

Research Article

Reading Stories Activates Neural Representations of Visual and Motor Experiences

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ABSTRACT—*To understand and remember stories, readers integrate their knowledge of the world with information in the text. Here we present functional neuroimaging evidence that neural systems track changes in the situation described by a story. Different brain regions track different aspects of a story, such as a character's physical location or current goals. Some of these regions mirror those involved when people perform, imagine, or observe similar real-world activities. These results support the view that readers understand a story by simulating the events in the story world and updating their simulation when features of that world change.*

The information available to readers when reading a story is vastly richer than the information provided by the text alone. For example, when reading about a soccer game, readers with a rudimentary knowledge of the sport are quickly able to grasp the meaning of the sentence “The midfielder scored a goal,” even though the text does not explicitly state how the goal was made, what other people were involved, or where the action took place. These elaborate representations of the situations described by text—situation models—arise through the integration of a reader's knowledge of the world with information explicitly presented in text (Kintsch & van Dijk, 1978). Researchers have proposed that situation models guide ongoing comprehension, and thereby affect later memory (van Dijk & Kintsch, 1983).

Situation models are thought to function by maintaining and updating representations of information that is presented in a story. Multiple dimensions of the situation are maintained in situation models; these dimensions include the characters and

objects present, the spatial and temporal layout of the situation, and the characters' goals and intentions (Gernsbacher, 1990). Readers can use these different aspects of story-relevant information to index the degree of overlap between what they are currently reading and what has happened previously in the story. Readers may update their situation models at points when overlap is low (Gernsbacher, 1990; Zwaan & Radvansky, 1998).

Recent theories of reading comprehension suggest that the representations of these various situation-model dimensions are based on the activity of brain regions involved in analogous perceptions and actions in the real world (Barsalou, 1999; Glenberg, 1997; Zwaan, 2004). These theories suggest that the same representations used for making or watching a goal kick are activated when one reads about a goal kick. Behavioral evidence provides some support for this claim: After reading a sentence describing an action, people are faster to recognize a picture that is consistent with the action than a picture that is inconsistent with the action (Zwaan, Stanfield, & Yaxley, 2002), and are faster to make movements that are consistent with the action than movements that are inconsistent with the action (Glenberg & Kaschak, 2002).

Neuroimaging studies of single-word reading have also provided some initial support for the hypothesis that readers' representations of word meaning are grounded in visual and motor representations. These studies have demonstrated that brain regions involved in reading action words are some of the same regions involved in performing analogous actions in the real world. For example, reading verbs such as “run” or “kick” activates brain regions that are selectively activated when moving one's foot (Pulvermüller, 2005). One limitation of these studies is that they have used restricted lists of single words or phrases. The processing of such stimuli may differ substantially from the processing of meaningful stories. However, these results do suggest a strong but untested prediction about the brain regions that should be active during story reading: The brain regions involved in tracking different dimensions of a reader's situation

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model should correspond to regions that have a role in seeing and acting out similar activities in the real world.

To test this prediction, we used functional magnetic resonance imaging (fMRI) to record participants' brain activity while they read four short narratives. Each narrative was coded on six different dimensions of story information thought to be relevant to readers' situation models (Zwaan & Radvansky, 1998): references to temporal information (e.g., "immediately"), initiations of new causal chains (i.e., when something that happened was not caused by something described previously), points when the subject of the text changed (character changes), changes in characters' spatial locations (e.g., moving from one room to another or from one point to another within a room), changes in characters' interactions with objects (e.g., when characters picked something up or put something down), and points when a character initiated a new goal (see Fig. 1a). We then identified brain regions whose activity increased significantly when each of these aspects of the story situation changed. In this way, we were able to determine whether the regions activated at these points were similar to the regions activated when observers or actors perceive or carry out analogous activities in the real world.

METHOD

Participants

All 28 participants were right-handed, native English speakers (ages 19–34; 20 women, 8 men), and all gave informed consent according to the guidelines set forth by Washington University. For 5 participants, we had data from only two ($n = 1$) or three ($n = 4$) stories because of equipment malfunction or participant fatigue.

Materials

The four narratives were taken from the book *One Boy's Day* (Barker & Wright, 1951) and described the everyday activities of Raymond, a 7-year-old boy. The narratives described Raymond getting up and eating breakfast ("Waking Up"), playing with his friends on the school ground ("Play Before School"), performing an English lesson in school ("Class Work"), and participating in a music lesson ("Music Lesson"). For this study, all references to Raymond's interactions with the observers who recorded his activities were deleted (these references were rare), and the scenes were shortened as necessary to keep the length of each narrative below 1,500 words ("Waking Up": 1,368 words; "Play Before School": 1,104 words; "Class Work": 1,182 words; "Music Lesson": 1,404 words). All stimuli can be downloaded from <http://dcl.wustl.edu/DCL/stimuli.html>.

