# Personal Experience With Narrated Events Modulates Functional Connectivity Within Visual and Motor Systems During Story Comprehension

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**Abstract:** Past experience of everyday life activities, which forms the basis of our knowledge about the world, greatly affects how we understand stories. Yet, little is known about how this influence is instantiated in the human brain. Here, we used functional magnetic resonance imaging to investigate how past experience facilitates functional connectivity during the comprehension of stories rich in perceptual and motor details. We found that comprehenders' past experience with the scenes and actions described in the narratives selectively modulated functional connectivity between lower- and higher-level areas within the neural systems for visual and motor processing, respectively. These intramodal interactions may play an important role in integrating personal knowledge about a narrated situation with an evolving discourse representation. This study provides empirical evidence consistent with the idea that regions related to visual and motor processing are involved in the reenactment of experience as proposed by theories of embodied cognition. *Hum Brain Mapp 36:1494–1505, 2015.* © 2014 Wiley Periodicals, Inc.

**Key words:** embodiment; discourse; simulation; knowledge; language

## INTRODUCTION

Language comprehension during everyday communication entails not only the decoding of semantic and syntactic information from linguistic inputs but also the incorporation of one's knowledge about the world. By integrating these two sources of information, a mental representation of the described situation is constructed, known as a situation model [Hagoort and van Berkum, 2007; Johnson-Laird, 1983; Kintsch, 1988; van den Broek, 2010]. A crucial factor that influences a comprehender's ability to construct such a mental representation is whether or not she has had experiences similar to those being described [Barsalou et al., 2003; Bransford and Johnson, 1972; Kendeou and Van den Broek, 2007; Maguire et al., 1999]. In particular, past perceptual or motor experiences can flesh out the details of the described situation. For example, if presented with a story that includes the iconic four-faced clock in New York's Grand Central Station, those who are familiar with this station and the clock are likely to create a more detailed and vivid mental representation of this scene than those who are not. Confirming this intuition, behavioral research has demonstrated that past experience plays an important role in story comprehension [Bartlett, 1932; Green, 2004; Krajcik and Sutherland, 2010; Larsen and Seilman, 1988; McNamara and Kintsch, 1996].

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: NIDCD Intramural Research Funds ZIA-DC000031-19 (to A.R.B.)

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Received for publication 5 May 2014; Revised 27 October 2014; Accepted 4 December 2014.

DOI: 10.1002/hbm.22718
Published online 25 December 2014 in Wiley Online Library (wileyonlinelibrary.com).

How do our past experiences modulate neural processing during story comprehension? The crux of this issue centers on the neuroanatomical organization of knowledge acquired through past experience. It is generally agreed on that sensory-motor knowledge is at least partially represented in the same neural systems that are responsible for perception and action. For example, various basic visual features and action concepts are represented in different parts of the visual and motor cortices [Albright, 2012; Gainotti et al., 2009; Goldberg et al., 2006; Grezes and Decety, 2001; Hauk et al., 2004; Haxby et al., 2001; Mahon and Caramazza, 2003; Martin and Chao, 2001]. Recent studies show that more complex representations are formed through interactions between primary and higher-order association areas within the visual or motor processing systems. [Freeman et al., 2011; Singer and Gray, 1995; Yanagisawa et al., 2012; Zhu et al., 2011]. Recent theories further propose that the interactions instantiated in the visual and motor processing systems play an important role in organizing high-level conceptualizations that support language comprehension [Barsalou, 2009; Binder and Desai, 2011; Damasio, 1989; Friston, 2002; Thut et al., 2012]. From this perspective, a comprehender's past visual and motor experience with a situation being described should facilitate the interactions between regions representing visual and motor knowledge, localized within the visual or motor processing system.

To test this hypothesis, this study used a functional connectivity approach to examine how past experience with everyday scenes and actions influences interactions between regions in visual/motor processing systems and the rest of the brain during narrative comprehension. We predicted that experience with visual scenes would evoke richer representations of visual knowledge to be integrated with the semantic information delivered by the text. This would lead to the enhancement of connectivity among regions recruited for visual processing as the visual components of the situation model are being constructed. By the same token, experience with bodily actions should result in greater connectivity among regions for motor processing. An alternative hypothesis is also possible, however, in which less experience with the events described triggers strategic processes similar to mental imagery, resulting in increased connectivity for those less experienced. Although this is a possibility, elaborative mental imagery is effortful and slow, and may be unlikely to occur during the progress of natural story comprehension as studied here [Zwaan and Radvansky, 1998].

## MATERIALS AND METHODS

### Participants

Participants were 24 native speakers of English (11 females and 13 males; aged 21–33) with no history of neurological or psychiatric disease. All were right-handed according to the Edinburgh Handedness Inventory [Oldfield, 1971]. Informed written consent was obtained from each participant in accordance with the protocol approved by the NIH CNS Institutional Review Board. Participants were compensated for participating in the study.

### Text Stimuli

The stimuli consisted of 18 stories, written by the authors. Each story was made up of three paragraphs conforming to a typical story structure, including setting, initiation of events, and resolution. Four types of content were manipulated between paragraphs, namely descriptions of scenes (Perception Condition), bodily actions (Action condition), emotionally charged events (Emotion Condition), and abstract factual description or typical everyday events (Control condition). The data collected were previously analyzed to examine the effect of content, unrelated to past personal experience, for a separate publication [Chow et al., 2014].

To ensure that participants had a wide range of experience with the situations to be described during the experiment, the story topics were selected based on the results of a pilot survey. This survey was completed by separate sample of subjects chosen from the same population from which the sample of fMRI participants was drawn. Thirty four participants (mean age $25.4 \pm 0.1$ years; ranging from 22.2 to 35.6) rated the degree to which they had direct, past personal experience with a broad array of topics including 52 scenes, 61 activities involving bodily movements, and 32 emotionally charged events on a scale from 1 (not at all) to 5 (very much). Story stimuli were then created around the topics that the sample reporting having a wide variety of experience with (defined as 15% or more participants reporting experience in at least three out of the five possible levels of experience. This approach was used to maximize the variability in personal experience for our sample, decreasing potential problems associated with restriction of range.

This study focused on the modulatory effects of experience during comprehension of the visually vivid (Perception Condition) and action-rich (Action Condition) content. We focused on these two types of content because participants reported a relatively evenly distributed range of experience with these topics. For the events in the Emotion Condition, participants reported either having or not having had experience with the situations described, which did not provide sufficient variability to relate to fluctuations in functional connectivity. The key conditions (Perception and Action) each consisted of 12 paragraphs, out of a total of 54 paragraphs. We matched the paragraphs in each condition on a variety of linguistic features including the number of syllables, words, words per sentence, as well as readability, word frequency and imageability (see Table S1 in the Supporting Information for details). In addition, stories were recorded so that they could be presented aurally. A pre-study with 19 participants (3 males and 16 females; aged 22–34) was performed to confirm that the story content had been manipulated as intended (i.e., that story segments in the Perception condition were rated as more visually vivid whereas those in the Action condition were rated as more intense in action). For the details of this pre-study and the audio recording procedure, please see the Supporting Information.

