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The Anterior Temporal Lobe Semantic Hub Is a Part of the Language Neural Network: Selective Disruption of Irregular Past Tense Verbs by rTMS

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There is growing evidence from patient and neuroimaging studies that the anterior temporal lobe (ATL) should be considered a crucial part of the neural network that underpins language. Specifically, this region supports semantic representations that play a key role in various aspects of language processing. In this study, we tested the critical importance of this region for language processing in normal participants by applying repetitive transcranial magnetic stimulation over the left ATL semantic region. The ability to generate the past tense of English verbs has often been used as a test case for neurocognitive models of language. Accordingly, we used this aspect of language to investigate the impact of repetitive transcranial magnetic stimulation (rTMS) over the left ATL. As predicted by single mechanism accounts of past-tense generation, ATL rTMS had a selective impact on participants' ability to generate the past tense of irregular verbs. When combined with other evidence, these results confirm that the ATL semantic hub is a key component of the neural network for language.

Keywords: anterior temporal lobe, language, semantic memory, TMS

Introduction

Since the seminal aphasiological studies of Broca, Wernicke, and their colleagues, researchers have attempted to understand which brain regions are implicated in language processing. Both traditional and some contemporary models of the language network tend to focus upon classical, perisylvian language centers such as Wernicke's and Broca's areas and supramarginal and angular gyri (e.g., Mesulam 1998; Catani and Ffytche 2005; Friederici 2009). There is growing evidence, however, that regions beyond these classical regions should be included within the language neural network (Wise 2003; Hickok and Poeppel 2007). The target of this study was one such region—the anterior temporal lobe (ATL). It is likely that this region was not considered in the classical aphasiological models because cerebrovascular accident rarely affects the anterior temporal region. This may be for 2 reasons: 1) although the exact arterial distribution varies from individual to individual, the ATL most often has a double blood supply (the anterior temporal cortical artery of the middle cerebral artery and the anterior temporal branch of the distal posterior cerebral artery: Conn 2003; Borden 2006) and 2) the anterior temporal cortical artery branches below the main trifurcation of the middle cerebral artery and thus may be less vulnerable to emboli. This absence of evidence for the contribution of the ATL to language processing has been exacerbated by both technical limitations of standard functional magnetic resonance imaging (fMRI; the ATL suffers from magnetic field inhomogeneities that distort and degrade the blood oxygen level–dependent signal: Devlin et al. 2000) and because many positron emission tomography (PET)/fMRI studies have used a restricted field-of-view thereby failing to sample the ATL (Visser et al. 2010).

The hypothesis that the ATL is a critical part of the language neural network is formulated in 2 steps. The first reflects the observation that this region is critically important in semantic memory. In the context of pronounced atrophy and hypometabolism of the inferior and lateral aspects of the ATL, semantic dementia (SD) patients present with a progressive yet selective degradation of amodal semantic representations (Nestor et al. 2006; Patterson et al. 2006; Lambon Ralph and Patterson 2008). This converges with PET- and magnetoencephalography (MEG)-based studies that find ATL activations when participants are required to comprehend words or pictures (Vandenberghe et al. 1996; Marinkovic et al. 2003). Importantly for this study, when repetitive transcranial magnetic stimulation (rTMS) is applied to the lateral ATL, normal participants exhibit a selective slowing on semantic tasks (the same stimulation does not affect nonsemantic tasks matched for overall difficulty: Pobric et al. 2007; Lambon Ralph et al. 2009).

The second step in our working hypothesis derives from computational models of language processing (Plaut et al. 1996; Joanisse and Seidenberg 1999). The core idea underpinning these approaches is that many different language activities (reading, repetition, naming, past tense generation, etc.) are supported by interactions between a small set of primary brain systems (including semantics, phonology, vision, etc.: Patterson and Lambon Ralph 1999), rather than each activity being housed in a separate, dedicated brain region. When one of these primary systems is impaired by brain damage (or temporarily suppressed by rTMS), a predictable impact should be felt across a variety of different language activities. Previous studies of SD patients indicate that, in face of the degradation of semantic knowledge, there is a predictable effect on a range of verbal and nonverbal activities that are not traditionally associated with semantic memory (Patterson et al. 2006). The hypothesis arising from these studies is that the ATL semantic system contributes to these language activities through its interactions with the other language centers. This idea rests, however, solely upon these SD data, and these have been challenged on the basis that 1) SD patients might have a combination of semantic impairment combined with deficits to task-specific representations (though see: Patterson et al. 2006) and 2) because SD arises from a neurodegenerative disease, there is never an absolute boundary to the patients' brain damage and there could be subtle damage or invasion of pathology remote to the ATL that is causing or contributing to each language impairment. As a consequence, it is critically important to test this hypothesis in alternative ways and in neurologically intact participants. We achieved this aim for the first time by the use of rTMS over the ATL in order to generate a temporary suppression of semantic memory (Pobric et al. 2007; Lambon Ralph et al. 2009).

