UC Merced

Proceedings of the Annual Meeting of the Cognitive Science Society

Title

Neural bases of semantic-memory deficits for events

Permalink

https://escholarship.org/uc/item/586917r9

Journal

Proceedings of the Annual Meeting of the Cognitive Science Society, 38(0)

Authors

Lei, Chia-Ming Dresang, Haley C. Holcomb, Michelle B. <u>et al.</u>

Publication Date 2016

Peer reviewed

Neural bases of semantic-memory deficits for events

Chia-Ming Lei (chl162@pitt.edu)

Department of Communication Science and Disorders, 6035 Forbes Tower Pittsburgh, PA 15260 USA

Haley C. Dresang (haleydresang@pitt.edu)

Department of Communication Science and Disorders, 6035 Forbes Tower Pittsburgh, PA 15260 USA

Michelle B. Holcomb (mbh32@pitt.edu)

Department of Psychology, Learning Research & Development Center, 3939 O'Hara Street Pittsburgh, PA 15260 USA

Tessa C. Warren (tessa@pitt.edu)

Department of Psychology, Learning Research & Development Center, 3939 O'Hara Street Pittsburgh, PA 15260 USA

Michael Walsh Dickey (mdickey@pitt.edu)

VA Pittsburgh Healthcare System, University Dr C Department of Communication Science and Disorders, 6035 Forbes Tower Pittsburgh, PA 15260 USA

Abstract

This study investigated the neural bases of event-related semantic-memory deficits among people with aphasia due to left-hemisphere (LH) stroke. A novel task using naturalistic photographic stimuli and patient-friendly procedures was used to test event-related semantic knowledge. In the task, participants decided whether depicted events were normal (represented in semantic memory) or were abnormal (not represented in semantic memory). Performance on this Event task was correlated with deficits in action- and object-concept processing and on standardized language measures, especially action- and verb-processing deficits. Logistic regression analyses examined lesion correlates of patient performance on the Event task. Surprisingly, increasing LH lesion size in action ROIs was associated with improved performance on the event-knowledge task. These findings suggest that action processing may play a special role in event-related semantic memory representations. Furthermore, they are consistent with recent claims that the right hemisphere may be especially important for activation of event-related knowledge.

Keywords: semantic memory; event-related knowledge; lefthemisphere lesion; aphasia; lesion-deficit analysis

Introduction

Semantic memory refers to an individual's core world knowledge, ranging from general facts to specific features of objects and actions (Squire, 1987; Tulving, 1972; Yee, Chrysikou, & Thompson-Schill, 2013). Semantic memory therefore impacts a wide variety of cognitive domains, including language. Semantic memory representations have been examined clinically through standardized assessments for object-related conceptual semantics, such as the Pyramids and Palm Trees task (PPT; Howard & Patterson, 1992), and action-related conceptual semantics, such as the Kissing and Dancing Task (KDT; Bak & Hodges, 2003). However, the focus of most research has been on concrete concepts (e.g., object semantics). There has been much less investigation of abstract concepts (e.g. event-related semantics).

Event-related semantic memory consists of knowledge about common events, such as playing soccer or eating breakfast. Event-related representations bind together information about actions and their common participants (such as agents, themes, and locations: Ferretti, McRae & Hatherell, 2001; McRae & Matsuki, 2009). Event-related semantic memory representations are especially important for rapid language comprehension and online language prediction (Matsuki et al., 2011; Metusalem et al., 2012). Event-related semantic knowledge can be quickly activated agent-verb combinations, by isolated words, or morphosyntactic cues, and has been shown to guide expectations for upcoming words and concepts (Hare et al., 2009; Kamide, Scheepers & Altmann, 2003; McRae & Matsuki, 2009). These event-related expectations contribute to comprehension at both the sentence and the discourse level (Metusalem et al., 2012). Semantic-memory impairments for events can thus contribute to debilitating communication deficits.