### Experimental Design

Stories containing different content types were presented in random order, without repetition, in a single fMRI session. To allow the hemodynamic response to return to baseline, paragraphs within a story were separated by 12 sec; the interval between stories was 16 sec. Participants were instructed to listen to the stories carefully and to do nothing during interstimulus intervals. To measure whether or not participants paid attention to the stimuli, they were asked to answer three yes–no comprehension questions after each run, responding via button press. The mean accuracy of the 24 participants included in the subsequent fMRI analyses was $88.5\% \pm 4.3\%$ (S.D.), indicating that participants paid attention to the story stimuli.

### Experience Ratings

Immediately after the fMRI experiment, written versions of the stories were presented to participants in random order. For each paragraph of the Perception and Action conditions, participants were asked to rate how much direct, past personal experience they had with the described situation on a scale from 1 (not at all) to 5 (very much). Specifically, when rating their experience they were instructed to consider both how often they had encountered the described situation in the past along with the intensity of those experiences. Additionally, participants rated the vividness of each paragraph on a five-point scale, which was used to evaluate whether personal experience contributes to building up a vivid story representation.

### MRI Data Acquisition

Whole-brain gradient-echo echo-planar imaging (EPI) data were acquired on a 3-T GE Signa scanner with an eight-channel head coil (repetition time = 1500 ms, echo time = 30 ms, flip angle = 90°, $64 \times 64$ matrix, field of view 224 mm, 30 sagittal slices acquired in interleaved order, slice thickness: 5 mm, acceleration factor: 2). High resolution structural images were acquired using a magnetization prepared rapid acquisition gradient echo sequence (MPRAGE: voxel size: $0.81 \times 0.81 \times 1.0$ mm).

### fMRI Data Preprocessing

Using AFNI [Cox, 1996], functional images of each participant were aligned to the first images on a slice-by-slice basis, timing differences in acquiring each slice were corrected, and then, each volume was aligned to the first volume using rigid body rotation. To remove the physiological and motion-related artifacts, spatial independent component analysis (sICA, [McKeown et al., 1998]) was applied to the motion and slice-time corrected functional data for each subject using the GIFT toolbox (http://mialab.mrn.org/software/gift/index.html). In sICA, each functional image was treated as a mixture of multiple spatially independent signal and noise components. The number of components in each dataset was estimated by minimum description length criterion [Li et al., 2007]. Classification of artifactual and neuronal ICA components was based on their degree of spatial clustering, location of major positively weighted clusters, and neighborhood connectedness between positively and negatively weighted clusters. Using these criteria, the noise components were identified by human experts and their variances were then subtracted from the original dataset [AbdulSabur et al., 2014; Xu et al., 2014]. The functional and anatomical images of each participant were coregistered and normalized to the stereotaxic space of the Montreal Neurological Institute (MNI) using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). All coordinates are reported in MNI space. The functional images were resampled to a voxel size equal to $3 \times 3 \times 3$ mm and smoothed with an isotropic 6-mm full-width-half-maximum Gaussian kernel.

### Seed Regions Selection

As we hypothesized that visual and motor experience with the narrated situations would selectively modulate connectivity associated with the regions involved in visual and motor processing, we defined seed regions for the connectivity analyses using two criteria. First, we confined the search space for the seed regions to the vicinity of the cortical areas previously shown to play an essential role in the processing of visual scenes and motor actions [Epstein, 2008; Fogassi and Luppino, 2005; Gazzola and Keysers, 2009; Kravitz et al., 2011]. To reduce the potential arbitrariness of this process, we used the WFU PickAtlas to define areas related to visual and motor processing [Maldjian et al., 2003]. The visual processing areas we chose included the occipital lobe, the fusiform gyrus, the hippocampus, the parahippocampal gyrus, the precuneus, and the posterior cingulate cortex including the retrosplenial cortex (WFU PickAtlas regions 35–40, 43–56, and 67–68). The motor processing areas included the precentral gyrus, the postcentral gyrus, the supplementary motor area, and the paracentral lobule (WFU PickAtlas regions 1–2, 17–20, 57–70). We extended the regions of the precentral and postcentral gyri defined in the atlas 15 mm anteriorly to the frontal lobe and 15 mm posteriorly to the parietal lobe to include the dorsal premotor and the anterior intraparietal areas, both of

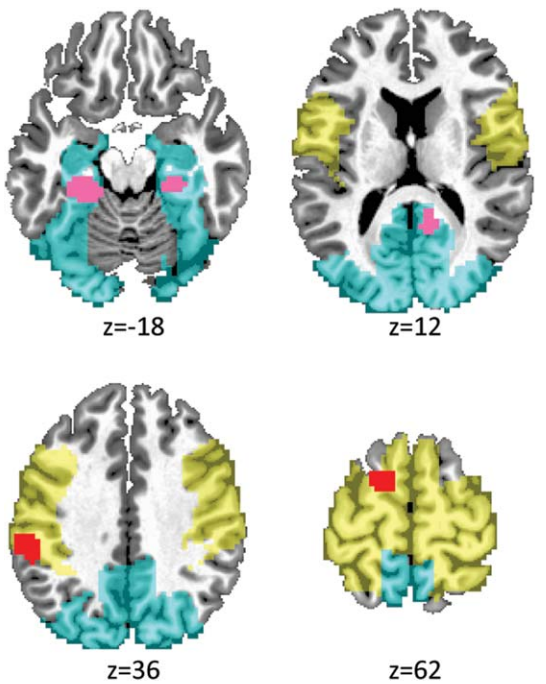


**Figure 1.**
The visual (indicated in turquoise) and motor (indicated in yellow) areas defined in this study. In these areas, three visual seeds (indicated in pink) and two motor seeds (indicated in red) were defined by the clusters significantly activated in the direct comparisons between Perception and Action conditions. The underlays are axial slices of a single subject's T1 image.

which have been shown to be important to motor processing [Van Overwalle and Baetens, 2009]. We then identified peak activations from the contrasts between the Perception and Action conditions that overlapped with the visual and motor processing areas defined by the atlas; these peaks constituted the locations of our visual and motor seed regions. The final seeds regions, which fulfilled the above two criteria, were located in the parahippocampal gyrus, the retrosplenial cortex, the dorsal premotor area, and the anterior intraparietal area. Although these are not primary or secondary visual or motor areas, they are higher-order association areas unambiguously linked to visuospatial and motor processing. The search space for the seed regions and content-related activations are shown in Figure 1.