An LCD projector was used to project stimuli onto a screen positioned at the foot of the scanner, and participants viewed the stimuli through a mirror connected to the head coil. Stimulus presentation and timing were controlled by PsyScope software

(Cohen, MacWhinney, Flatt, & Provost, 1993) running on an Apple PowerMac G4 computer (Apple, Cupertino, CA). A PsyScope button box was used to record responses during the behavioral testing session.

Task and Procedure

Each narrative was presented one word at a time to minimize eye movements; each word remained on the screen for 200 ms and was followed by a blank delay of 150 ms per syllable. Participants practiced this reading method on a separate narrative prior to scanning until they reported being comfortable with word-by-word reading.

The four narratives ranged in length from 8.5 to 10.9 min, and the order of the narratives was counterbalanced across participants. The first and fourth authors coded the narratives for situation changes at the clause level. A clause was identified as a verb together with its arguments. Complement clauses, subordinate clauses, and relative clauses that were dominated by a larger unit were grouped with that larger unit.

We assessed whether or not a given clause contained a change in any of six situational dimensions (see Zacks, Speer, & Reynolds, 2009). *Spatial changes* consisted of changes in the locations of characters, such as when a character moved from one room in a house to another or from one region of interaction within a room to another (e.g., "Raymond raced down the terrace"). *Object changes* occurred when a character interacted with an object in a new way (e.g., Raymond picking up a candy Easter egg). *Character changes* occurred whenever the subject of a clause was different from the subject of the previous clause. *Causal changes* occurred whenever a clause described an activity that was not directly caused by an activity described in the previous clause (e.g., a character initiated a new action). *Goal changes* occurred whenever a character started an action with a new goal. Although there were no temporal changes, each clause was coded for the presence or absence of a *temporal reference* (e.g., "immediately" or "slowly"). Mean interrater reliability across the situation changes was .77 as measured by Cohen's kappa, and disagreements were resolved by discussion.

Participants were told in advance that they would be given a comprehension test at the end of the session. Mean accuracy on this 20-item, four-alternative, multiple-choice test was 82.74% ($SEM = 2.14\%$), indicating that participants comprehended the narratives. Participants returned for a second testing session during which there was no scanning (see Speer, Reynolds, & Zacks, 2007), but only the data from the scanning session are relevant to the current study.

Imaging

Images were acquired on a 3-T Siemens Vision MRI scanner (Erlangen, Germany). High-resolution ($1 \times 1 \times 1.25$ mm) structural images were acquired using a sagittal MP-RAGE (magnetization-prepared rapid acquisition with gradient echo)

a

Clause	Cause	Character	Goal	Object	Space	Time
As soon as [Mrs. Logan] made a check mark on his paper,		●				●
[Raymond] hurried back to his desk.		●	●		●	
Nearing his desk,						
he crumpled the paper, seemingly without any disappointment or anxiety.	●		●	●		
His expression was one of “Well, that’s that and I’m through.”						
The teacher called to him pleasantly, “Did I grade your book?”	●	●	●			
Raymond answered with a negative shake of his head.		●	●			
He picked up his English workbook and returned to her desk.				●		
He walked briskly.						●
He laid his workbook on the desk.				●		

