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Hemispheric Asymmetry in Event Knowledge Activation During Incremental Language Comprehension: A Visual Half-Field ERP Study

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Abstract

During incremental language comprehension, the brain activates knowledge of described events, including knowledge elements that constitute semantic anomalies in their linguistic context. The present study investigates hemispheric asymmetries in this process, with the aim of advancing our understanding of the neural basis and functional properties of event knowledge activation during incremental comprehension. In a visual half-field event-related brain potential (ERP) experiment, participants read brief discourses in which the third sentence contained a word that was either highly expected, semantically anomalous but related to the described event, or semantically anomalous but unrelated to the described event. For both visual fields of target word presentation, semantically anomalous words elicited N400 ERP components of greater amplitude than did expected words. Crucially, event-related anomalous words elicited a reduced N400 relative to event-unrelated anomalous words only with left visual field/right hemisphere presentation. This result suggests that right hemisphere processes are critical to the activation of event knowledge elements that violate the linguistic context, and in doing so informs existing theories of hemispheric asymmetries in semantic processing during language comprehension. Additionally, this finding coincides with past research suggesting a crucial role for the right hemisphere in elaborative inference generation, raises interesting questions regarding hemispheric coordination in generating event-specific linguistic expectancies, and more generally highlights the possibility of functional dissociation between event knowledge activation for the generation of elaborative inferences and for linguistic expectancies.

Keywords

language; event knowledge; event-related brain potentials; ERP; N400; hemispheric asymmetry

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1. Introduction

Language often describes scenarios or events. Comprehending such language entails mapping between linguistic input and knowledge stored in semantic memory of the type of event described, such as the typical event location, entities and actions involved, and temporal and causal relations. Research suggests that event knowledge supports incremental (i.e., word-by-word) language comprehension, including linguistic expectancy generation (Altmann & Mirković, 2009; Elman, 2009; McRae & Matsuki, 2009). Additionally, event knowledge activation can extend beyond those elements expected to appear in the unfolding sentence to include elements that constitute semantic anomalies in sentence context (Metusalem et al., 2012). Given this complex interplay between linguistic input and event knowledge, specifying the neural basis of event knowledge activation during incremental comprehension is an important goal. The present study advances this goal by investigating asymmetries across the cerebral hemispheres in the activation of semantic information that is related to a described event but is semantically anomalous in sentence context. While understanding the neural basis of event knowledge activation is important in its own right, the utility of this investigation extends further; against the backdrop of previous research suggesting systematic functional asymmetries across the hemispheres in the activation of semantic information triggered by linguistic input, this investigation informs our understanding of the functional properties of event knowledge activation more generally. The present study thus examines event knowledge activation with respect to both its neural basis and functional profile.

1.1. Activating event knowledge during incremental comprehension

Sentence and discourse comprehension can be characterized as construction of a mental representation of the described scenario or event, often called a mental or situation model (Johnson-Laird, 1983; Van Dijk & Kintsch, 1983; Zwaan & Radvansky, 1998). Constructing such representations crucially involves integrating linguistic input with general knowledge stored in semantic memory of the type of event described, and comprehenders deploy this knowledge to guide comprehension as a sentence unfolds word-by-word (Altmann & Mirković, 2009; Elman, 2009; McRae & Matsuki, 2009). For example, the influence of event knowledge on the processing of post-verbal patient nouns has been demonstrated in reading times (Bicknell, Elman, Hare, McRae, & Kutas, 2010; Matuski et al., 2011), anticipatory looking behavior in the Visual World Paradigm (Borovsky, Elman, & Fernald, 2012; Kamide, Altmann, & Haywood, 2003; Kukona, Fang, Aicher, Chen, & Magnuson, 2011) and event-related brain potentials (ERPs; Bicknell et al., 2010). Bicknell et al.'s participants read sentences such as *The mechanic checked the brakes* or *The journalist checked the brakes*, in which the critical patient noun *brakes* is congruent with knowledge of what a mechanic might check, but is incongruent with knowledge of what a journalist might check. They found that the congruence of the patient noun with the event implied by the combination of the preceding agent and verb influenced the amplitude of the N400 ERP component. The N400 is a negative-going deflection in the ERP waveform peaking around 400ms after the onset of a word or other potentially meaningful stimulus, and its amplitude is inversely related to the degree to which the stimulus aligns with or is expected in its context (Kutas & Hillyard, 1980, 1984; see Kutas and Federmeier, 2000, 2011 for review) –

the greater the semantic fit between a word and its context, the smaller the N400 (assuming other factors are held constant). Bicknell et al. found that N400 amplitude was smaller for congruent relative to incongruent patient nouns, indicating that the brain's response to these words was affected by the fit between the word and the event implied by the preceding sentential context within several hundred milliseconds of word onset.