Cognitive neuropsychology has a long history of investigating individuals with semantic deficits (e.g., Warrington & Shallice, 1984). Persons with aphasia (PWA) and persons with neurodegenerative disorders such as semantic dementia or fronto-temporal dementia often experience semantic-memory impairments. These impairments can impact both language production and comprehension. Size, location, and relative atrophy of lesions, as well as cortical and cognitive reorganization post-stroke, yield individual differences in semanticmemory deficits (Antonucci & Reilly, 2008). For example, patients with either lesions or neurodegenerative disorders affecting left-hemisphere (LH) temporal regions exhibit deficits in object processing (e.g., Bak & Hodges, 2003; Binney et al., 2010; Kim & Thompson, 2004; see discussion in Lambon Ralph, 2014). In contrast, patients with atrophy or lesions affecting LH frontal regions exhibit deficits in action-concept processing (Bak & Hodges, 2003; Hillis, Oh & Ken, 2004; Kemmerer et al., 2012; for a review see Mätzig, et al., 2009). There is also evidence that action or verb processing activates posterior LH superior temporal gyrus and adjacent angular gyrus (Boylan, Trueswell, Thompson-Schill, 2015; den Ouden, et al., 2009).

Still, it remains unclear how event-related semanticmemory representations are organized within the brain. Events are complex, abstract concepts, and involve constellations of actions, objects, spatial, and temporal information. We know little about how these different components contribute to the neural representation of eventrelated conceptual semantic knowledge. The evidence described above suggests that distinct cortical networks are associated with action versus object conceptual processing. Event-related semantic representations may lean more strongly on action-related networks, given that actions are at the core of event-related knowledge (McRae & Matsuki, 2009), but this remains unknown.

One study to date has directly examined how this type of event-related knowledge is represented in the brain. Metusalem et al. (2016) used divided visual-field presentation to examine how event-related knowledge is activated in the two cerebral hemispheres. They presented short discourses from a previous ERP study (Metusalem et al., 2012) that were intended to activate event-related knowledge representations. These short discourses were followed by sentences with a critical word that was expected (*snowman*), unexpected but related to the event activated by the previous context (*jacket*), or unexpected and unrelated to the event (*towel*):

 A huge blizzard swept through town last night. My kids ended up getting the day off from school. They spent the whole day outside building a big [snowman/jacket/towel] in the front yard.

Metusalem et al. (2012) found that the expected word elicited a smaller N400 response than the two unexpected words. In addition, they found that the event-related word elicited an attenuated N400 response compared to the unrelated, unexpected word. This is parallel to many other ERP findings showing that words that are semantically related to a strongly expected word elicit attenuated N400 responses (Federmeier, 2007). Metusalem et al. (2016)

found that the advantage for event-related words was present when the critical word was presented to the left visual field/right hemisphere (RH), but absent when it was presented to the right visual field/LH. This finding suggests that event-related knowledge may be activated or represented primarily in the RH. This finding is in contrast to the lesion-based and neuroimaging evidence noted above, which suggests a LH bias in action and object conceptual representations.

The current study examined the neural basis of eventrelated semantic memory via a combination of behavioral testing and lesion-deficit analyses. Participants with lefthemisphere lesions were tested on a novel, patient-friendly assessment of event knowledge, along with standardized measures of object- and action-related conceptual processing and language performance. The influence of lesions to LH action- and object-related regions of interest on performance in the Event task was then modeled. The study tested two hypotheses: (1) that participants' performance on the Event task will be more strongly correlated with their action-concept/verb processing deficits than their object-concept/noun processing deficits; and (2) that lesions to LH action-processing regions will negatively impact event-knowledge task performance, but lesions to object-processing regions will not.

On the other hand, if Metusalem et al.'s (2016) claim regarding the RH bias for event-related representations is correct, LH lesions may be unrelated or even positively related to event task performance. Increasing LH lesion may force participants to lean more heavily on RH to perform the Event task, much as larger LH lesion prompts PWA to recruit RH regions for language tasks (Saur et al., 2006). Although this RH recruitment may be maladaptive for language processing, it could result in better performance if event-related semantic memory is RH-biased.