b

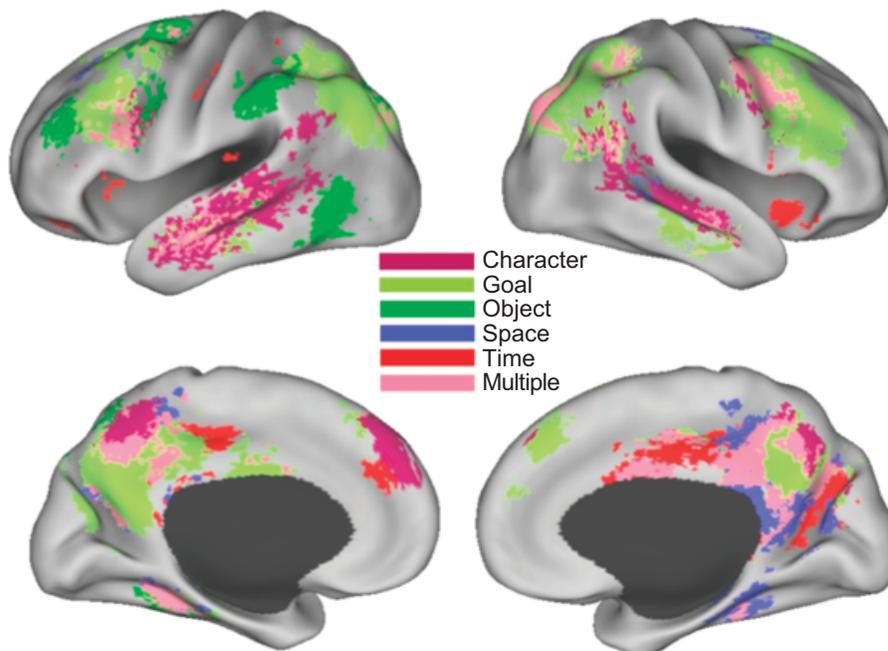


Fig. 1. Coding of a sample passage from the “Waking Up” narrative (a) and brain maps illustrating the location of regions involved in comprehending changes in the narrated situation (b). Each clause was coded for the presence or absence of causal change, character change, goal change, object change, spatial change, and temporal reference (see the text for details). The color coding in (b) indicates which brain regions increased in activity in response to each type of situation change (or two or more types). The top images give inflated left and right lateral views of cortex, and the bottom images give the corresponding inflated medial views.

T1-weighted sequence. Blood-oxygen-level-dependent (BOLD) functional images were acquired using a T2*-weighted asymmetric spin-echo echo-planar sequence, with 32 slices (4.0- × 4.0-mm in-plane resolution) acquired every 2.048 s. A T2-weighted fast turbo spin-echo scan was acquired in the same planes as the functional scans to map the functional data to the

structural data. The functional data were preprocessed to correct for timing offsets, slice intensity differences, and participant movement, and warped to a standard stereotactic space with isotropic voxels (3 × 3 × 3 mm; Talairach & Tournoux, 1988). Data were then smoothed with a Gaussian filter (2-mm full-width at half-maximum).

Analysis of the Imaging Data

To identify regions whose activity depended on situation changes, we used a two-stage procedure using participant as a random effect. In the first stage, each participant's brain response to each of the situation changes was estimated using a general linear model (GLM). Individual clauses were treated as trials in a rapid-event-related data analysis. The *clause-start* variable coded the onset of each trial. Clauses varied considerably in duration, and the interval between successive instances of each type of change varied considerably, which made it possible to accurately estimate the independent effects of each type of change (Zacks et al., 2001). Six additional variables coded which (if any) situation changes occurred during each clause. Clause starts and situation changes were each coded as a 500-ms impulse at the beginning of the clauses and convolved with a canonical hemodynamic response function (time constant = 1.25 s; delay = 2.0 s; Boynton, Engel, Glover, & Heeger, 1996) to generate regressors for the GLM. Ten additional regressors coded for effects of no interest (terminal and nonterminal punctuation, differences across BOLD runs, and the linear trend within each BOLD run). Participants with fewer than four BOLD runs had fewer regressors coding for differences across and linear trends within BOLD runs.

In the second stage of analysis, paired-sample *t* tests compared effect estimates from the GLMs for each of the situation changes with the effect estimates for the clause-start variable, generating maps of *t* statistics for each of the six situation changes. The *t*-statistic maps were converted to *z*-statistic maps and thresholded to control the map-wise false positive rate at .01, by retaining only clusters of at least 4 contiguous voxels with *z* values greater than 4.5 (McAvoy, Ollinger, & Buckner, 2001). These maps were combined to create a composite map illustrating the voxels that responded significantly to each situation change or to multiple situation changes. (To simplify the visualization, we used a single category for those voxels that responded to more than one change.) This composite map was projected onto the cortical surface using CARET with the PALS atlas (Van Essen, 2002; Van Essen, 2005).

To characterize the activated regions, we identified local maxima in the statistical map for each situation change, subject to the constraint that no two maxima could be closer than 20 mm. Each significant voxel was assigned to the closest local maximum to define regions of interest for reporting and for further analyses. In order to test regional selectivity, we conducted region-based analyses that tested whether, after removal of the variance in the BOLD data associated with the situation change used to define a given region, any of the remaining situation changes accounted for substantial additional variance. We used a hierarchical regression approach. In Stage 1, for each region, we fit linear models predicting the fMRI signal for each participant from the nuisance variables, the clause-start variable, and the situation-change variable used to define the region. In Stage 2, we used each of the remaining situation-change vari-

ables as the sole predictor in a simple regression model of the residuals from the Stage 1 model. This analysis was performed separately for each participant, and the regression coefficients from the Stage 2 models were compared with zero in *t* tests with subject as the random effect ($df = 27$). Regions for which none of the *t* statistics exceeded 1.0 were characterized as selective for a single situation change. If a region were to have a medium-sized effect ($d = 0.5$) of one other situation change in addition to the one used to define the region, the power to detect that effect by this criterion was .89; if a region were to have medium-sized effects of two of the other situation changes, the power was .99.