## Conventional Activation Analysis

As mentioned in the previous paragraph, the results of the activation analysis were one of the criteria used to define seed regions for our functional connectivity analyses. An activation analysis was conducted using the framework of the general linear model (GLM) implemented in SPM8. At the subject level, separate regressors were constructed by convolving the box-car function of each condition with the canonical hemodynamic response function. The model also included regressors of no interest to account for variance due to low-frequency (<1/128 Hz) scanner drift, global signal fluctuations, and acoustic features of the story stimuli including pitch and loudness. Subject-level GLM was computed using classical restricted maximum likelihood estimation. Individual model parameters were entered into a second-level random effects analysis. The contrast between Perception and Action conditions was computed using paired *t*-tests. The statistical threshold was set at $P < 0.001$ with a cluster size threshold of $k > 30$, corresponding to a corrected $P < 0.01$ based on Monte Carlo simulations (computed by 3dClustSim in AFNI; [Ward, 2000]).

## Modulatory Effect of Experience on Functional Connectivity

The residual time-series of each voxel for the individual GLMs was band-pass filtered with cutoff frequencies at 0.03 and 0.3 Hz, which ensured that the connectivity between regions was not affected by high frequency physiological noise or low frequency scanner drift. For each paragraph containing vivid descriptions of scenes or actions (30 sec, 20 TRs), the time-series of the voxels within a 5 mm radius sphere at each seed location were extracted and averaged. A Pearson correlation coefficient ($r$) between the seed region time-series and each voxel in the whole brain was computed, generating 12 functional connectivity maps corresponding to the 12 paragraphs in each condition. For each set of functional connectivity maps, a Spearman correlation coefficient ($\rho$) was calculated to quantify the monotonic relationship between functional connectivity ($r$) and the associated experience ratings voxel by voxel. The Spearman correlation coefficients ($\rho$) were then converted to Fisher's $z$. For each seed, individual $z$-maps of each condition were entered into a second-level random-effects analysis. As we expected that experience would facilitate functional connectivity between regions, for each voxel we used a one-sample $t$-test to examine whether the modulatory effect of experience on connectivity associated with each condition was significantly larger than zero. $T$-tests were used to compare the modulatory effect of experience on connectivity between conditions. Specifically, we compared whether the modulation of experience was stronger in the Perception condition than in the Action condition for the visual seeds and whether the modulation of experience was stronger in the Action condition than in the Perception condition for the motor seeds. The statistical threshold was set at $P < 0.0075$ and $k > 51$, corresponding to corrected $P < 0.05$ based on Monte Carlo simulations (computed by 3dClustSim in AFNI).

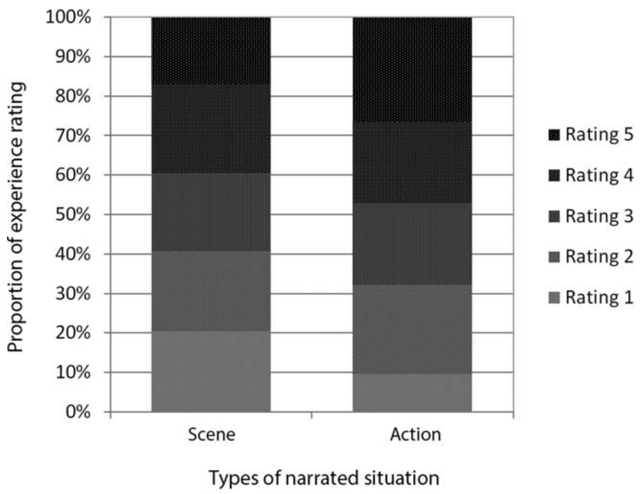


**Figure 2.**
The proportion of experience ratings averaged across participants. Experience with each depicted scene or action was rated on a scale from 1 (not at all) to 5 (very much).

### Modulatory Effect of Experience on Activation Magnitude

The participants' experience ratings for paragraphs describing scenes and actions were also included as parametric modulators in the activation analyses described above, capturing the modulatory effect of experience on hemodynamic responses (i.e., parametric modulation of activation magnitude). Individual model parameters were entered into a second-level random effect analysis. The modulatory effect of experience on activation magnitude associated with each condition was compared with zero using a one-sample *t*-test. Statistical threshold was set at the same threshold used in the analyses of modulatory effect on functional connectivity ($P < 0.0075$ and $k > 51$, corresponding to a corrected $P < 0.05$).

## RESULTS

### Experience and Vividness Ratings

Ratings of past experience, shown in Figure 2, demonstrate that the participants had a wide range of experience with the scenes and actions described in our stories. The average proportion of ratings was roughly evenly distributed across the full range of the scale. Moreover, the profile of experience with the depicted situations varied widely across participants. This is reflected by the low level of consistency of experience ratings among subjects, as illustrated by low intraclass correlations (Perception: ICC = 0.18, Action: ICC = 0.20; [Landis and Koch, 1977; McGraw and Wong, 1996]).

In addition to experience ratings, participants also rated the vividness of each story segment. For each condition, we evaluated the effect of experience on perceived vividness of story segments using an ANOVA model with experience-ratings acting as a fixed-effect factor and subject as a random-effect factor. We found that perceived vividness varied with experience in the Perception condition ($F[4, 92] = 7.3$, $P < 0.05$) and the Action condition ($F[4, 92] = 3.4$, $P < 0.05$). To illustrate the relationship between experience and vividness, the average vividness ratings for each level of experience is shown in Figure 3, with greater past experience clearly predicting greater perceived vividness. This is consistent with evidence from past behavioral research demonstrating that personal experience contributes to the construction of a more vivid mental representation of stories [Green, 2004; Long et al., 2008].

### Modulatory Effect of Experience on Functional Connectivity Between Regions

Our primary aim was to examine whether personal experience with the situations described in a story affects the functional connectivity of related brain regions. Toward this aim, we first identified clusters activated in response to the visual and action content of our stories within the visual and motor processing systems; these were used as seeds in the connectivity analysis (for details, see Methods). A total of five clusters were identified and their approximate peaks are indicated by green dots in Figures 4 and 5.

For each condition, we performed whole-brain analyses that identified regions whose functional connectivity with each seed co-varied with experience ratings. As predicted, these analyses showed that past experience with the described situations modulated the functional connectivity within the visual and motor systems themselves (see Table I). Importantly, the modulatory effect of experience depended on the type of content being processed. While processing visually vivid content, a greater degree of personal experience was associated with increases in functional connectivity between all three visual seeds and other regions in the visual processing system, including the cuneus, the lingual gyrus, the fusiform gyrus, and the parahippocampal gyrus (Fig. 4 and Table I). For the Perception condition, there were no statistically significant modulatory effects found between any visual seed and any other brain region outside of the visual processing system.

In stark contrast, during the processing of action content, greater experience was associated with increases in functional connectivity between the motor seeds and other motor processing areas, including the bilateral precentral/postcentral gyri, the supplementary motor area, and the ventral premotor area (Fig. 5 and Table I). During the Action condition, there was no modulatory effect between any motor seed and any other brain region outside of the motor processing areas.