Although there is a range of language activities that could act as a target (Patterson et al. 2006), we selected past tense generation of English verbs because this topic has been used as a test case for neurocognitive models of language processing for many years (Rumelhart and McClelland 1986; Joanisse and Seidenberg 1999). As per the primary systems hypothesis, connectionist models of verb inflection contend that phonological and semantic systems make joint contributions to each verb type (Joanisse and Seidenberg 1999; Patterson et al. 2001; Bird et al. 2003). Phonological factors play a crucial role in this domain because the past tense for both regular and irregular verbs is underpinned by various different phonological regularities and consistencies (Seidenberg 1997; Joanisse and Seidenberg 1999). Via the interaction between phonology and semantics, verb meaning provides a second source of constraint. Although this is present for all real verbs, semantic memory is critically important for irregular verbs because it can counteract the overwhelming tendency for the phonological system to compute the regular form (following the phonological statistics of language: Patterson et al. 2001). Patterson et al. (2001) demonstrated that SD patients have a significant deficit for generating and recognizing the irregular past tense, and the extent of the irregular verb deficit was correlated with the patients' degree of semantic impairment. The present study represents the first attempt to derive evidence from neurologically intact participants that the ATL semantic system is critical for irregular past tense verbs and for language more generally. One might expect functional neuroimaging to be the major source of evidence for processing in neurologically intact participants. This is overshadowed, however, by the fact that standard fMRI suffers from significant field inhomogeneities in the inferiorolateral and polar aspects of the ATL (Devlin et al. 2000). Thus, although the literature contains a small number of fMRI studies of past tense, including careful analyses of phonological factors (e.g., Desai et al. 2006), none has highlighted ATL activation.

Materials and Methods

Participants

Twelve participants took part in the study (mean age 24 years). Ten of them had participated in our previous investigation that demonstrated a temporary, selective semantic slowing after ATL stimulation (Pobric et al. 2007). All were native English speakers and strongly right handed, yielding a laterality quotient of at least +90 on the Edinburgh Handedness Inventory (Oldfield 1971). None had a previous history of implants, seizures, neurological, or psychiatric disease. Local ethics approval was granted for all procedures.

Design

A within-participant factorial design was used with TMS (pre-TMS baseline vs. post-TMS performance) and item type (regular, irregular, or nonverb) as the 2 factors. We used the "virtual lesion" method in which a train of rTMS is delivered offline (in the absence of a concurrent behavioral task) and behavioral changes are probed during the extended refractory period. Behavioral testing began immediately after the last TMS pulse was delivered and performance was compared with baseline levels obtained prior to stimulation.

Materials and Task

In order to provide direct comparison with the results from SD patients (see Introduction), the 100-verb set was taken directly from Patterson et al. (2001). All verbs were monosyllabic in the present tense. Regular and irregular verbs were matched for frequency, familiarity, and imageability. Fifty verbs (25 regular, 25 irregular) were presented prior to any rTMS to determine baseline performance and 50 verbs (25 regular, 25 irregular) after rTMS. The 2 sets were counterbalanced across participants. Fifty nonwords derived from a single initial phoneme alteration of the uninflected form for each verb were also included before and after rTMS. Additionally, due to the strong tendency to regularize novel or nonce words (Pinker 1998), 25 filler irregular verbs were added to each pre and poststimulation set. Items were presented in a random order during both test phases. A PC running SuperLab software (Cedrus Corporation, United states) allowed presentation of stimuli and recorded responses. Participants sat in front of a 15″ monitor and were instructed to generate the past-tense form as quickly and as accurately as possible. Each verb stem was presented in the center of the computer screen after a 400-ms fixation point and 250-ms interstimulus interval. The verb remained on screen until a response was detected. Response latencies were recorded via a voice-activated key, and spoken responses were recorded on a digital voice recorder for offline error analysis.