RESULTS

Responses to Individual Situation Changes

The regions responding to situation changes are illustrated in Figure 1b and listed in Table 1. Figure 1b shows all brain voxels that were associated with one or more situation changes. Activity in a number of regions changed during processing of the different types of situation changes. Furthermore, the neural responses to particular types of changes in the stories occurred in the vicinity of regions that increase in activity when people view similar changes or carry out similar activities in the real world.

Characters and Goals

Adjacent and overlapping regions in bilateral posterior superior temporal cortex (Brodmann's area, BA, 22/39) responded to changes in characters and goals. These regions also increase in activation when participants observe goal-directed, intentional actions, relative to non-goal-directed, meaningless motion (Decety & Grezes, 1999). Changes in characters' goals also were associated with increased activation in prefrontal cortex (BA 9, 44, 46), damage to which results in impaired knowledge of the typical order and structure of daily goal-directed activities (Wood & Grafman, 2003).

Interactions With Objects

Regions whose activity increased for character-object interactions included several regions considered part of the human grasping circuit (Cacioppo, 2005). One of these regions was in the lateral precentral sulcus (BA 6) and likely corresponds to the premotor hand area (e.g., Ehrsson, Geyer, & Naito, 2003); another was in the postcentral cortex (BA 2/40) and likely corresponds to the somatosensory hand representation (Porro et al., 1996) and adjacent anterior intraparietal cortex (Johnson et al., 2002). Consistent with these regions' involvement during grasping, both the precentral and the postcentral activations were lateralized to the left hemisphere. The object changes that were associated with these increases typically referred to characters putting down or picking up objects (e.g., "Raymond laid down his pencil").

TABLE 1
Regions That Increased Significantly in Activation in Response to Situation Changes

Coordinates			Hemisphere	Region	BA	Size (mm ³)
x	y	z				
Causal change						
29	-70	37	Right	Intraparietal sulcus	19	1,620
42	6	32	Right	Middle frontal gyrus	6	1,161
Character change						
* -54	-28	-9	Left	Superior temporal sulcus	21	4,320
* -52	-61	18	Left	Temporo-parietal junction	39	621
-44	8	29	Left	Inferior/middle frontal gyrus	9/44	1,107
-40	-79	28	Left	Superior occipital gyrus	19	243
-31	-59	43	Left	Superior intraparietal sulcus	7	297
-23	-34	27	Left	White matter	—	216
* -6	48	26	Left	Superior frontal gyrus	9	270
* -3	42	46	Left	Superior frontal gyrus	8	1,134
-2	-59	38	Left	Precuneus	7/31	4,941
30	-66	40	Right	Intraparietal sulcus	7	810
44	12	30	Right	Inferior/middle frontal gyrus	9/44	2,430
51	-22	-10	Right	Superior temporal gyrus	22	2,214
* 54	-51	13	Right	Temporo-parietal junction	22/39	1,107
Goal change						
-54	-27	-12	Left	Anterior superior temporal sulcus	21	1,431
-46	12	-19	Left	Anterior superior temporal sulcus	21	216
-45	-54	17	Left	Temporo-parietal junction	39	135
* -37	2	49	Left	Middle frontal gyrus	6/8	648
* -35	14	29	Left	Middle frontal gyrus	44	3,159
-34	-66	38	Left	Inferior parietal lobule	39/40	11,799
-27	-36	-17	Left	Hippocampus	35	405
-22	17	56	Left	Superior frontal gyrus	8	702
-12	-24	8	Left	Thalamus	—	270
-9	-64	22	Left	Posterior cingulate gyrus/precuneus	7/23/31	6,318
-9	30	46	Left	Medial frontal gyrus	8	810
-8	-78	-31	Left	Medial cerebellum	—	567
-3	42	27	Left	Medial frontal gyrus	9/32	297
0	-47	36	Medial	Posterior cingulate gyrus	5/31	7,614
5	-7	32	Medial	Cingulate gyrus	24	1,431
8	-19	9	Right	Thalamus	—	270
14	-62	24	Right	Posterior cingulate gyrus/precuneus	7/31	2,754
18	16	52	Right	Superior frontal gyrus	6/8	675
32	-66	43	Right	Inferior/superior parietal lobule	7/19/39	8,154
32	-14	34	Right	Inferior frontal gyrus	44	837
38	6	44	Right	Precentral sulcus	6	5,832
42	-49	52	Right	Superior parietal lobule	7	3,240
* 43	22	26	Right	Inferior frontal gyrus	44/45/46	4,023
45	-57	24	Right	Inferior parietal lobule	39	1,728
56	-29	-11	Right	Middle temporal gyrus	21/22	1,377
Object change						
-59	-35	39	Left	Postcentral gyrus	2/40	1,134
-52	-33	-5	Left	Superior temporal sulcus	22	189
* -50	-62	-10	Left	Posterior middle temporal gyrus	37/39	1,701
* -45	1	27	Left	Precentral gyrus	6	270
-42	35	24	Left	Middle frontal gyrus	46	486
-41	-46	42	Left	Intraparietal sulcus	37	324
-33	-77	33	Left	Inferior parietal sulcus	7/19/39	1,188
-30	-43	-16	Left	Fusiform gyrus	20/36	1,188