Next, we directly compared the effect of experience between the two conditions. The modulation of

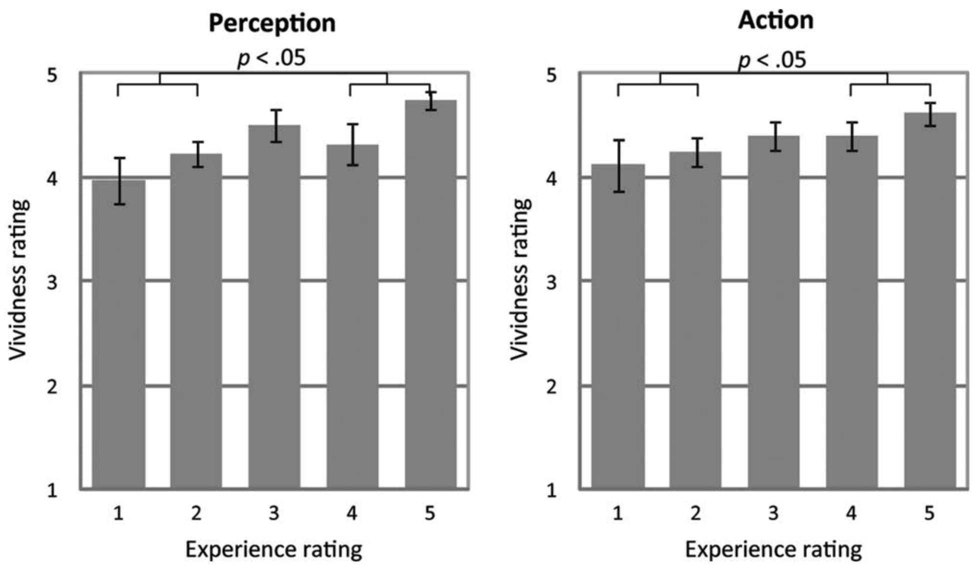


**Figure 3.**
The mean vividness ratings in each level of experience in the Perception (left panel) and Action (right panel) conditions. Consistent across conditions, participants rated the story segments as more vivid if they had personal experience with the described events. The error bar indicates the standard error of mean.

connectivity between the visual seeds in the parahippocampal gyri and a number of visual areas (including the cuneus and the lingual gyrus) was stronger in the Perception condition than in the Action condition (Table I). However, there was no significant difference for the same comparison based on the seed in the retrosplenial cortex. For both motor seeds, the modulatory effect with at least one of the motor areas (including the premotor area and the precentral gyrus) was stronger in the Action condition than in the Perception condition (Table I).

**TABLE I. Effects of experience on functional connectivity in the Perception and Action conditions**

| | | Perception | | | Perception − Action | | |
|---|---|---|---|---|---|---|---|
| Seed regions | Modulated regions | *x*, *y*, *z* | *T* | cm$^3$ | *x*, *y*, *z* | *t* | cm$^3$ |
| Visual seeds[a] | | | | | | | |
| Left parahippocampal gyrus | R. cuneus | 24, −72, 18 | 4.28 | 2.9 | 24, −75, 27 | 4.42 | 8.5 |
| | R. lingual gyrus | 15, −63, −3 | 3.79 | 2.5 | 12, −69, −12 | 3.40 | 1.7 |
| | L. lingual gyrus/L. cuneus | −21, −60, −6 | 3.59 | 1.5 | −9, −87, 0 | 3.34 | 1.4 |
| Right parahippocampal gyrus | L. fusiform/lingual gyrus | −27, −57, −15 | 3.68 | 1.6 | | | |
| | R. precuneus/R. cuneus | | | | 12, −75, 36 | 4.26 | 2.8 |
| Right retrosplenial cortex | R. parahippocampal gyrus | 30, −48, −12 | 4.85 | 3.1 | | | |
| | L. middle temporal gyrus/L. middle occipital gyrus | −45, −66, 3 | 3.93 | 2.2 | | | |
| Motor seeds[b] | | Action | | | Action − Perception | | |
| Left anterior intraparietal area | L. post/precentral gyrus | −63, −18, 33 | 4.20 | 1.6 | | | |
| | R. ventral premotor area | 60, 9, 12 | 4.06 | 1.5 | 63, 9, 9 | 4.30 | 1.7 |
| | R. post/precentral gyrus | 63, −18, 27 | 3.40 | 2.4 | | | |
| Left dorsal premotor area | L. ventral precentral gyrus | −60, −9, 9 | 3.85 | 3.4 | −57, −18, 12 | 3.58 | 1.4 |
| | R. ventral precentral gyrus | 54, −12, 12 | 4.11 | 1.9 | | | |
| | L./R. supplementary motor area | −3, −6, 72 | 4.28 | 1.5 | | | |

[a]For all visual seeds, no significant modulatory effect was found in the Action condition.
[b]For all motor seeds, no significant modulatory effect was found in the Perception condition.