Method

Participants

All participants (n=26, 8 female) had unilateral lefthemisphere (LH) strokes. They ranged in age from 50 to 82 (mean=73.4) and were between 17 and 276 months poststroke (mean=73.4). They all had diagnosed aphasia, confirmed by their performance on the Comprehensive Aphasia Test (Howard, Swinburn, & Porter, 2004; CAT Modality Mean T-score mean=55.42). All 26 participants completed behavioral testing designed to measure their event-related knowledge and its connection to action and object processing. A subset of these participants (n=10, 4 female) also completed neuroimaging procedures. They ranged in age from 54 to 80 (mean=68), were between 19 and 276 months post-stroke (mean=102.7) and had a mean CAT Modality Mean T-score of 54.17.

Behavioral Tasks

A novel task utilizing naturalistic photographic stimuli and patient-friendly procedures (the Event task) was used to test event-related semantic knowledge. Participants were presented with images that depicted either typical events (n=130; left image, Fig. 1) or events that involved one or more abnormal event participants, such as a highly unlikely agent, theme, location, or instrument (n=130; right image, Fig. 1). These images were taken from an ERP study by Proverbio and Riva (2009) that found that the images of abnormal events elicited a robust centro-parietally distributed N400 response compared to the typical-event images in college-aged adults. In the Event task, participants had to decide whether the depicted events were normal (represented in semantic memory) or were abnormal (not represented in semantic memory).



Figure 1: Sample images from the Event task.

Participants also completed standardized measures of language performance and of action and object processing. Language performance was tested using the CAT (Swinburn, et al., 2004). Action processing was tested by the Kissing and Dancing Test (KDT: Bak & Hodges, 2003), whereas object processing was tested by Pyramids and Palm Trees (PPT: Howard & Patterson, 1992). KDT and PPT are picture-based tasks in which participants indicate which of two actions (KDT) or objects (PPT) best matches a reference action/object (e.g., a palm tree matches a pyramid better than a pine tree does).

Procedure

Event task stimuli were presented on a computer using E-Prime 2.0 (Schneider, Eschmann & Zuccolotto, 2012) and participants responded by pressing one of two keys on the keyboard. They were instructed to press a left-hand key marked with a '1' label if the image showed "something that might normally happen," and to press a right-hand key marked with a '5' label if it showed "something that might not normally happen." Participants had 5 seconds to respond. Each participant was given 4 practice trials with feedback. The remaining trials did not have feedback. KDT and PPT stimuli were also presented via E-Prime, with participants pressing the keys labeled with '1' and '5' to indicate whether the left-hand (1) or right-hand (5) image better matched the reference action or object. The CAT was administered and scored by a trained speech-language pathologist. The Action Naming and Object Naming subtests of the CAT were intended to measure verb and

noun processing, respectively. The CAT, KDT, PPT, and the Event task were all administered in a single session.

Neuroanatomical Data

Scan Protocol

Magnetic resonance imaging procedures were performed at the Neuroscience Imaging Center (http://www.nic.pitt.edu/) using a Siemens Allegra 3T scanner. High-resolution T1weighted structural images were collected from each participant using an MPRAGE sequence. The scan parameters for the T1 image were as follows: Field of View: 256mm x 256mm; 192 slices in sagittal plane, 1mm thick; Flip angle: 8° ; TE/TR = 3.04/1540 ms; Voxel size: 1mm x 1mm x 1mm. In addition to T1 images, either highdefinition 3D T2-weighted or 3D FLAIR images were collected for each participant. Scan parameters for the 3D FLAIR image were as follows: Field of View: 256mm x 220mm; 160 slices in sagittal plane, 1mm thick; Flip angle: $180^{\circ} - 90^{\circ} - 180^{\circ}$, IR sequence; TE/TR/TI = 353/6200/2000ms; Voxel size: 1mm x 1mm x 1mm. Scan parameters for the 3D T2 image were as follows: Field of View: 256mm x 192mm; 160 slices in sagittal plane, 1mm thick; Flip angle: $90^{\circ} - 180^{\circ}$, spin-echo sequence; TE/TR = 354/3500 ms; Voxel size: 1mm x 1mm x 1mm. All structural images were collected in a single scanning session.