Additional sentence comprehension research has suggested that event knowledge influences the processing of syntactic structures (Hare, Elman, Tabaczynski, & McRae, 2009; McRae, Spivey-Knowlton, & Tanenhaus, 1998) and that grammatical cues such as verb aspect serve to differentially activate event knowledge (Ferretti, Kutas, & McRae, 2007). Outside of sentence comprehension research, lexical priming studies have shown that processing of isolated words activates knowledge of events with which those words are associated (Chwilla & Kolk, 2005; Hare, Jones, Thomson, Kelly, & McRae, 2009; McRae, Hare, Elman, & Ferretti, 2005), suggesting that activating event knowledge is a central component of the brain's response to individual words as well as sentences.

Noting the centrality of event knowledge to incremental comprehension, Altmann and Mirković (2009) assert that comprehension fundamentally entails mapping between sentence and event structures in the service of predicting how the language (and described event) will unfold in time. This notion highlights an interesting question with respect to event knowledge activation during incremental comprehension. Many concepts might relate to the type of event being described, but at a specific point in a sentence, only some (or none) of these will be expected to appear in the immediately upcoming linguistic input. Is real-time event knowledge activation limited to only these elements? Metusalem et al. (2012) investigated this question in an ERP experiment in which participants read three-sentence discourses describing typical events. The third sentence always presented a sentence-medial word that was either strongly expected (Expected), related to the described event but semantically anomalous in sentence context (Event-Related), or unrelated to the described event and semantically anomalous in sentence context (Event-Unrelated). (For example, *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*, in which both *jacket* and *towel* are semantically anomalous, but *jacket* is event-related by virtue of being likely to be worn by children playing in the snow.) Metusalem et al. found a three-way split in amplitude of the N400, with Expected targets eliciting the smallest N400, Event-Unrelated targets eliciting the largest N400, and Event-Related targets eliciting an intermediate N400. This finding has been replicated (Amsel, DeLong, & Kutas, 2015; see Huettig, in press). Metusalem et al. interpreted N400 reduction for the Event-Related targets as indicating that at any point in a particular sentence the real-time activation of event knowledge is extends beyond those words that are expected to appear to include words that are semantically anomalous in sentence context.

During incremental comprehension, how does the brain activate contextually anomalous but event-related information? The present study addresses this question by investigating if and how the cerebral hemispheres differ with respect to this process. As will now be reviewed, the cerebral hemispheres appear to exhibit functional asymmetries in the activation of semantic information during language comprehension. In the context of this research, the present study additionally advances our understanding the functional properties of event knowledge activation.

1.2. Hemispheric asymmetries in language comprehension

Hemispheric asymmetries in language have been appreciated since the early discoveries by Broca (1861) and Wernicke (1874) of profound language deficits following lesion to only the left hemisphere. Much subsequent research has been based on a view of the left hemisphere as the dominant hemisphere for language, although modern functional imaging has made clear that language processing is supported by a complex bilateral brain network (Gernsbacher & Kaschak, 2003; Grodzinsky & Friederici, 2006; Hickok & Poeppel, 2007; Price, 2012). Within this network, the left and right hemispheres exhibit systematic functional asymmetries in semantic processing during sentence and discourse comprehension.

Processing of a word in sentence context is highly sensitive to the message-level meaning of the sentence or discourse. ("Message-level" meaning refers to the propositional semantic content of a sentence or discourse abstracted away from the words and syntactic structures used to convey that meaning). Early work suggested that only the left hemisphere is sensitive to message-level semantic cues in the processing words in sentences and discourse (e.g., Faust, Kravetz, & Babkoff, 1993; see Faust (1998) for review), though this view was soon revised to include a degree of sensitivity to message-level cues by the right hemisphere (Chiarello, Liu, & Faust, 2001). ERP studies have made clear that the both hemispheres are sensitive to message-level cues, but in different ways (Coulson, Federmeier, Van Petten, & Kutas, 2005; Federmeier & Kutas, 1999b; Federmeier, Mai, & Kutas, 2005; Wlotko & Federmeier, 2007, 2013). ERP studies on hemispheric asymmetries in the semantic processing of words in sentence and discourse contexts typically focus on the N400 component and utilize visual half-field presentation of critical words. Visual half-field methods lateralize presentation of a target stimulus to either the right or left visual field. Only the hemisphere contralateral to the visual field of presentation receives direct sensory input, and processing proceeds unilaterally through area V2; the ipsilateral hemisphere receives information only via subsequent callosal transfer, which is delayed and can result in loss of information fidelity (see discussion by Banich, 2003). Visual half-field presentation thus provides a processing advantage to the contralateral hemisphere, and observation of differing responses to the same stimulus when presented to the left versus right visual fields can support inferences regarding hemispheric asymmetries in processing.[1] Visual half-field presentation methods have been used to great effect in both behavioral and ERP studies of hemispheric asymmetries in language processing (see Chiarello, 1988, Federmeier, 2007, and Federmeier, Wlotko, and Meyer, 2008, for reviews).