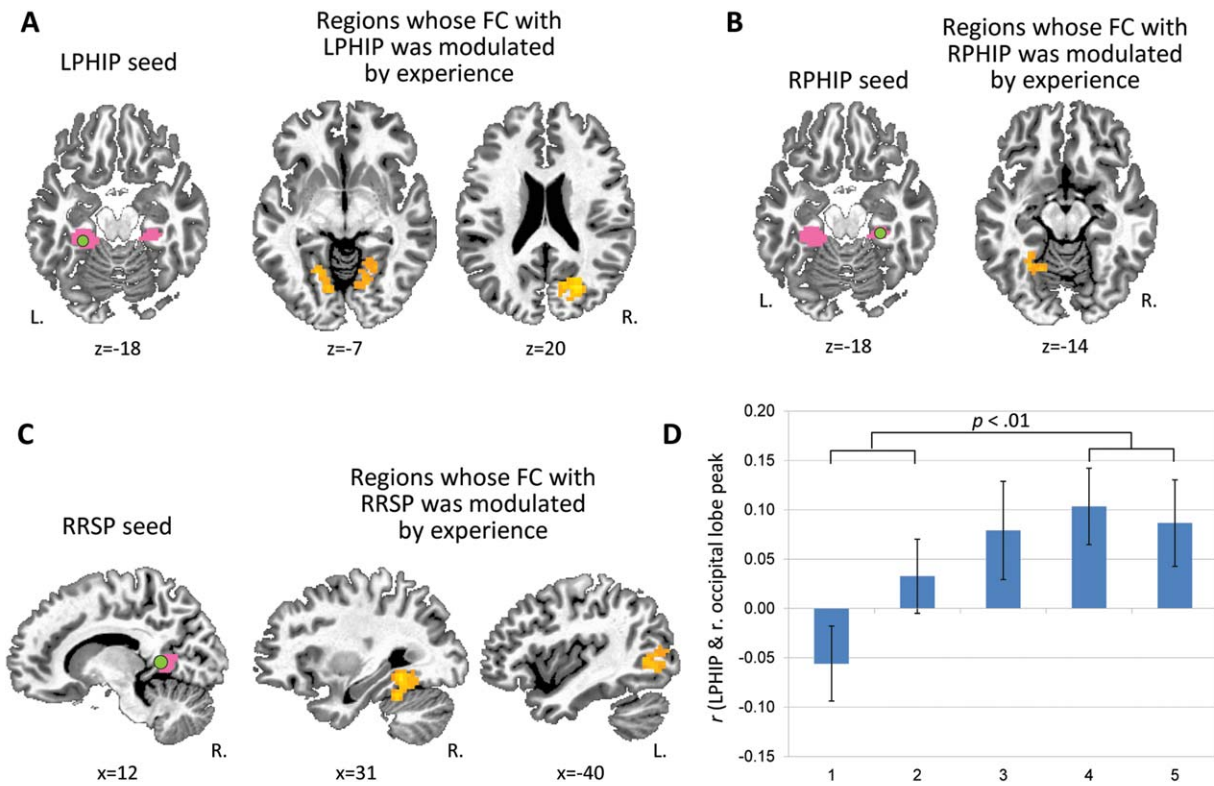


**Figure 4.**

The modulatory effects of experience on functional connectivity (FC) of the visual seeds while participants were listening to stories with vivid visual content. The clusters indicated in orange are regions whose FC with (A) the left parahippocampal gyrus (LPHIP), (B) the right parahippocampal gyrus (RPHIP), and (C) the right retrosplenial cortex (RRSP) was significantly modulated by the participant's experience with the narrated situation ($P < 0.05$, corrected). In these panels, the approximated locations of the seeds (indicated in green) were overlaid on the regions significantly activated in the Perception condition compared with the Action condition (indicated in pink). The underlays are axial or sagittal slices of a single subject's T1 image. (D) An example of the modulatory effect of experience on FC in the Perception condition. The bar chart shows the correlation (Pearson's *r*, averaged across participants) between the LPHIP seed and a region in the right occipital lobe that showed the strongest experience-related FC modulatory effect, at each level of experience rating. The error bars indicate the standard error of mean across participants. There was a significant difference in FC between low (rating 1 and 2) and high (rating 4 and 5) experience with the narrated situation ($P < 0.01$).

### Modulatory Effect of Experience on Activation

One possible explanation of the foregoing results is that the modulation effects observed might simply be attributed to differences in the magnitude of activation, rather than functional connectivity per se. To examine this possibility, we used a parametric modulation method to directly quantify the relationship between the magnitude of hemodynamic responses and the experience ratings in each condition. In contrast to the modulation effects of experience on functional connectivity, activation per se was not significantly modulated by experience in visual or motor processing areas, or any other brain region for the Perception or Action conditions.

## DISCUSSION

In this study, we found that a subject's experience with the content of a narrated situation has dramatic effects on the functional connectivity of regions within visual and motor processing systems. Specifically, experience with visual and action story content selectively modulated functional connectivity between regions within the visual and motor-processing systems, respectively. This indicates that past personal experience influences the construction of a story representation during comprehension. We propose that the selective augmentation of intramodal interactions plays a role in integrating past experiential knowledge and textual information into a complex, "fleshed out," representation of the narrative.

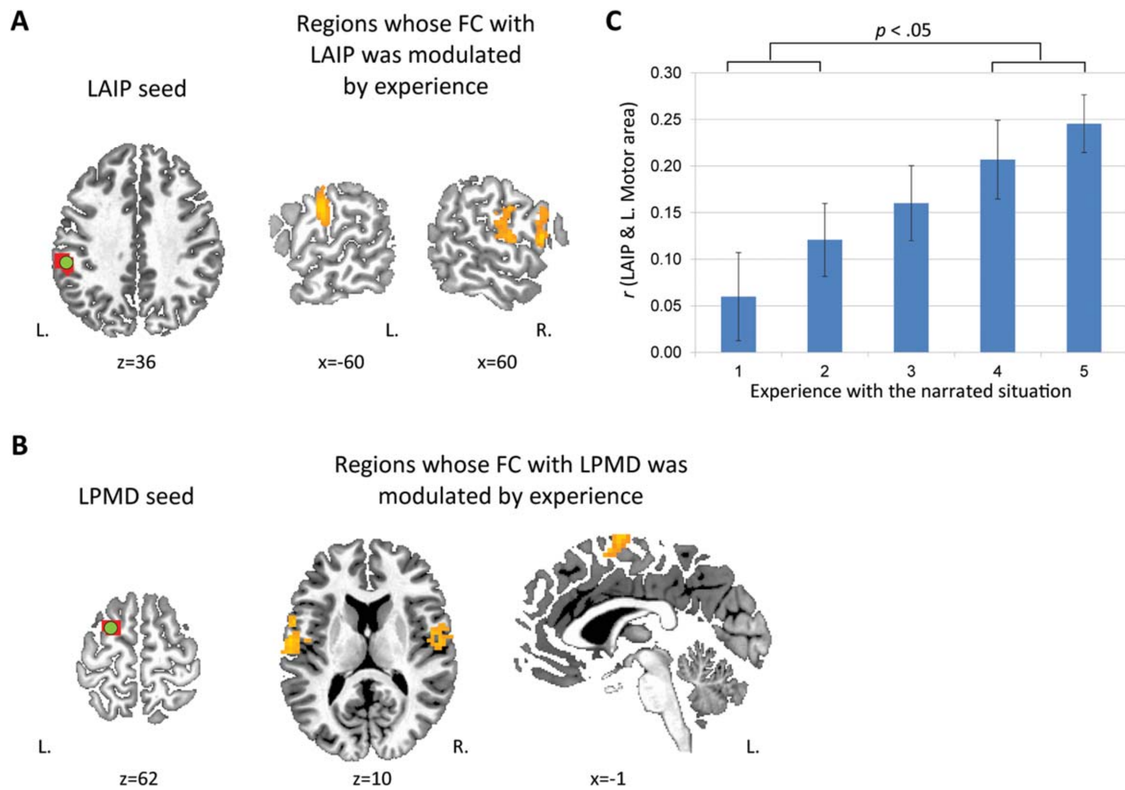


**Figure 5.**

The modulatory effects of experience on function connectivity (FC) of the motor seeds while participants were listening to stories with action-rich content. The clusters indicated in orange are regions whose FC with (A) the left anterior parietal area (LAIP) and (B) the left dorsal premotor area (LPMD) was significantly modulated by the participants' experience with the narrated situation ($P < 0.05$, corrected). In these panels, the approximated locations of the seeds (indicated in green) were overlaid on the region significantly activated in the Action condition compared with the Perception condition (indicated in red). The underlays are axial or sagittal slices of a single subject's T1 image. (C) An example of the modulatory effect of experience on FC in the Action condition. The bar chart shows the correlation (Pearson's *r*, averaged across participants) between the LAIP seed and a region in the left primary motor cortex that showed the strongest experience-related FC modulatory effect, at each level of experience rating. The error bars indicate the standard error of mean across participants. There was a significant difference in FC between low (rating 1 and 2) and high (rating 4 and 5) experience with the narrated situation ($P < 0.05$).