Procedure

Exactly the same stimulation site and a very similar procedure as in Pobric et al. (2007) were adopted. Focal magnetic stimulation of the ATL was delivered using a Magstim SuperRapid^2 (www.magstim.com) stimulator with a dual 70-mm coil. For each participant, motor threshold was determined using visible twitch of the relaxed contralateral abductor pollicis brevis muscle. Repetitive TMS was applied for a total of 10 min (600 pulses at a frequency of 1 Hz and an intensity of 120% motor threshold). To guide positioning of the TMS coil, structural T1-weighted anatomical images were acquired for each participant. Coregistration of the scalp surface with underlying cortical surface in each participant was achieved using the Ascension MiniBird tracking system and MRIreg freeware (http://www.sph.sc.edu/comd/rorden/mrireg.html). Six facial landmarks (the vertex, inion, lower vermillion of the lip, nasion, and the tragus of each ear), selected as reproducible landmarks that would enable stereotaxic coregistration at test, were identified and marked on each participant using oil capsules prior to the structural scan. The ATL site was defined as 10 mm posterior from the tip of the left temporal lobe along the middle temporal gyrus. This point was used in each participant as the anatomical landmark of the temporal pole. The average Montreal Neurological Institute coordinates for the ATL in standard space were (–53, 4, –32). The stimulating coil was held on the scalp surface over the marked site of stimulation with the handle directed posteriorly for all participants.

Data Analysis

Only reaction times for correct responses were analyzed. A further 2.5% of the trials were removed due to voice key mistriggers or participant false starts. The novel experience of rTMS had a generalized alerting effect on the participants leading to a generic speeding of reaction times after rTMS. The mean elicitation time (irrespective of verb type) prior to rTMS was 931 ms, and after stimulation, it was 865 ms (there was no change in accuracy rates: 90% correct at baseline and 91% poststimulation). This nonspecific speeding of reaction times after rTMS has been observed in studies applying a train of pulses during an intertrial interval (e.g., Campana et al. 2002) and after offline rTMS (Knecht et al. 2002). In this study, the raw elicitation times were entered into an ANOVA to explore the impact of TMS and verb type. In order to observe the verb-specific TMS effect more clearly, Figure 1 shows the adjusted means (calculated by dividing raw reaction times for each participant by the mean reaction time of pre or post-TMS

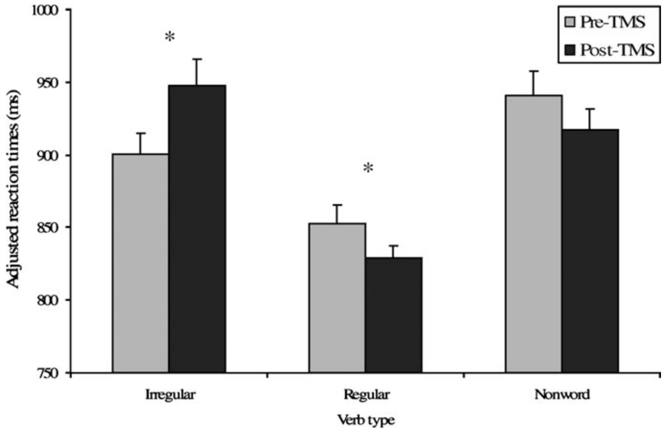

Figure 1. Past tense elicitation time before and after ATL rTMS. Error bars denote standard error of the mean per condition. Asterisks mark significant effect of rTMS on elicitation times.

condition, as appropriate. Each proportion was then scaled according to the grand mean to remove the generic speeding effect and equalize the reaction times in pre and poststimulation sessions). Planned comparison t-tests (one-tailed) were conducted on these adjusted values in order to compare the effect of ATL rTMS on each verb type. Following the primary systems hypothesis and previous results from SD patients (see Introduction), we expected to observe a relative slowing of elicitation times for the irregular verbs but no differences for regular or nonverbs.

Results

The effect of rTMS to the ATL on each verb type is summarized in Figure 1. The results are clear and conform directly to the primary systems hypothesis (see Introduction). The ANOVA of elicitation times confirmed main effects of rTMS and verb type ($F(1,11) = 9.88$, $P = 0.009$; $F(2,22) = 7.51 = 0.003$, respectively), and most importantly, there was a significant interaction between the 2 factors ($F(2,22) = 4.28$, $P = 0.03$). Planned comparisons demonstrated that this interaction reflected a relative slowing of elicitation times for irregular verbs ($t(11) = 2.79$, $P = 0.02$) in the context of an overall speeding up of responses after TMS as observed in the regular and nonce-verb conditions ($t(11) = 2.37$, $P = 0.04$; $t(11) = 1.63$, $P = 0.13$, respectively). As can be seen in Figure 1, the relative slowing of elicitation times for irregular verbs cannot be due to overall difficulty because the baseline reaction times for this verb type was intermediate between regular and nonce verbs (both of which showed a trend toward quicker elicitation times after stimulation).