[1]It is important to note that due to interhemispheric communication in the healthy adult brain, studies using visual half-field presentation methods cannot support strong inferences that attribute a process exclusively to one hemisphere. Visual half-field methods provide a processing advantage to the contralateral hemisphere but do not rule out involvement of the ipsilateral hemisphere. No claims in this paper regarding visual half-field studies are meant to imply that a cognitive process is carried out exclusively in one hemisphere or the other, but only that one hemisphere appears to play a greater or more central role than the other hemisphere in that process.

Federmeier and Kutas (1999a,b) found evidence that the hemispheres differ in their use of message-level cues to pre-activate semantic features of likely upcoming words. In an experiment utilizing central presentation of target words (1999a), they demonstrated that unexpected words from the same semantic category as an expected word (within-category violations) elicit a reduced N400 relative to an equally unexpected word that does not belong to the same category as the expected word (between-category violations; e.g. smaller N400 to *pines* than *roses* following *They wanted to make the hotel look more like a tropical resort, so along the driveway they planted rows of…*, where *palms* is expected). They showed that N400 reduction for within-category violations was larger for more highly constraining contexts, suggesting that when strong message-level cues are available, the brain more strongly pre-activates semantic features of likely upcoming input. Under this view, N400 amplitude then captures the degree to which the presented word matches the pre-activated semantic features. In a visual half-field version of the experiment (1999b), they found that right visual field/left hemisphere (RVF/LH) presentation of target words led to the same pattern as with central presentation: the smallest N400 for expected words, largest for between-category violations, and intermediate for within-category violations. With left visual field/right hemisphere (LVF/RH) presentation, they observed a two-way split in N400 amplitudes, with expected words eliciting a smaller N400 than both within- and between-category violations, which patterned together. The authors argued that left hemisphere processing appears to apply message-level context in top-down fashion to pre-activate semantic features of likely upcoming input.

The notion of the left hemisphere making greater top-down use of message-level context has been bolstered by several additional findings. The N400 elicited by an expected word is reduced by the presence of lexical associates in the preceding sentence context only for LVF/RH presentation, indicating that the left hemisphere more strongly weights message-level context over lexical associations than does the right hemisphere (Coulson et al., 2005). In addition, expected words elicit larger amplitude P2 ERP components in strongly constraining versus weakly constraining contexts with RVF/LH but not LVF/RH presentation, suggesting that left hemisphere processing utilizes message-level context to generate high-level perceptual predictions for upcoming words (Federmeier et al., 2005). Finally, N400 reduction for expected relative to unexpected words in weakly constraining contexts is greater for RVF/LH than LVF/RH presentation, suggesting that left hemisphere processing supports a boost to the activation level of expected words when message-level constraint is present but weak (Wlotko & Federmeier, 2007, 2013).

Right hemisphere processing of words in sentence and discourse contexts is affected by message-level cues, as well (Federmeier, Wlotko, & Meyer, 2008). Expected words generally elicit smaller N400s than unexpected words with LVF/RH presentation, just as with RVF/LH presentation (Coulson et al., 2005; Federmeier & Kutas, 1999b; Wlotko & Federmeier, 2007, 2013). Expected words elicit smaller N400s in strongly constraining than in weakly constraining contexts with LVF/RH presentation, even when the effect of lexical association is controlled (Federmeier et al., 2005). The question then is not whether, but in what way, the right hemisphere is sensitive to message-level contextual cues during processing.