For a long time, behavioral research has shown that prior knowledge has a marked effect on narrative comprehension. Personal memories are evoked during reading [Larsen and Seilman, 1988], relevant personal experience results in greater engagement with a text [Green, 2004] and experience also shapes the recall of story content [Bartlett, 1932; Bransford and Johnson, 1972; Kintsch, 1994]. Long et al. [2008] argue that the facilitatory effect of prior knowledge on text memory is due to the construction of a content-rich representation during comprehension. Consistent with this proposal, our own behavioral data show that personal experience is associated with greater subjective vividness of story passages. This further supports our interpretation that past experience contributes to the formation of a rich narrative representation.

How might past experience enrich narrative comprehension? What degree of similarity between the depicted situation and past experience is required in order for these heightened intramodel interactions to be observed? Although conjectural at this point, we believe that a one-to-one mapping is not necessary for experience to play a role in comprehension. That is, as the stories we presented involved quite specific situations, it is unlikely that our participants had personally experienced these exact scenarios. In light of this, listeners likely drew on similar categories of experience to enrich their situation models. For example, even if a participant listening to a tale about baking a caramel custard has never baked that specific dessert, past experience with baking will likely be drawn from to produce a more detailed representation of the scenario.

In addition, experience-related enrichment during mental reconstruction may involve the retrieval of both semantic and episodic memories. The degree of similarity between the depicted situation and past experience may result in a differential contribution of episodic memories and semantic knowledge to enrichment of representations during story comprehension. In the example of baking a caramel custard, a comprehender might draw on semantic knowledge of baking in general (e.g., remembering to preheat the oven) as well as episodic memories (e.g., the time they had such trouble separating egg yolks from the whites that they wasted five eggs), even when these episodic memories do not match all the parameters of the described situation but rather resonate with the theme (e.g., making mistakes while baking).

Our results relate to a series of past imaging studies that investigated the effect of experience on sentence comprehension by comparing experts with novices. Beilock et al. [2008] showed that professional hockey players exhibit greater activation in the left premotor area and left inferior frontal gyrus during the comprehension of hockey-related sentences, compared to novices. This pattern of results likely reflects the retrieval of specialized motor concepts that professional hockey players possess but that novices lack. In this way, it is similar to previous studies that have found activation of premotor regions when subjects comprehend text associated with actions, compared to nonaction text [Tettamanti et al., 2005]. It also parallels our contrast between the Action and Perception conditions (see Fig. 1), which similarly demonstrated that comprehending action language evokes activation in premotor areas.

The effect of expert knowledge, however, might be quite different from the effect of everyday experience during comprehension. To the best of our knowledge, no previous brain imaging study has investigated the effect of everyday experience on language comprehension. In contrast to expert knowledge, our results showed that experience with everyday life activities did not modulate the magnitude of activation in motor or visual processing regions. This is likely due to the fact that our participants may have sufficient knowledge of these everyday situations to support basic comprehension. Rather than a difference in activation, what we observed was modulation of intranetwork connectivity. This may reflect the role of experience in enhancing the ability to efficiently retrieve details of actions or scenes and integrate them within a burgeoning mental model. This interpretation is partially consistent with the results of recent studies suggesting that experience enhances processing efficiency, accompanied by an increase of connectivity and concomitant attenuation of activation in the relevant brain regions [Gotts et al., 2012]. It is also congruent with other accounts arguing that connectivity reflects integrative processes [Damasio, 1989; Zhu et al., 2011].

On the basis of our results, and in light of previous work, we propose that functional connectivity is a plausible mechanism through which detailed visuomotor knowledge is made available for the construction of a story representation. This interpretation is consistent with the idea that functional connectivity reflects the encoding and representation of our past experience [Baldassarre et al., 2012; Koyama et al., 2011; Lewis et al., 2009; Zhu et al., 2011]. Moreover, the nature of the regions in which connectivity was selectively modulated by experience supports this interpretation. Although all of our seed regions were higher-level areas in the visual and motor-processing systems, connectivity with at least one lower-level area within these systems was, in each case, modulated by experience (Table I). Based on functional-anatomical hierarchies, lower-level areas may support the retrieval and maintenance of specific visuomotor features whereas higher-level areas represent more complex and abstract concepts [Grill-Spector and Malach, 2004; Uithol et al., 2012]. Enhanced connectivity between higher- and lower-level areas may, therefore, reflect the integration of specific information with a growing unified representation of the described situation, as suggested in previous studies on visual perception [Damasio, 1989; DeGutis et al., 2007; Freeman et al., 2011; Fries, 2009; Singer and Gray, 1995; Zhu et al., 2011].

Recent theories of embodied cognition have proposed that language comprehension is a mental simulation process, through which relevant perceptual or motor experience is reenacted, leading to the engagement of modality-specific brain regions [Barsalou, 2008]. A growing body of literature has shown that activations in the sensory, motor, and affective areas during comprehension are indeed content-dependent [e.g., Chow et al., 2014; Desai et al., 2010; Ferstl et al., 2005; Speer et al., 2009]. However, these activations alone do not necessarily indicate that past personal experience, as predicted by embodied cognition theories, plays an instrumental role in this process. In contrast, this study provides empirical evidence that past experience systemically modulates relevant neural processes during comprehension. This modulatory effect seems likely to reflect an important constituent of the enactment process.

Although incidental, our results may also help to clarify a currently ongoing debate regarding the role of lower-level visual and motor areas in the occipital lobe and precentral/postcentral gyri during language comprehension [Meteyard et al., 2012]. On the one hand, the majority of previous imaging studies (using conventional activation analysis methods) did not find content-related activation in these areas during language comprehension, unless conscious imagery was encouraged [Thompson-Schill, 2003; Tomasino et al., 2007; Willems et al., 2010]. On the other hand, another line of research has shown that disruption of the primary motor cortex (using transcranial magnetic stimulation) impairs action-word comprehension [Gerfo et al., 2008; Oliveri et al., 2004; Repetto et al., 2013]. In our own data, descriptions of scenes and actions activated higher-level regions such as the parahippocampal gyrus and the premotor areas, but did not elicit increased responses in the occipital lobe or primary motor and somatosensory cortices, consistent with previous imaging studies [e.g., Desai et al., 2010; Martin and Chao, 2001]. However, our connectivity analyses show that these lower-level regions exhibit enhanced connectivity with higher-level regions as a function of experience. In fact, 9 out of the 12 regions exhibiting enhanced connectivity with the seed regions (all of which are higher-level areas) were located in the occipital lobe or precentral/postcentral gyri (lower-level areas; see Table I). In other words, the lower-level visual and motor areas appear to be involved in natural story comprehension through their interactions with higher-level areas within each processing stream. These interactions may represent the neural mechanism underlying the implicit imagery that is engaged during language comprehension [Willems et al., 2010] and cognitive simulation—"the reenactment of perceptual, motor, and introspective states acquired during experience with the world, body, and mind" proposed by Barsalou (2008, p. 618).