Image Preprocessing

The acquired DICOM images were converted to NifTi format using MRIcron (Rorden & Brett, 2000). Brain lesions were demarcated directly on coronal slices of the T1 image using ITK-SNAP (Yushkevich et al., 2006). Lesion boundaries on coronal slices were compared to axial and sagittal slices, with T2/FLAIR images serving as reference images to help disambiguate lesion from cerebral-spinal fluid, ventricles, and white-matter atrophy. At least two tracers delineated the lesion boundaries in each brain. The tracers were blind to the individual's identity and languageimpairment profile. Inter-tracer reliability for lesion tracings was computed by comparing the discrepant areas voxel by voxel in AFNI (Cox, 1996). Less than 30% discrepancy was achieved for all brains (range: 8% - 27%). All lesion tracings were then reviewed by the first author and an additional experienced tracer (Michelle Gravier, Ph.D.), who was blind to the individual's identity and profile. The lesion tracing that was judged by the first author and the additional tracer to be the best for each brain was selected as the consensus lesion tracing for that brain.

The consensus lesion tracings served as the lesion mask for each participant. All lesion masks were normalized using SPM8 (Ashburner et al., 2012) to an age-matched brain template (Rorden, et al., 2012). Then, cost-function masking was applied to demarcate the lesion boundaries so as to reduce 'lesion bleeding' during transformation (Bates et al., 2003; Brett, et al., 2001). Finally, each patient's brain scan was warped onto the older brain template using the Clinical Toolbox for SPM8. The transformation matrix obtained was also applied to each patient's lesion mask, so that all the lesions were transformed to the template space.

Lesion Measures

Two LH ROIs were defined using the parcellations of the automated anatomical labeling (AAL: Tzourio-Mazoyer et al., 2002). These ROIs were derived from lesion-based and fMRI evidence regarding the neural correlates of object- and action-concept processing (see Table 1).

Table 1:	ROIs	used	in	analysis.
----------	------	------	----	-----------

ROI	Anatomical regions in LH
Object	Middle temporal gyrus
	Inferior temporal gyrus
	Fusiform gyrus
	Temporal pole
Action	Precentral gyrus
	Postcentral gyrus
	Inferior frontal gyrus (pars triangularis,
	orbitalis, and opercularis)
	Paracentral lobule
	Superior temporal gyrus
	Superior parietal gyrus
	Angular gyrus
	Temporal pole

These ROIs were intended to measure the influence of object- and action-related semantic processing on performance in the Event task. In addition to these ROIs, additional ROIs were defined for: (1) the whole brain and (2) LH Heschl's gyrus. The whole-brain ROI was intended to measure the influence of overall lesion volume on performance. It served as a control variable in regression models examining the effects of specific ROIs above. The Heschl's gyrus ROI served as an additional control ROI. Because the Event task does not involve auditory stimuli, lesion to primary auditory cortex (Heschl's gyrus) should not affect Event-task performance.

The SPM toolbox MarsBaR (Brett, Anton, Valabregue, Poline, 2002) was applied to extract masks for the ROIs described above. These masks were intersected with lesion masks, to determine the overlapping area between the normalized lesions and the ROIs. The voxels of the overlapping areas were then used to calculate the lesion volume (proportion of lesioned voxels) in each ROI for each participant. The proportion of lesion in each ROI was used as predictors in lesion-deficit models.

Results

Behavioral Tasks

Data from the behavioral tasks came from the full set of 26 participants. Accuracy for the Event task ranged from 47.7% to 94.5%, with a mean of 86.2%. Accuracy was higher for normal events than abnormal events (88.3% vs. 84.1%), suggesting there may have been a 'yes' bias among

our participants (e.g., Mitchum, Haendiges & Sloan Berndt, 2004). A logistic regression analysis of trial-level Event data in R using lme4 (Bates, et al., 2015) confirmed this, showing that stimulus type (normal versus abnormal) predicted the likelihood of a correct response (estimate=0.552; z=2.656, p<0.01). Given this bias, we used d-prime as our measure of Event task performance and included stimulus type as a nuisance variable in the lesion-deficit models reported below.