In line with our previous studies (Pobric et al. 2007; Lambon Ralph et al. 2009), we found that the rTMS effect was carried by reaction times and not by accuracy rates. An ANOVA found no main effect of TMS ($F(1,11) < 1$), a main effect of verb type ($F(2,22) = 16.2$, $P < 0.001$: regular > nonword = irregular) and no interaction ($F(2,22) < 1$).

Discussion

This study used rTMS to confirm that the ATL semantic system should be included along with other classical perisylvian regions within the language neural network (Wise 2003; Hickok and Poeppel 2007). There is already convergent evidence for the first part of this hypothesis that the ATL contributes an amodal representational system to semantic memory. This includes studies of patients with ATL damage (Bozeat et al. 2000; Jefferies and Lambon Ralph 2006; Lambon Ralph et al. 2007), PET- and MEG-based investigations (Vandenberghe et al. 1996; Marinkovic et al. 2003) and rTMS to the lateral ATL (Pobric et al. 2007; Lambon Ralph et al. 2009). Strong evidence for the involvement of semantic memory in a variety of "nonsemantic" language tasks has been derived from studies of patients with semantic dementia (Patterson et al. 2006) and thus, by implication, the ATL. Some researchers have urged caution, however, when linking the semantic impairment of SD solely to the ATL given that the boundary of pathology or dysfunction is graded in neurodegenerative conditions (Martin 2007). Thus, evidence in support of this idea from normal participants is a critical step. Previous studies have shown that rTMS to the lateral ATL produces a temporary, specific slowing of performance on semantic tasks (Pobric et al. 2007; Lambon Ralph et al. 2009). In this study, therefore, we repeated the same rTMS protocol and confirmed that this produces a specific effect on language tasks. By investigating the ability to produce the past tense of English verbs, we were able to demonstrate that suppressing ATL semantic processing also leads to a relative slowing on irregular verbs alone. In contrast, elicitation times for regular verbs and novel verbs showed a tendency to be speeded.

This study adds to existing neuropsychological and computational investigations that suggest that language activities (e.g., reading and repetition) are not encapsulated within single modular processes but reflect the joint action of a network of brain regions, each of which supports sources of information, such as orthographic, phonological, or semantic representations, that provide varying constraints for different cognitive skills (Plaut et al. 1996; Joanisse and Seidenberg 1999; Patterson and Lambon Ralph 1999). In single word processing, phonological representations provide a key source of constraint both in terms of the surface representation of words, but also because there are important regularities and consistencies that can be extracted from the phonologically related statistics (Seidenberg 1997). Semantic representations also contribute to language activities even when the activity does not require comprehension of the words per se. Automatic interaction with word meaning is not instantiated in these models but is an emergent property of comprehension and speech production, which are core, everyday language activities (Plaut et al. 1996; Joanisse and Seidenberg 1999). This interaction with word meaning is computationally beneficial because semantic representations tend to be orthogonal to phonology (words of similar meaning have different phonological forms; phonologically similar items tend to have very different meanings). Like positions on any Cartesian-based map, words can be uniquely specified by a combination of these 2 orthogonal axes (semantics and phonology Marshall and Newcombe 1973; Lambon Ralph 1998). Semantic constraint is additionally important because, in most language activities, many words follow a strong statistical pattern (e.g., regular words in reading, e.g., MINT; or regular words for past tense, e.g, WALK → WALKED), but there are always exceptional patterns (e.g., PINT for reading, or RUN → RAN for past tense). In order to compute the correct form for these items, the strong statistical pattern can be counteracted in part by the constraint that comes from the interaction with meaning (Plaut et al. 1996; Joanisse and Seidenberg 1999).