Research suggests that the right hemisphere processes message-level context in support of high-level discourse comprehension functions (Johns, Tooley, & Traxler, 2008). The right hemisphere seems to support establishing coherence across multiple sentences (Hough, 1990; Robertson et al., 2000; Schneiderman, Murasugi, & Saddy, 1992; St. George, Kutas, Martinez, & Sereno, 1999; Wapner, Hamby, & Gardener, 1981). For example, behavior of right hemisphere damaged patients (Hough, 1990; Schneiderman et al., 1992) and functional imaging of healthy individuals (St. George et al., 1999) suggest that the right hemisphere uses information regarding the discourse topic or theme to integrate information across multiple sentences. Furthermore, the right hemisphere has been shown to support comprehension of numerous forms of nonliteral language, including novel metaphors (Cardillo et al., 2012; Mashal & Faust, 2009; Mashal, Faust, Hendler, & Jung-Beeman, 2007), indirect requests (Foldi, 1987), irony (Eviatar & Just, 2008), sarcasm (Giora et al., 2000; Shamay-Tsoory, Tomer, & Aharon-Peretz, 2005), and humor (Brownell, Michel, Powelson, & Gardner, 1983; Coulson & Williams, 2005; Coulson & Wu, 2005; Gardner, Ling, Flamm, & Silverman, 1975). Interestingly, the right hemisphere seems to support the literal interpretation of idiomatic expressions, as well (Mashal, Faust, Hendler, & Jung-Beeman, 2008), suggesting that the right hemisphere does not simply support nonliteral interpretations, but the maintenance of alternative or subordinate meanings of ambiguous input. Indeed, numerous priming studies indicate a role for the right hemisphere in maintaining multiple or alternative interpretations of ambiguous input (Atchley, Keeney, & Burgess, 1999; Burgess & Simpson, 1988; Faust & Chiarello, 1998).

The right hemisphere also appears to play an important role in inference (Beeman, 1993; Brownell, Potter, & Bihrle, 1986; Beeman, Bowden, & Gernsbacher, 2000; Mason & Just, 2004; Virtue et al., 2006). A distinction is often made between bridging or coherence inferences, which are required to maintain discourse coherence across sentences, and elaborative or predictive inferences, which can be generated to enrich the discourse representation but are not required to maintain coherence.[2] Beeman et al.'s (2000) participants performed a cross-modal naming task as they listened to stories that promoted an inference corresponding to a target word presented to either the right or left visual field. For example, one story described a space shuttle launch but never mentioned the launch itself, and *launch* was the target word. At early points in the story, the target word probed an elaborative inference (e.g. *The shuttle sat on the ground in the distance, waiting for the signal to be given*), and at later points in the story probed a coherence inference (*After a huge roar and a bright flash, the shuttle disappeared into space*). They found that targets probing elaborative inferences were primed only with LVF/RH presentation, and that targets probing coherence inferences were primed only with RVF/LH presentation. This finding indicates that the right hemisphere may be responsible for maintaining activation of unstated information that is not necessary to maintain discourse coherence, but nevertheless enriches the discourse representation.

[2]"Predictive inference" refers to inferences about unmentioned but likely upcoming events or consequences of previously stated events, and should not be confused with "prediction" as referring to the anticipation of upcoming linguistic input. Predictive inference can be thought of as a subtype of elaborative inference, and to avoid confusion, the remainder of this paper will use the term "elaborative inference", including with reference to Beeman et al. (2000), who specifically tested predictive inference.

In sum, the cerebral hemispheres exhibit functional asymmetries in the processing of message-level context. The left hemisphere appears to make top-down use of message-level cues in order to pre-activate semantic features of likely upcoming input. The right hemisphere, on the other hand, appears to use message-level context to activate a wide array of conceptual information in the service of higher-level comprehension functions, such as elaborative inference generation. With these functional asymmetries in mind, we now turn to the present study.

1.3. The present study

During incremental comprehension, event knowledge elements can be activated even at points in a sentence in which they are unexpected and constitute semantic anomalies (Metusalem et al., 2012). With the goal of better understanding how the brain activates event knowledge during incremental comprehension, the present study investigates if and how the cerebral hemispheres differ with respect to this process. We utilize the stimuli from Metusalem et al. (2012) in conjunction with the visual half-field ERP methodology described above. Analyses focus on the amplitude of the N400 elicited by the Expected, Event-Related, and Event-Unrelated anomalous target words, presented to either the right or left visual field.