The modulatory effects of experience on functional connectivity observed in this study provide empirical evidence consistent with aspects of embodied cognition theories, specifically those that postulate that modality-specific regions serve as modal convergence zones, binding sensory-motor features into entities [Barsalou, 2003; Binder and Desai, 2011; Damasio, 1989]. Although these theories also predict that the generation of higher-level representations involves direct or indirect interactions between modality-specific systems, these cross-modal interactions were not evident in this study. This is may be a function of our experimental design, in which only one type of content was manipulated in each condition. Cross-modal interactions would likely be enhanced by experience if subjects had processed stories in which integration of sensory-motor information was required for comprehension.

Additionally, it is possible that under certain circumstances the relationship between experience and functional connectivity might differ from what we observed in this study. For example, a comprehender's lack of experience with the described situation may trigger strategic processes similar to mental imagery. These processes could be initiated in two circumstances: (1) When the comprehender's experience is not sufficient to fully understand what is being described in the text, and/or (2) when the comprehender consciously imagines the described situation to achieve a specific goal [Graesser et al., 1994]. In these cases, additional information is retrieved and integrated into a discourse representation, which may lead to increased connectivity. However, neither of these circumstances is likely to occur within the design of this experiment. First, all of the situations described in our stimuli are related to everyday activities (e.g., baking, playing basketball, encountering natural scenes). Although some participants reported that they had not had much direct experience with these activities, it is reasonable to believe that they have ample indirect experience with these activities through TV and other sources. It is highly unlikely that they were so unfamiliar with these activities that they could not comprehend them. Moreover, the process of generating visual imagery is considered to be effortful, slow, and initiated consciously. Since detailed visual images take time to form (on the scale of seconds), it seems unlikely that conscious mental visualization was occurring during comprehension of the aurally-presented stories we used [Zwaan and Radvansky, 1998]. Moreover, we provided no specific instructions to consciously visualize the stories, so it seems unlikely that our participants would do so unnecessarily. Further research will be necessary to understand the effect of experience on functional connectivity during the aforementioned circumstances.

## CONCLUSION AND IMPLICATIONS

We conclude that interactions between higher- and lower-level areas within the visual and motor processing systems, strongly modulated by personal experience, represent an underlying neural mechanism through which visual and motor knowledge is retrieved and integrated into a rich mental representation during narrative comprehension. As experiential knowledge is not only used during language comprehension but is also crucial for memory recall and prospection, this work may have implications for the role of functional connectivity in other processes that rely on mental reconstruction.

## ACKNOWLEDGMENT

The authors thank Maja Djikic for her assistance in story composition.

## REFERENCES

AbdulSabur NY, Xu Y, Liu S, Chow HM, Baxter M, Carson J, Braun AR (2014): Neural correlates and network connectivity underlying narrative production and comprehension: A combined fMRI and PET study. Cortex 57:107–127.

Albright TD (2012): On the perception of probable things: Neural substrates of associative memory, imagery, and perception. Neuron 74:227–245.

Baldassarre A, Lewis CM, Committeri G, Snyder AZ, Romani GL, Corbetta M (2012): Individual variability in functional connectivity predicts performance of a perceptual task. Proc Natl Acad Sci USA 109:3516–3521.

Barsalou LW (2003): Situated simulation in the human conceptual system. Lang Cogn Process 18:513–562.

Barsalou LW (2008): Grounded cognition. Annu Rev Psychol 59: 617–645.

Barsalou LW (2009): Simulation, situated conceptualization, and prediction. Philos Trans R Soc Lond B Biol Sci 364:1281–1289.

Barsalou LW, Kyle Simmons W, Barbey AK, Wilson CD (2003): Grounding conceptual knowledge in modality-specific systems. Trends Cogn Sci 7:84–91.

Bartlett FC (1932): Remembering: A Study in Experimental and Social Psychology. Cambridge, UK: Cambridge University Press.

Beilock SL, Lyons IM, Mattarella-Micke A, Nusbaum HC, Small SL (2008): Sports experience changes the neural processing of action language. Proc Natl Acad Sci USA 105:13269–13273.

Binder JR, Desai RH (2011): The neurobiology of semantic memory. Trends Cogn Sci 15:527–536.

Bransford JD, Johnson MK (1972): Contextual prerequisites for understanding: Some investigations of comprehension and recall. J Verbal Learning Verbal Behav 11:717–726.

Chow HM, Mar RA, Xu Y, Liu S, Wagage S, Braun AR (2014): Embodied Comprehension of Stories: Interactions between Language Regions and Modality-specific Neural Systems. J Cogn Neurosci 26:279–295.

Cox RW (1996): AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Comput Biomed Res 29:162–173.

Damasio AR (1989): Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. Cognition 33:25–62.

DeGutis JM, Bentin S, Robertson LC, D'Esposito M (2007): Functional plasticity in ventral temporal cortex following cognitive rehabilitation of a congenital prosopagnosic. J Cogn Neurosci 19:1790–1802.

Desai RH, Binder JR, Conant LL, Seidenberg MS (2010): Activation of sensory-motor areas in sentence comprehension. Cereb Cortex 20:468–478.

Epstein RA (2008): Parahippocampal and retrosplenial contributions to human spatial navigation. Trends Cogn Sci 12:388–396.

Ferstl EC, Rinck M, von Cramon DY (2005): Emotional and temporal aspects of situation model processing during text comprehension: An event-related fMRI study. J Cogn Neurosci 17: 724–739.

Fogassi L, Luppino G (2005): Motor functions of the parietal lobe. Curr Opin Neurobiol 15:626–631.

Freeman J, Donner TH, Heeger DJ (2011): Inter-area correlations in the ventral visual pathway reflect feature integration. J Vis 11:1–23.

Fries P (2009): Neuronal gamma-band synchronization as a fundamental process in cortical computation. Annu Rev Neurosci 32:209–224.

Friston K (2002): Functional integration and inference in the brain. Prog Neurobiol 68:113–143.

Gainotti G, Ciaraffa F, Silveri MC, Marra C (2009): Mental representation of normal subjects about the sources of knowledge in different semantic categories and unique entities. Neuropsychology 23:803–812.

Gazzola V, Keysers C (2009): The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fMRI data. Cereb Cortex 19:1239–1255.

Gerfo EL, Oliveri M, Torriero S, Salerno S, Koch G, Caltagirone C (2008): The influence of rTMS over prefrontal and motor areas in a morphological task: Grammatical vs. semantic effects. Neuropsychologia 46:764–770.

Goldberg RF, Perfetti CA, Schneider W (2006): Perceptual knowledge retrieval activates sensory brain regions. J Neurosci 26: 4917–4921.