Table 1. (Contd.)

Coordinates			Hemisphere	Region	BA	Size (mm ³)	
x	y	z					
-28	1	60	Left	Precentral gyrus	6	2,079	
-27	20	50	Left	Middle frontal gyrus	8	351	
-9	-68	54	Left	Precuneus	7	189	
Spatial change							
-27	-37	-16	Left	Hippocampus/parahippocampal gyrus	35/36	1,242	
-27	1	57	Left	Superior frontal gyrus	6	243	
-26	22	43	Left	Superior frontal gyrus	8/9	135	
-12	-56	17	Left	Parieto-occipital sulcus	19	324	
-6	-43	39	Left	Posterior cingulate gyrus	5/31	2,970	
14	-57	23	Right	Parieto-occipital sulcus	18/19	2,781	
14	-32	11	Right	Thalamus	—	216	
22	7	57	Right	Superior frontal gyrus	6	135	
29	-35	-14	Right	Hippocampus/parahippocampal gyrus	35/36	999	
34	-70	38	Right	Superior parietal lobule	7/19	270	
39	-48	43	Right	Intraparietal sulcus	7	864	
53	-38	1	Right	Posterior superior temporal sulcus	22	162	
Temporal reference							
*	-38	10	0	Left	Insula	44	243
	-33	-67	38	Left	Intraparietal sulcus	7	810
	-32	34	4	Left	Inferior frontal gyrus	45/47	513
	-30	-24	29	Left	White matter	—	1,512
	-29	-36	-14	Left	Fusiform gyrus	20	189
	-22	-48	18	Left	Posterior cingulate gyrus	23/31	3,834
*	-21	2	37	Left	White matter	—	270
	-16	-24	5	Left	Thalamus	—	1,296
	-15	-50	46	Left	Posterior cingulate gyrus	31	918
	-13	36	24	Left	Anterior cingulate gyrus	32	162
	2	-11	32	Right	Cingulate gyrus	24	1,620
	15	-21	8	Right	Thalamus	—	1,134
	15	16	40	Right	Cingulate gyrus	31	135
	17	-59	21	Right	Posterior cingulate gyrus/precuneus	30/31	3,240
	20	-39	39	Right	Posterior cingulate gyrus	5/23/31	2,160
	24	-41	13	Right	White matter	—	3,186
	33	24	-3	Right	Inferior frontal gyrus	47	621
	34	-58	45	Right	Intraparietal sulcus	7	3,105
	38	2	37	Right	Precentral gyrus	6	1,782

Note. The coordinates listed are the coordinates of peaks in Talairach space. Asterisks indicate regions showing significant activity that was unique to a single type of situation change. BA = Brodmann's area.

Space

Two bilateral superior frontal regions (BA 6) responded to changes in characters' spatial locations. The locations of these regions fall within the 95% confidence intervals for functionally defined frontal eye fields, which increase in activation during saccadic eye movements, relative to fixation (Speer, Swallow, & Zacks, 2003). Regions in right and left parahippocampal cortex (BA 35–36), which increase in activation during processing of changes in spatial location (Burgess, Maguire, & O'Keefe, 2002), also showed increased activation in response to changes in characters' spatial locations.

Time

Regions whose activity increased during temporal references included the inferior frontal gyrus (BA 45/47), insula (BA 44), intraparietal sulcus (BA 7), medial posterior cortex (precuneus and cingulate gyrus, especially BA 23/31), and anterior cingulate gyrus (BA 32), as well as posterior and anterior white matter tracts. The neurophysiology of time perception in this range of durations (seconds to minutes) is not well understood, so there are few, if any, neuroimaging data with which to compare these results. However, the cortical activations do correspond well with those observed in a recent study comparing stories with

temporal inconsistencies and stories with emotional inconsistencies (Ferstl, Rinck, & von Cramon, 2005). (The extensive activations in white matter were unexpected and await further empirical confirmation.)