Correlation analyses examined the relationship between Event task performance and (1) action/object-processing deficits (KDT, PPT performance) and (2) languageprocessing impairments (CAT performance). Accuracy data for KDT and PPT and d-prime data for the Event task were z-score transformed. These z-scores were used for correlation analyses. Scores on the Event task were significantly correlated with both KDT and PPT, but more strongly correlated with KDT than PPT (KDT: r=.637, PPT: r=.526; both p<0.01). Event performance was compared to performance on the CAT Action Naming and Object Naming subtests. Event z-scores were significantly correlated with both Action Naming and Object Naming Tscores, but more strongly correlated with Action Naming than Object Naming (Action Naming: r=.411, Object Naming: r=.331; both p<0.05).

Neuroimaging Data

The distribution of lesions for the 10 participants who were scanned is depicted in Figure 2.



Figure 2: Lesion overlap for scanned participants

Logistic regression models examined the relationship between trial-level Event responses and lesions to control, action, and object ROIs. All models contained whole-brain lesion volume as a covariate, in order to measure the effect of lesions to a specific ROI while controlling for the effect of overall lesion volume. In addition, all models contained fixed effects of stimulus type (normal vs. abnormal), to control for the effect of response bias on Event performance, as well as stimulus-type-by-ROI interaction. The main effect of stimulus type was significant in all models.

As expected, there was no effect of lesion to the control ROI (Heschl's gyrus) on Event performance (estimate=0.878; z=1.090, p>0.2), and no interaction between control ROI lesion and stimulus type (estimate=0.556; z=-1.627, p>0.1). There was also no effect of lesion to the object ROI (estimate=-0.168; z=-0.078,

p>0.9), though there was a negative interaction of object ROI lesion and stimulus type (estimate=-1.846; z=-2.073, p<0.05). In contrast, there was a marginally significant effect of lesion to action ROI (estimate=10.42; z=1.674, p=0.094) and a significant interaction of action ROI lesion and stimulus type (estimate=-2.311; z=-1.973, p<0.05). Interestingly, the effect of action ROI lesion was positive: participants with larger lesions to the LH action ROI were *more* likely to respond accurately in Event, as shown in Figure 3. Similarly, the interactions of action and object ROI lesion and stimulus type (a measure of response bias) were negative: participants with larger sponse bias.



Figure 3: Relationship between Action ROI lesion and Event performance

Discussion and Conclusions

This study examined the neural bases of semanticmemory deficits for events in a sample of people with LH damage and aphasia, using a novel task (the Event task) that is picture-based and patient-friendly. Results from the behavioral tasks showed that Event-task performance is strongly correlated with performance on other picture-based measures of semantic memory, especially action-related measures (KDT). Furthermore, Event-task performance is correlated with deficits in language processing, especially verb processing (Action Naming on the CAT). These findings suggest that semantic memory representations for events may be closely aligned with action-concept representations and verb processing. This is consistent with evidence linking verb processing and event-related knowledge (e.g., Hare, et al., 2009).

Consistent with the behavioral evidence, lesion-deficit analyses showed that Event-task performance was most strongly related to lesions in LH action-related ROIs. However, this relationship was a negative one: greater LH lesion was associated with better Event-task performance, as well as a reduction in response bias. This finding suggests that damage to LH regions responsible for action processing may force participants to rely on complementary RH regions to perform the Event task. This LH damage may impair action-related language performance (such as verb processing), since language is a LH-localized function. However, it could result in better Event-task performance if event-related representations are partially or primarily RHlocalized. This finding is thus consistent with evidence that event-related knowledge may be activated or represented primarily in the RH (Metusalem, et al., 2016).