This is perhaps the first study to demonstrate that the ATL semantic system in normal participants provides this form of semantic constraint in language activities. To date, the sole albeit strong evidence in favor of this idea derives from patients with semantic dementia (Patterson et al. 2006). There is growing evidence from MR tractography that the ATL is connected into perisylvian language centers (both prefrontal and temporoparietal regions: Catani and Thiebaut de Schotten 2008; Makris et al. 2009). Thus, there is the requisite structural connectivity to permit interaction between the ATL semantic system and classical language areas, as specified in the connectionist computational models of language (Plaut et al. 1996; Joanisse and Seidenberg 1999). Given this body of evidence from different methods, one might wonder why the ATL has not played a prominent role in classical models of aphasia or in the results of functional neuroimaging studies of language processing. As noted in the Introduction, this is most likely to reflect absence of evidence rather than evidence of absence. Classical aphasiological models are based primarily upon the results of stroke-induced aphasia and, given the privileged vascular supply of the ATL, there are very few cases of patients with stroke-induced ATL damage. In addition, given that fMRI suffers from distortion artifacts in this region and many previous PET-based studies have used a restricted field-of-view (Devlin et al. 2000; Visser et al. 2010), then it is possible that the role of the ATL in these language activities has not been sampled on a consistent basis. This possibility will need to be tested in future neuroimaging studies that overcome these technical limitations of standard fMRI.

We finish by considering what implications these results have for theories of past tense verb processing. This domain is dominated by 2 opposing views (Ullman et al. 1997; Patterson et al. 2001; Bird et al. 2003). The current results fit directly with the single mechanism connectionist models of past tense (Joanisse and Seidenberg 1999). As noted above, these suggest that the past tense is computed by a conjunction of phonological and semantic information. The regular past tense, as well as consistencies among irregular items, are primarily encoded and supported by the phonological component of these models (Seidenberg 1997; Joanisse and Seidenberg 1999). Although meaning is activated for all real verbs, the interaction between semantics and phonology is most critical for the irregular items as this form of semantic constraint helps to overcome the tendency to generate a regularized form. This form of constraint, although present for regular verbs, is superfluous. Novel verbs, by definition, have no associated meaning (Patterson et al. 2001). The results of the ATL rTMS in this study fit precisely with this framework. When the ATL semantic system is suppressed by rTMS then the semantic input to verb elicitation is partially compromised. This would be expected to have an effect on irregular verb generation (indexed by slower elicitation times) but to leave regular and novel verb generation unaffected. The alternative account suggests that the past tense is captured best by 2 separate elements: a rule-based procedure that generates the regular inflection and a lexicon that stores the irregular past tense form (Ullman et al. 1997). Proponents of this approach have associated the lexical component broadly within the temporal lobe but have not specified which exact area is critical for this function. Without greater neuroanatomical specificity, it is impossible to use rTMS methods to test this theory. In any event, this theory is silent, however, on the role of semantic memory in language processing or how this might be underpinned by the ATL.

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Notes

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References

Bird H, Lambon Ralph MA, Seidenberg MS, McClelland JL, Patterson K. 2003. Deficits in phonology and past-tense morphology: What's the connection? J Mem Lang. 48(3):502-526.

Borden NM. 2006. 3D angiographic atlas of neurovascular anatomy and pathology. Cambridge (MA): Cambridge University Press.

Bozeat S, Lambon Ralph MA, Patterson K, Garrard P, Hodges JR. 2000. Non-verbal semantic impairment in semantic dementia. Neuropsychologia. 38:1207-1215.

Campana G, Cowey A, Walsh V. 2002. Priming of motion direction and area V5/MT: a test of perceptual memory. Cereb Cortex. 12(6):663-669.

Catani M, Ffytche DH. 2005. The rises and falls of disconnection syndromes. Brain. 128:2224-2239.

Catani M, Thiebaut de Schotten M. 2008. A diffusion tensor imaging tractography atlas for virtual in vivo dissections. Cortex. 44(8): 1105-1132.

Conn M. 2003. Neuroscience in medicine. Totowa (NJ): Humana Press.

Desai R, Conant LL, Waldron E, Binder JR. 2006. fMRI of past tense processing: the effects of phonological complexity and task difficulty. J Cogn Neurosci. 18(2):278-297.

Devlin JT, Russell RP, Davis MH, Price CJ, Wilson J, Moss HE, Matthews PM, Tyler LK. 2000. Susceptibility-induced loss of signal: comparing PET and fMRI on a semantic task. Neuroimage. 11(6; PART 2):589-600.

Friederici AD. 2009. Pathways to language: fiber tracts in the human brain. Trends Cogn Sci. 13(4):175-181.

Hickok G, Poeppel D. 2007. The cortical organization of speech processing. Nat Rev Neurosci. 8(5):393-402.

