neuroscience, 4,* 417–422.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15,* 527–536.

Buchsbaum, B. R., Baldo, J. V., Okada, K., Berman, K. F., Dronkers, N., D'Esposito, M., et al. (2011). Conduction aphasia, sensory-motor integration, and phonological short-term memory—An aggregate analysis of lesion and fMRI data. *Brain and Language, 119,* 119–128.

Chen, Q., & Mirman, D. (2012). Competition and cooperation among similar representations: Toward a unified account of facilitative and inhibitory effects of lexical neighbors. *Psychological Review, 119,* 417–430.

Chen, Q., & Mirman, D. (under review). Interaction between phonological and semantic representations: Time matters.

Cloutman, L., Gottesman, R., Chaudhry, P., Davis, C., Kleinman, J. T., Pawlak, M., et al. (2009). Where (in the brain) do semantic errors come from? *Cortex, 45,* 641–649.

Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. R. (2004). Neural systems behind word and concept retrieval. *Cognition, 92,* 179–229.

Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature, 384,* 159–161.

Fridriksson, J., Kjartansson, O., Morgan, P. S., Hjaltason, H., Magnusdottir, S., Bonilha, L., et al. (2010). Impaired speech repetition and left parietal lobe damage. *The Journal of Neuroscience, 30,* 11057–11061.

Goldrick, M., Folk, J. R., & Rapp, B. (2010). Mrs. Malaprop's neighborhood: Using word errors to reveal neighborhood structure. *Journal of Memory & Language, 62,* 113–134.

Gordon, J. K. (2002). Phonological neighborhood effects in aphasic speech errors: Spontaneous and structured contexts. *Brain and Language, 82,* 113–145.

Gow, D. W. (2012). The cortical organization of lexical knowledge: A dual lexicon model of spoken language processing. *Brain and Language, 121,* 273–288.

Graves, W. W., Grabowski, T. J., Mehta, S., & Gupta, P. (2008). The left posterior superior temporal gyrus participates specifically in accessing lexical phonology. *Journal of Cognitive Neuroscience, 20,* 1698–1710.

Hayward, R. W., Naeser, M. A., & Zatz, L. M. (1977). Cranial computed tomography in aphasia: Correlation of anatomical lesions with functional deficits. *Radiology, 123,* 653–660.

Hickok, G. S. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience, 13,* 135–145.

Hickok, G. S., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8,* 393–402.

Ide, N., & Suderman, K. (2004). The American National Corpus first release. In M. T. Lino, M. F. Xavier, F. Ferreira, R. Costa, & R. Silva (Eds.), *Proceedings of the Fourth Language Resources and Evaluation Conference (LREC)* (pp. 1681–1684). Lisbon: ELRA—European Language Resources Association.

Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. (2012). Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex, 48,* 826–848.

Kertesz, A. (1982). *Western Aphasia Battery*. New York: Grune & Stratton.

Kertesz, A., Harlock, W., & Coates, R. (1979). Computed tomographic localization, lesion size, and prognosis in aphasia and nonverbal impairment. *Brain and Language, 8,* 34–50.

Kimberg, D. Y., Coslett, H. B., & Schwartz, M. F. (2007). Power in voxel-based lesion-symptom mapping. *Journal of Cognitive Neuroscience, 19,* 1067–1080.

Kittredge, A. K., Dell, G. S., Verkuilen, J., & Schwartz, M. F. (2008). Where is the effect of frequency in word production? Insights from aphasic picture-naming errors. *Cognitive Neuropsychology, 25,* 463–492.

Luce, P. A. (1986). Neighborhoods of words in the mental lexicon. Research on Speech Perception, Technical Report No. 6. Bloomington, IN: Speech Research Laboratory, Department of Psychology, Indiana University.

Luce, P. A., & Pisoni, D. B. (1998). Recognizing spoken words: The neighborhood activation model. *Ear and Hearing, 19,* 1–36.

Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behavior Research Methods, Instruments & Computers, 28,* 203–208.

Magnuson, J. S., Dixon, J. A., Tanenhaus, M. K., & Aslin, R. N. (2007). The dynamics of lexical competition during spoken word recognition. *Cognitive Science, 31,* 1–24.

McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: Part 1. An account of basic findings. *Psychological Review, 88,* 375–407.

McRae, K., Cree, G. S., Seidenberg, M. S., & McNorgan, C. (2005). Semantic feature production norms for a large set of living and nonliving things. *Behavior Research Methods, 37,* 547–559.