Selectivity of Responses

Figure 1b suggests that a core network comprising the medial posterior cortex (precuneus, posterior cingulate cortex, temporo-parietal junction) and the lateral posterior frontal cortex was activated by multiple situation changes. Note that all the regions that responded to causal changes also responded to other situation changes. However, Figure 1 also suggests that some brain regions were selectively activated by only one type of situation change. Given that a region shows a significant response to one situation change, the mere failure to detect significant responses to other changes is weak evidence of selectivity—particularly given the stringent statistical thresholds we used. To directly assess selectivity for a single change, we performed a set of hierarchical regression analyses (see Analysis of the Imaging Data). The regions that were determined to respond selectively to a single type of situation change are marked with asterisks in Table 1 and illustrated in Figure 2. The selective responses included responses to character changes in the temporo-parietal junction and in medial frontal cortex (superior frontal gyrus), responses to goal changes in lateral frontal cortex (middle frontal gyrus), responses to object changes in premotor cortex (precentral gyrus), and responses to time changes in the left insula.

Responses to Increasing Numbers of Situation Changes

An additional analysis was conducted to identify regions that might play a role in determining when perceptual and motor representations of narrative elements should be updated in a reader's situation model. Because readers update their situation models when incoming information conflicts with information maintained in their active situation models (Zwaan & Radvansky, 1998), the greater the number of dimensions that change at a given point in a story, the more likely it is that the active situation model will be updated. To identify the regions that might be involved in such updating, we coded each clause for the total number of situation changes present (1, 2, or ≥ 3 changes). A linear contrast identified voxels whose activation increased linearly with increasing numbers of changes, and the resulting *t* statistics were generated in the same manner as the *t* statistics for the individual situation-model changes.

The number of changes in a given clause was related to activation in many of the change-related regions, such as dorsolateral prefrontal cortex (BA 9/46), posterior parietal cortex (BA 7/40), posterior cingulate cortex (BA 7/31), and bilateral hippocampi (BA 36; cf. Fig. 1 and Fig. 3, and see Table 2).

DISCUSSION

These results suggest that readers dynamically activate specific visual, motor, and conceptual features of activities while reading about analogous changes in activities in the context of a narrative: Regions involved in processing goal-directed human activity, navigating spatial environments, and manually ma-

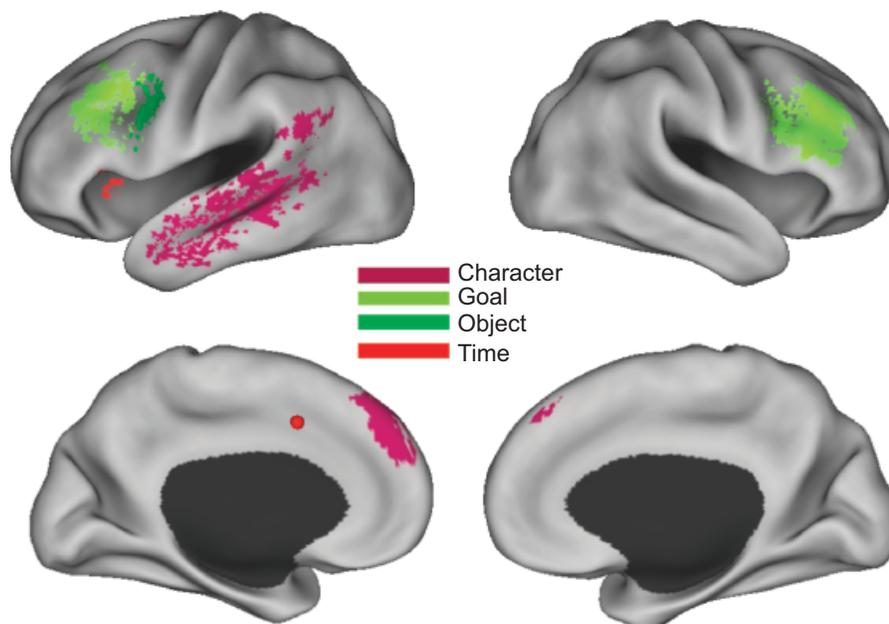


Fig. 2. Illustration of those regions in Figure 1 that responded selectively to only one type of change (as indicated by the color coding). The top images give inflated left and right lateral views of cortex, and the bottom images give the corresponding inflated medial views. The left medial time-specific region was internal to the cortical surface; its approximate location is indicated by the red circle.