With the left hemisphere appearing to engage in the pre-activation of semantic features of likely upcoming input, and with event knowledge being a crucial component of linguistic expectancy generation, it is possible that the left hemisphere processes are crucial to Metusalem et al.'s findings. However, the Event-Related and Event-Unrelated targets in that study were semantically anomalous in sentence context, making it unlikely that they would be activated by a left hemisphere mechanism that makes top-down use of context cues to guide expectancy generation. Perhaps then it is likely that right hemisphere processes underlie the activation of contextually anomalous but event-related information. This hypothesis would align with the notion of the right hemisphere as using message-level context not for expectancy generation, but rather for higher-level discourse functions such as elaborative inference generation. We therefore predicted that with LVF/RH but not RVF/LH presentation of Metusalem et al.'s target words, we will observe reduction in N400 amplitude for Event-Related relative to Event-Unrelated targets. Such a finding not only would contribute to our knowledge of the neural basis of event knowledge activation, specifically in terms of hemispheric asymmetries, but also would be consistent with an underlying functional distinction in the activation of event knowledge for generation of linguistic expectancies and of elaborative inferences.

2. Methods

2.1. Participants

Sixty-one undergraduates at the University of California, San Diego participated for course credit. All were native English speakers with normal or corrected-to-normal vision. All were right handed, and none reported any left handed immediate family members. None reported any cognitive or neurological deficits. Thirteen participants' data were excluded due to excessive EEG artifacts, resulting in data from 48 participants (25 male, 23 female; mean age: 21.5 years, age range: 18–33 years) being included in the analysis. This relatively large number of participants was run due to the relatively small number of items per condition available for the experiment (see *Stimuli*).

2.2. Stimuli

Participants read the 72 three-sentence discourses from Metusalem et al. (2012). The first two sentences of each item established the event context. The third and final sentence presented one of three types of target word: highly expected (Expected), related to the described event but semantically anomalous in sentence context (Event-Related), or unrelated to the described event and semantically anomalous in sentence context (Event-Unrelated). All target words appeared in sentence-medial position. Stimulus generation began with creation of three-sentence discourses in which the third sentence was deemed to create a strong expectation for a specific word to appear. Expected target words were then obtained via a cloze task. Thirty UCSD undergraduates read each discourse up to the word preceding target position and provided the word they felt was most likely to come next. For each item, cloze probability for a word was calculated as the proportion of participants that provided that word as a continuation of the discourse, and the word with the highest cloze probability was chosen as the Expected target word. Expected targets had a mean cloze probability of 0.81, indicating that they were strongly expected in context.

The Event-Related targets were obtained via a norming task in which a separate group of 45 UCSD undergraduates read each discourse up to and including the Expected target word and were asked to “paint a mental picture” of the described event. They were then asked to list up to five people or objects they imagined as being present at or involved with the event but were not mentioned in the discourse itself. Each participant’s responses for an item were given a weighted score based on order of mention: five points for the first listed response, four points for the second, three points for the third, two points for the fourth, and one point for the fifth. Within each item, scores for a given response were then summed across the 45 participants, yielding a highest possible event-relatedness score of 255 (if all 45 participants provided the same response in first position). The highest scoring response that was both zero-cloze according to the previous cloze task and deemed to be semantically anomalous in sentence context was chosen as the Event-Related target. Event-Related targets had a mean event-relatedness score of 92.36.

After this procedure, the 72 experimental items were split into six different groups of 12 items, allowing six experimental lists to be created by rotating each item group through the six conditions (where a condition is defined at the intersection of target word type and visual field of presentation). Across lists, Expected target words were matched on several factors known to influence N400 amplitude: cloze probability, frequency, length, and orthographic neighborhood size. Similarly, Event-Related target words were matched across lists on the following factors: length, orthographic neighborhood size, frequency, and event-relatedness norming score. Orthographic neighborhood sizes were taken from the Medical College of Wisconsin Orthographic Wordform Database (http://www.neuro.mcw.edu/mcword/). Frequency matching was based on log frequency per 51 million words taken from the SUBTLEXus corpus (Brysbaert & New, 2009).

After creation of the six rotation groups, Event-Related targets were shuffled across items within each group to obtain the Event-Unrelated targets, thereby matching Event-Related and Event-Unrelated target words on all lexical variables. All Event-Unrelated targets were zero-cloze and had an event-relatedness norming score of zero. Care was taken to match Event-Related and Event-Unrelated targets within each item for degree of contextual anomaly. The full set of experimental items is provided in the Appendix.