Although the current findings suggest that event-related knowledge (measured by Event-task performance) is most closely related to action-concept processing, Event-task performance was also related to both object and noun processing. It was also somewhat related to damage to LH object ROIs. This pattern is consistent with the fact that events connect actions, objects, spatial, and temporal information. Further research with larger samples of participants is needed to elucidate the nature of these relationships.

Ackowledgments

This research was supported by the National Institutes of Health through grant R01DC011520 to the last two authors. It is the result of work supported with resources and the use of facilities at the VA Pittsburgh Healthcare System. Thanks to Michelle Gravier for assistance with lesion-tracing analysis, normalization, and visualization procedures, to Anish Kumar and Derrick Krieder for help with lesiontracing procedures, and to Alice Proverbio and Federica Riva for sharing stimuli from Proverbio and Riva (2009).

References

- Antonucci, S. M., & Reilly, J. (2008). Semantic memory and language processing: A primer. Seminars in Speech and Language, 29(1), 5-17.
- Ashburner, J., Barnes, G., Chen, C. –C., Daunizeau, J., Flandin, G., Friston, K., ... & Phillips, C. (2012). SPM8 manual. Functional Imaging Lab, Inst. of Neurology. http://www.fil.ion.ucl.ac.uk/spm/doc/maual.pdf.
- Bak, T. H., & Hodges, J. R. (2003). Kissing and dancing- a test to distinguish the lexical and conceptual contributions to noun/verb and action/object dissociation. *Journal of Neurolinguistics*, 16(2), 169-181.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H. ...Rcpp, L. (2015). Package "Ime4." *Convergence*, *12*, 1.
- Bates, E., Wilson, S. M., Saygin, A. P., Dick, F., Sereno, M. I., Knight, R. T., & Dronkers, N. F. (2003). Voxel-based lesion-symptom mapping. *Nature Neuroscience*, 6(5), 448-450.
- Binney, R. J., Embleton, K. V., Jefferies, E., Parker, G. J. M., & Ralph, M. A. L. (2010). The ventral and inferolateral aspects of the anterior temporal lobe are crucial in semantic memory. *Cerebral Cortex*, 20(11), 2728-2738.
- Boylan, C., Trueswell, J. C., & Thompson-Schill, S. L. (2015). Compositionality and the angular gyrus: A multivoxel similarity analysis of the semantic composition of nouns and verbs. *Neuropsychologia*, 78, 130-141.
- Brett, M., Leff, A. P., Rorden, C., & Ashburner, J. (2001). Spatial normalization of brain images with focal lesions

using cost function masking. *Neuroimage*, 14(2), 486-500.

- Brett, M., Anton, J. L., Valabregue, R., & Poline, J. B. (2002). Region of interest analysis using an SPM toolbox. Presented at the 8th International Conference on Functional Mapping of the Human Brain (June, Sendai, Japan). Available on CD-ROM in *Neuroimage*, *16*(2).
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 29(3), 162-173.
- Den Ouden, D. –B., Fix, S., Parrish, T. B., & Thompson, C. K. (2009). Argument structure effects in action verb naming in static and dynamic conditions. *Journal of Neurolinguistics*, 22(2), 196-215.
- Federmeier, K. D. (2007). Thinking ahead: The role and roots of prediction in language comprehension. *Psychophysiology*, *44*(4), 491–505.
- Ferretti, T. R., McRae, K., & Hatherell, A. (2001). Integrating verbs, situation schemas, and thematic role concepts. *Journal of Memory and Language*, 44(4), 516-547.
- Hare, M., Jones, M., Thomson, C., Kelly, S., & McRae, K. (2009). Activating event knowledge. *Cognition*, 111(2), 151-167.
- Hillis, A. E., Oh, S., & Ken, L. (2004). Deterioration of naming nouns versus verbs in primary progressive aphasia. *Annals of Neurology*, 55(2), 268-275.
- Howard, D., & Patterson, K. E. (1992). *The Pyramids and Palm Trees Test: A test of semantic access from words and pictures.* Thames Valley Test Company.
- Howard, D., Swinburn, K., & Porter, G. (2004). *Comprehensive aphasia test*. Psychology Press.
- Kamide, Y., Scheepers, C., & Altmann, G. T. (2003). Integration of syntactic and semantic information in predictive processing: Cross-linguistic evidence from German and English. *Journal of Psycholinguistic Research*, 32(1), 37-55.
- 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*(7), 826-848.
- Kim, M., & Thompson, C. K. (2004). Verb deficits in Alzheimer's disease and agrammatism: Implications for lexical organization. *Brain and Language*, 88(1), 1-20.
- Lambon Ralph, M. A. (2014). Neurocognitive insights on conceptual knowledge and its breakdown. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369*(1634).
- Matsuki, K., Chow, T., Hare, M., Elman, J. L., Scheepers, C., & McRae, K. (2011). Event-based plausibility immediately influences on-line language comprehension. *Journal of Experimental Psychology: Learning, Memory,* and Cognition, 37(4), 913.
- Mätzig, S., Druks, J., Masterson, J., & Vigliocco, G. (2009). Noun and verb differences in picture naming: Past studies and new evidence. *Cortex*, 45(6), 738-758.