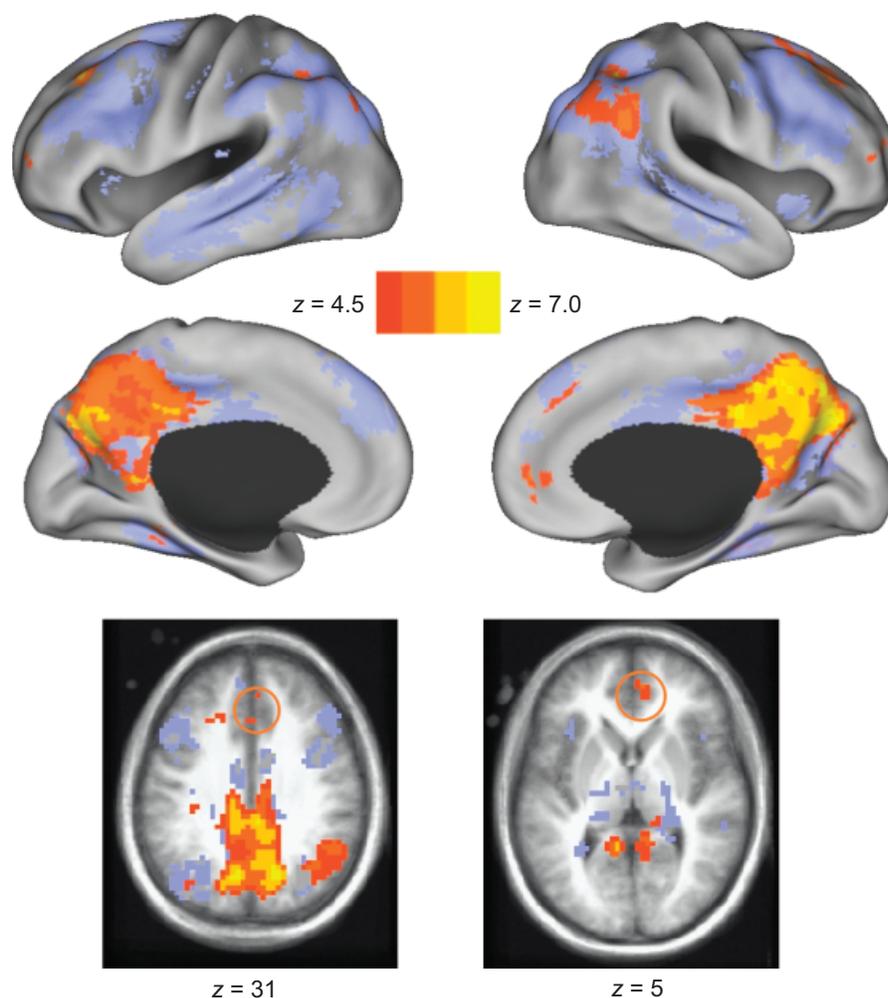


Fig. 3. Voxels whose activation increased with increasing numbers of situation changes. For reference, all the regions from Figure 1 are shown as a light-blue underlay. The color coding corresponds to values of the z statistics. The top four images give inflated views of the cortical surface, as in Figures 1 and 2; the bottom two images are axial slices (z coordinates are given) providing views of regions in anterior cingulate cortex that responded to increasing numbers of situation changes, but did not show significant increases in response to any individual change (orange circles).

nipulating objects in the real world increased in activation at points when those specific aspects of the narrated situation were changing. For example, when readers processed changes in a character's interactions with an object, precentral and parietal areas associated with grasping hand movements increased in activation. Previous studies of motor execution and motor imagery provide strong evidence that the portion of premotor cortex identified in this study performs computations that are specific to motor planning and execution (Ehrsson et al., 2003; Michelon, Vettel, & Zacks, 2006). These results suggest that readers use perceptual and motor representations in the process of comprehending narrated activity, and that these representations are dynamically updated at points when relevant aspects of the situation are changing.

Several recent studies have identified modality-specific brain activation using paradigms in which participants made judgments about individual words (Goldberg, Perfetti, & Schneider,

2006; Hauk, Johnsrude, & Pulvermüller, 2004; Hauk & Pulvermüller, 2004) or phrases (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Noppeney, Josephs, Kiebel, Friston, & Price, 2005). However, such paradigms leave open the possibility that the evoked responses could reflect, in part, cognitive operations that are specific to the specific judgment task. By contrast, the current paradigm used continuous reading of extended passages with no overt judgment task.