Gotts SJ, Chow CC, Martin A (2012): Repetition priming and repetition suppression: A case for enhanced efficiency through neural synchronization. Cogn Neurosci 3:227–237.

Graesser AC, Singer M, Trabasso T (1994): Constructing inferences during narrative text comprehension. Psychol Rev 101:371–395.

Green MC (2004): Transportation into narrative worlds: The role of prior knowledge and perceived realism. Discourse Process 38:247–266.

Grezes J, Decety J (2001): Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. Hum Brain Mapp 12:1–19.

Grill-Spector K, Malach R (2004): The human visual cortex. Annu Rev Neurosci 27:649–677.

Hagoort P, van Berkum J (2007): Beyond the sentence given. Philos Trans R Soc Lond B Biol Sci 362:801–811.

Hauk O, Johnsrude I, Pulvermuller F (2004): Somatotopic representation of action words in human motor and premotor cortex. Neuron 41:301–307.

Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P (2001): Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293:2425–2430.

Johnson-Laird PN (1983): Mental Models. Cambridge, MA: Harvard University Press.

Kendeou P, Van den Broek P (2007): The effects of prior knowledge and text structure on comprehension processes during reading of scientific texts. Mem Cognit 35:1567–1577.

Kintsch W (1988): The role of knowledge in discourse comprehension: A construction-integration model. Psychol Rev 95:163–182.

Kintsch W (1994): Text comprehension, memory, and learning. Am Psychol 49:294–303.

Koyama MS, Di Martino A, Zuo XN, Kelly C, Mennes M, Jutagir DR, Castellanos FX, Milham MP (2011): Resting-state functional connectivity indexes reading competence in children and adults. J Neurosci 31:8617–8624.

Krajcik JS, Sutherland LM (2010): Supporting students in developing literacy in science. Science 328:456–459.

Kravitz DJ, Saleem KS, Baker CI, Mishkin M (2011): A new neural framework for visuospatial processing. Nat Rev Neurosci 12: 217–230.

Landis JR, Koch GG (1977): The measurement of observer agreement for categorical data. Biometrics 33:159–174.

Larsen SF, Seilman U (1988): Personal meanings while reading literature. Text 8:411–429.

Lewis CM, Baldassarre A, Committeri G, Romani GL, Corbetta M (2009): Learning sculpts the spontaneous activity of the resting human brain. Proc Natl Acad Sci USA 106:17558–17563.

Li YO, Adali T, Calhoun VD (2007): Estimating the number of independent components for functional magnetic resonance imaging data. Hum Brain Mapp 28:1251–1266.

Long DL, Prat C, Johns C, Morris P, Jonathan E (2008): The importance of knowledge in vivid text memory: An individual-differences investigation of recollection and familiarity. Psychon Bull Rev 15:604–609.

Lyons IM, Mattarella-Micke A, Cieslak M, Nusbaum HC, Small SL, Beilock SL (2010): The role of personal experience in the neural processing of action-related language. Brain Lang 112: 214–222.

Maguire EA, Frith CD, Morris RG (1999): The functional neuroanatomy of comprehension and memory: The importance of prior knowledge. Brain 122(Pt 10):1839–1850.

Mahon BZ, Caramazza A (2003): Constraining questions about the organisation and representation of conceptual knowledge. Cogn Neuropsychol 20:433–450.

Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003): An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19:1233–1239.
Martin A, Chao LL (2001): Semantic memory and the brain: Structure and processes. Curr Opin Neurobiol 11:194–201.
McGraw KO, Wong SP (1996): Forming inferences about some intraclass correlation coefficients. Psychol Methods 1:30–46.
McKeown MJ, Makeig S, Brown GG, Jung TP, Kindermann SS, Bell AJ, Sejnowski TJ (1998): Analysis of fMRI data by blind separation into independent spatial components. Hum Brain Mapp 6:160–188.
McNamara DS, Kintsch W (1996): Learning from texts: Effects of prior knowledge and text coherence. Discourse Processes 22: 247–282.
Meteyard L, Cuadrado SR, Bahrami B, Vigliocco G (2012): Coming of age: A review of embodiment and the neuroscience of semantics. Cortex 48:788–804.
Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97–113.
Oliveri M, Finocchiaro C, Shapiro K, Gangitano M, Caramazza A, Pascual-Leone A (2004): All talk and no action: A transcranial magnetic stimulation study of motor cortex activation during action word production. J Cogn Neurosci 16:374–381.
Repetto C, Colombo B, Cipresso P, Riva G (2013): The effects of rTMS over the primary motor cortex: The link between action and language. Neuropsychologia 51:8–13.
Singer W, Gray CM (1995): Visual feature integration and the temporal correlation hypothesis. Annu Rev Neurosci 18:555–586.
Speer NK, Reynolds JR, Swallow KM, Zacks JM (2009): Reading stories activates neural representations of visual and motor experiences. Psychol Sci 20:989–999.
Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D (2005): Listening to action-related sentences activates fronto-parietal motor circuits. J Cogn Neurosci 17:273–281.
Thompson-Schill SL (2003): Neuroimaging studies of semantic memory: Inferring "how" from "where". Neuropsychologia 41: 280–292.
Thut G, Miniussi C, Gross J (2012): The functional importance of rhythmic activity in the brain. Curr Biol 22:R658–R63.
Tomasino B, Werner CJ, Weiss PH, Fink GR (2007): Stimulus properties matter more than perspective: An fMRI study of mental imagery and silent reading of action phrases. Neuroimage 36(Suppl 2):T128–T141.
Uithol S, van Rooij I, Bekkering H, Haselager P (2012): Hierarchies in action and motor control. J Cogn Neurosci 24:1077–1086.
van den Broek P (2010): Using texts in science education: Cognitive processes and knowledge representation. Science 328:453–456.
Van Overwalle F, Baetens K (2009): Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. Neuroimage 48:564–584.
Ward BD (2000): Simultaneous inference for fMRI data. Available at: http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf.
Willems RM, Toni I, Hagoort P, Casasanto D (2010): Neural dissociations between action verb understanding and motor imagery. J Cogn Neurosci 22:2387–2400.
Xu Y, Tong Y, Liu S, Chow HM, AbdulSabur NY, Mattay GS, Braun AR (2014): Denoising the speaking brain: Toward a robust technique for correcting artifact-contaminated fMRI data under severe motion. Neuroimage 103:33–47.
Yanagisawa T, Yamashita O, Hirata M, Kishima H, Saitoh Y, Goto T, Yoshimine T, Kamitani Y (2012): Regulation of motor representation by phase-amplitude coupling in the sensorimotor cortex. J Neurosci 32:15467–15475.
Zhu Q, Zhang J, Luo YL, Dilks DD, Liu J (2011): Resting-state neural activity across face-selective cortical regions is behaviorally relevant. J Neurosci 31:10323–10330.
Zwaan RA, Radvansky GA (1998): Situation models in language comprehension and memory. Psychol Bull 123:162–185.