Jefferies E, Lambon Ralph MA. 2006. Semantic impairment in stroke aphasia vs. semantic dementia: a case-series comparison. Brain. 129:2132-2147.

Joanisse MF, Seidenberg MS. 1999. Impairments in verb morphology after brain injury: a connectionist model. Proc Natl Acad Sci U S A. 96:7592-7597.

Knecht S, Floel A, Drager B, Breitenstein C, Sommer J, Henningsen H, Ringelstein EB, Pascual-Leone A. 2002. Degree of language lateralization determines susceptibility to unilateral brain lesions. Nat Neurosci. 5(7):695-699.

Lambon Ralph MA. 1998. Distributed versus localist representations: evidence from the study of item consistency in a case of classical anomia. Brain Lang. 64:339-360.

Lambon Ralph MA, Lowe C, Rogers TT. 2007. Neural basis of category-specific semantic deficits for living things: evidence from semantic dementia, HSVE and a neural network model. Brain. 130:1127-1137.

Lambon Ralph MA, Patterson K. 2008. Generalisation and differentiation in semantic memory: insights from semantic dementia. Ann N Y Acad Sci. 1124:61-76.

Lambon Ralph MA, Pobric G, Jefferies E. 2009. Conceptual knowledge is underpinned by the temporal pole bilaterally: convergent evidence from rTMS. Cereb Cortex. 19(4):832-838.

Makris N, Papadimitriou GM, Kaiser JR, Sorg S, Kennedy DN, Pandya DN. 2009. Delineation of the middle longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. Cereb Cortex. 19(4):777-785.

Marinkovic K, Dhond RP, Dale AM, Glessner M, Carr V, Halgren E. 2003. Spatiotemporal dynamics of modality-specific and supramodal word processing. Neuron. 38:487-497.

Marshall JC, Newcombe F. 1973. Patterns of paralexia: a psycholinguistic approach. J Psycholinguist Res. 1(3):175–199.

Martin A. 2007. The representation of object concepts in the brain. Annu Rev Psychol. 58:25–45.

Mesulam MM. 1998. From sensation to cognition. Brain. 121(6):1013–1052.

Nestor PJ, Fryer TD, Hodges JR. 2006. Declarative memory impairments in Alzheimer's disease and semantic dementia. Neuroimage. 30:1010–1020.

Oldfield RC. 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia. 9:97–113.

Patterson K, Lambon Ralph MA. 1999. Selective disorders of reading? Curr Opin Neurobiol. 9:235–239.

Patterson K, Lambon Ralph MA, Hodges JR, McClelland JL. 2001. Deficits in irregular past-tense verb morphology associated with degraded semantic knowledge. Neuropsychologia. 39(7):709–724.

Patterson K, Lambon Ralph MA, Jefferies E, Woollams A, Jones RW, Hodges JR, Rogers TT. 2006. "Presemantic" cognition in semantic dementia: six deficits in search of an explanation. J Cogn Neurosci. 18(2):169–183.

Pinker S. 1998. Words and rules. Lingua. 106(1–4):219–242.

Plaut D, McClelland JL, Seidenberg MS, Patterson K. 1996. Understanding normal and impaired word reading: computational principles in quasi-regular domains. Psychol Rev. 103:56–115.

Pobric GG, Jefferies E, Lambon Ralph MA. 2007. Anterior temporal lobes mediate semantic representation: mimicking semantic dementia by using rTMS in normal participants. Proc Natl Acad Sci U S A. 104: 20137–20141.

Rumelhart DE, McClelland JL. 1986. On learning the past tense of English verbs. In: McClelland JL, Rumelhart DE, and the PDP Research Group, editors. Parallel distributed processing: explorations in the microstructure of cognition, vol. 2. Psychological and biological models. Cambridge (MA): MIT Press.

Seidenberg MS. 1997. Language acquisition and use: learning and applying probabilistic constraints. Science. 275(5306):1599–1603.

Ullman MT, Corkin S, Coppola M, Hickok G, Growdon JH, Koroshetz WJ, Pinker S. 1997. A neural dissociation within language: evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. J Cogn Neurosci. 9(2):266–276.

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ. 1996. Functional-anatomy of a common semantic system for words and pictures. Nature. 383(6597):254–256.

Visser M, Jefferies E, Lambon Ralph MA. 2010. Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. J Cogn Neurosci. 22(6):1083–1094.

Wise R. 2003. Language systems in normal and aphasic human subjects: functional imaging studies and inferences from animal studies. Br Med Bull. 65:95–119.