Although a number of regions responded selectively to a particular type of change, there were several regions whose activity increased for more than one type of situation change (cf. Figs. 1 and 2). These regions may be particularly important for indicating when a reader's situation model should be updated. Because readers update an active situation model when incoming information conflicts with information maintained within that model, increasing the number of aspects of the situation that are changing may increase the likelihood that the

TABLE 2
Regions With a Linear Relationship to the Number of Changes in a Clause

Coordinates			Hemisphere	Region	BA	Size (mm ³)
<i>x</i>	<i>y</i>	<i>z</i>				
-28	6	53	Left	Middle frontal gyrus	6	1,242
-27	19	33	Left	Middle frontal gyrus	8/9	2,376
-33	47	10	Left	Middle frontal gyrus	10/46	351
-12	-43	8	Left	Posterior cingulate	29/30	2,079
-11	-63	22	Left	Posterior cingulate	29/30/31	11,583
-29	-19	36	Left	Posterior cingulate	31	189
-28	-34	-12	Left	Hippocampus	36	729
-32	-53	24	Left	Inferior parietal lobule	40	864
-39	-78	29	Left	Inferior parietal lobule	40	594
5	-59	42	Bilateral	Precuneus	7	16,470
-1	-42	64	Bilateral	Precuneus	7	513
6	-21	33	Bilateral	Posterior cingulate	23/31	3,105
-5	-42	33	Bilateral	Posterior cingulate	31	11,421
4	33	31	Bilateral	Anterior cingulate gyrus	32	1,215
-2	45	5	Bilateral	Anterior cingulate gyrus	32	1,026
34	6	39	Right	Middle frontal gyrus	6	27
25	20	52	Right	Middle frontal gyrus	6/8	4,617
38	30	34	Right	Middle frontal gyrus	8	783
34	51	13	Right	Middle frontal gyrus	10/46	1,350
36	-48	10	Right	Superior temporal gyrus	22	162
10	-58	21	Right	Posterior cingulate	29/30/31	11,853
22	-36	22	Right	Posterior cingulate	31	1,080
23	-35	-6	Right	Hippocampus	36	648
43	-58	37	Right	Inferior parietal lobule	39/40	10,017

Note. The coordinates listed are the coordinates of peaks in Talairach space. BA = Brodmann's area.

active situation model will be updated (Gernsbacher, 1990; Zwaan & Radvansky, 1998). This updating process should be associated with the perception that a new narrative event has begun (Zacks, Speer, Swallow, Braver, & Reynolds, 2007). Indeed, previously reported analyses of the data discussed in the present study provided evidence that when changes occur, readers tend to perceive that a new event has begun (Speer et al., 2007; see also Zacks et al., 2009).

Figure 3 indicates that the number of changes in a given clause was related to activation in many of the regions depicted in Figure 1, such as dorsolateral prefrontal cortex (BA 9/46), posterior parietal cortex (BA 7/40), posterior cingulate cortex (BA 7/31), and bilateral hippocampi (BA 36). Some of these increases in activation may come about simply because the more dimensions of the situation are changing, the more any particular dimension is likely to be changing. However, a region in the anterior cingulate cortex (within BA 32), which was not involved in processing any of the individual changes, also increased in activity with increasing numbers of changes. Given the role of the anterior cingulate cortex in monitoring external and internal conflict (Brown & Braver, 2005), activation in this region may serve as a cue for the reader to update the current situation model, or begin constructing a new model. Additional studies are needed to determine the reason for this relation between

activation in the anterior cingulate cortex and the number of changes in a narrative.

The collection of medial brain regions we found to be associated with situation changes closely resembles a network of regions that have been recently associated with the act of projecting one's self into a remembered, anticipated, or imagined situation (Buckner & Carroll, 2007). These regions are functionally connected to the hippocampi (Vincent et al., 2006), which were also observed to increase in activity with increasing numbers of situation changes. The convergence of these results is consistent with the idea that readers construct simulations of situations as they read a text, and that this process is similar to recalling previous situations or imagining potential ones.

Overall, these data make a strong case for embodied theories of language comprehension, according to which readers' representations of situations described in language are constructed from basic sensory and motor representations (Barsalou, 1999; Glenberg, 1997; Zwaan, 2004). However, the use of perceptual and motor representations to guide story comprehension may be an example of a more general, fundamental principle of cognitive function. Brain regions involved in motor function are active when a person views another person execute an action (Rizzolatti & Craighero, 2004). When one is viewing a movie, somatosensory and motor cortices increase in activity during

scenes showing close-ups of features such as hands and faces (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004), and the regions involved in perceiving and later remembering auditory and visual information show similar correspondences (Wheeler & Buckner, 2004). Thus, the use of sensory and motor representations during story comprehension may reflect a more general neural mechanism for grounding cognition in real-world experiences. Language may have adopted this general mechanism over the course of human evolution to allow individuals to communicate experiences efficiently and vividly.

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