Mirman, D. (2011). Effects of near and distant semantic neighbors on word production. *Cognitive, Affective, and Behavioral Neuroscience, 11,* 32–43.

Mirman, D., & Graziano, K. M. (2012). Damage to temporo-parietal cortex decreases incidental activation of thematic relations during spoken word comprehension. *Neuropsychologia, 50,* 1990–1997.

Mirman, D., & Magnuson, J. S. (2008). Attractor dynamics and semantic neighborhood density: Processing is slowed by near neighbors and speeded by distant neighbors. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 65–79.

Nozari, N., Schwartz, M. F., & Coslett, H. B. (2012). Fluency of speech depends on executive abilities: Evidence for two levels of conflict in speech production. *Procedia—Social and Behavioral Sciences, 61,* 183–184.

Okada, K., & Hickok, G. (2006). Identification of lexical-phonological networks in the superior temporal sulcus using functional magnetic resonance imaging. *NeuroReport, 17,* 1293–1296.

Patterson, K. E., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8,* 976–987.

Peramunage, D., Blumstein, S. E., Myers, E. B., Goldrick, M., & Baese-Berk, M. (2011). Phonological neighborhood effects in spoken word production: An fMRI study. *Journal of Cognitive Neuroscience, 23,* 593–603.

Pexman, P. M., Holyk, G. G., & Monfils, M.-H. (2003). Number-of-features effects and semantic processing. *Memory & Cognition, 31,* 842–855.

Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchison, E., & Britton, B. (2006). An event-related fMRI investigation of phonological-lexical competition. *Neuropsychologia, 44,* 2209–2221.

Righi, G., Blumstein, S. E., Mertus, J., & Worden, M. S. (2009). Neural systems underlying lexical competition: An eye tracking and fMRI study. *Journal of Cognitive Neuroscience, 22,* 213–224.

Roach, A., Schwartz, M. F., Martin, N., Grewal, R. S., & Brecher, A. R. (1996). The Philadelphia Naming Test: Scoring and rationale. *Clinical Aphasiology, 24,* 121–133.

Rorden, C., & Karnath, H.-O. (2004). Using human brain lesions to infer function: A relic from a past era in the fMRI age? *Nature Reviews Neuroscience, 5,* 813–819.

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences, 106,* 322–327.

Schwartz, M. F., Faseyitan, O., Kim, J., & Coslett, H. B. (2012). The dorsal stream contribution to phonological retrieval in object naming. *Brain, 135,* 3799–3814.

Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A. R., Faseyitan, O., Dell, G. S., et al. (2011). A neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences, 108,* 8520–8524.

Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Faseyitan, O., Brecher, A. R., Dell, G. S., et al. (2009). Anterior temporal involvement in semantic word retrieval: Voxel-based lesion-symptom mapping evidence from aphasia. *Brain, 132,* 3411–3427.

Shomstein, S., Lee, J., & Behrmann, M. (2010). Top–down and bottom–up attentional guidance: Investigating the role of the dorsal and ventral parietal cortices. *Experimental Brain Research, 206,* 197–208.

Smith, D. V., Clithero, J. A., Rorden, C., & Karnath, H.-O. (2013). Decoding the anatomical network of spatial attention. *Proceedings of the National Academy of Sciences, 110,* 1518–1523.

Snyder, H. R., Feigenson, K., & Thompson-Schill, S. L. (2007). Prefrontal cortical response to conflict during semantic and phonological tasks. *Journal of Cognitive Neuroscience, 19,* 761–775.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage, 15,* 273–289.

Vitevitch, M. S., & Sommers, M. S. (2003). The facilitative influence of phonological similarity and neighborhood frequency in speech production in younger and older adults. *Memory & Cognition, 31,* 491–504.

Walker, G. M., Schwartz, M. F., Kimberg, D. Y., Faseyitan, O., Brecher, A. R., Dell, G. S., et al. (2011). Support for anterior temporal involvement in semantic error production in aphasia: New evidence from VLSM. *Brain and Language, 117,* 110–122.

Wilson, S. M., Isenberg, A. L., & Hickok, G. (2009). Neural correlates of word production stages delineated by parametric modulation of psycholinguistic variables. *Human Brain Mapping, 30,* 3596–3608.

Zhuang, J., Randall, B., Stamatakis, E. A., Marslen-Wilson, W. D., & Tyler, L. K. (2011). The interaction of lexical semantics and cohort competition in spoken word recognition: An fMRI study. *Journal of Cognitive Neuroscience, 23,* 3778–3790.