- McRae, K., & Matsuki, K. (2009). People use their knowledge of common events to understand language, and do so as quickly as possible. *Language and Linguistics Compass*, *3*(6), 1417-1429.
- Metusalem, R., Kutas, M., Urbach, T. P., Hare, M., McRae, K., & Elman, J. L. (2012). Generalized event knowledge activation during online sentence comprehension. *Journal of Memory and Language*, 66(4), 545-567.
- Metusalem, R., Kutas, M., Urbach, T. P., & Elman, J. L. (2016). Hemispheric asymmetry in event knowledge activation during incremental language comprehension: A visual half-field ERP study. *Neuropsychologia*, 84, 252–271.
- Mitchum, C., Haendiges, A., & Sloan Berndt, R. (2004). Response strategies in aphasic sentence comprehension: An analysis of two cases. *Aphasiology*, *18*(8), 675–692.
- Proverbio, A. M., & Riva, F. (2009). RP and N400 ERP components reflect semantic violations in visual processing of human actions. *Neuroscience Letters*, 459(3), 142-146.
- Rorden, C., Bonilha, L., Fridriksson, J., Bender, B., & Karnath, H. O. (2012). Age-specific CT and MRI templates for spatial normalization. *Neuroimage*, 61(4), 957-965.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural neurology*, 12(4), 191-200.
- Saur, D., Lange, R., Baumgaertner, A., Schraknepper, V., Willmes, K., Rijntjes, M., & Weiller, C. (2006). Dynamics of language reorganization after stroke. *Brain*, 129(6), 1371-1384.
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2012). E-Prime v2.0. Pittsburgh, PA: Psychology Software Tools.
- Squire, L. R. (1987). Memory and the Brain. In S. L. Friedman, K. A. Klivington, & R. W. Peterson (Eds.), *The Brain, Cognition, and Education* (pp. 171-202). Orlando, FL: Academic Press, Inc.
- Tulving, E. (1972). Episodic and semantic memory. In E.Tulving & W. Donaldson (Eds.), *Organization of Memory* (pp. 381-402). New York, NY: Academic Press, Inc.
- Tzouriou-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subj. brain. *Neuroimage*, 15(1), 273-289.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107(3), 829-853.
- Yee, E., Chrysikou, E. G., & Thompson-Schill, S. L. (2013). The cognitive neuroscience of semantic memory. *Oxford Handbook of Cognitive Neuroscience, Vol.* 1, 353-374.
- Yushkevich, P. A., Piven, J., Hazlett, H. C., Smith, R. G., Ho, S., Gee, J. C., & Gerig, G. (2006). User-guided 3D active contour segmentation of anatomical structures: Significantly improved efficiency and reliability. *Neuroimage*, *31*(3), 1116-1128.