The six groups were then rotated through each condition to create six experimental lists containing 12 items per condition. Each item appeared exactly once per list and exactly once in each condition across all lists. Each list also included 24 filler items. All fillers were three sentence discourses describing common events and did not contain any contextually anomalous words. The inclusion of 24 fillers thus brought the total proportion of trials containing anomalous words to 50% for each list. Presentation of experimental and filler items was pseudo-randomized separately for each participant, such that no more than three trials in a row contained anomalous words or target words presented to the same visual field. Each list was seen by eight of the 48 participants included in the analysis.

2.3. Procedure

Participants sat in a dimly lit, sound attenuated, electromagnetically shielded chamber as they read the stimuli from a computer monitor. Each trial began with the first two sentences of the discourse presented in paragraph format at the center of the screen. Once the participants read and understood the sentences, they pressed a button to advance to the final sentence. A fixation cross then appeared at screen center, and participants were instructed to fixate the cross without blinking. The final sentence was then presented word-by-word via rapid serial visual presentation (RSVP) with a 500ms stimulus onset asynchrony (SOA) and a 200ms stimulus duration, yielding a 300ms interstimulus interval (ISI). All words except the target flashed one at a time centered immediately above the fixation cross. The target words appeared either to the right or left of central fixation, with 2 degrees visual angle between the inner edge of the word and screen center: For targets presented to the right visual field, two degrees separated the left edge of the word and screen center; for targets presented to the left visual field, two degrees separated the right edge of the word and screen center. In the setup used, participants were seated such that the nasion was 44 inches from the computer monitor, with two degrees of visual angle corresponding to 1.54 inches across the screen. Note that the RSVP parameters used here are different than those from Metusalem et al. (2012), who used a 350ms SOA and 150ms ISI. A slower RSVP rate was used here due to the first author's impression that the rate used by Metusalem et al. (2012) did not allow adequate time for reliable recognition of the laterally presented target words. This aligns with research showing that word recognition is slower for words presented peripheral to the point of fixation (Bouma, 1978; Rayner & Morrison, 1981; Schiepers, 1980).

After offset of the final word, the fixation cross remained on the screen for an additional 1400ms. A yes/no comprehension question appeared 1000ms following the offset of the fixation cross and remained on the screen until the participant entered a response with a button press of either the right or left hand. Yes/no response hand was counterbalanced across participants. Following the participant's response, the screen went blank for 1500ms before the next trial began.

Before the beginning of the experiment, participants completed 12 practice trials to familiarize themselves with the experimental procedure. These trials followed the same procedure outlined above. After the experiment, each participant completed adaptations of the Author and Magazine Recognition Tests described by Cunningham and Stanovich (1990) and Stanovich and Cunningham (1992). These were administered to form the basis of an analysis of individual differences parallel to that reported by Metusalem et al. (2012). As in Metusalem et al.'s study, performance was scored as the number of correct identifications minus the number of false alarms across both tests.

2.4. EEG recording & processing

Participants' electroencephalograms were recorded via 26 tin electrodes embedded in an elastic cap. Electrodes were spaced across the scalp in a laterally symmetric quasi-geodesic pattern of equilateral triangles (see Figure 1). Additional electrodes were placed over the left and right mastoids, as well as adjacent to the outer canthus and over the infraorbital ridge of each eye to monitor for eye movements and blinks. EEG was referenced online to the left mastoid and re-referenced offline to the average of the right and left mastoids. All electrode impedences were kept under 5 KΩ. Data was amplified with a band pass 0.01–100 Hz and digitized at 250 Hz.

The raw EEG was screened for artifacts before subsequent averaging and analysis. Target word epochs extended from 100ms pre-stimulus onset to 920ms post-stimulus onset. All epochs containing blinks, eye movements, excessive muscle tension, amplifier blocking, or excessive channel drift were rejected; importantly, any target epochs containing horizontal eye movements, which could have been launched to fixate a laterally presented target word, were rejected. Overall, 7.35% of target epochs were rejected, with the following rejection rates for each condition: Expected, RVF/LH – 8.68%; Expected, LVF/RH – 5.90%; Event-Related, RVF/LH – 9.03%; Event-Related, LVF/RH – 5.03%; Event-Unrelated, RVF/LH – 8.85%; Event-Unrelated, LVF/RH – 6.60%. Following artifact rejection, time-domain average ERPs for each condition were calculated relative to a 100ms pre-stimulus baseline.

2.5. Data Analysis

Several statistical analyses were conducted on mean ERP voltage measures in separate time windows. The first was 75–175ms post-stimulus, meant to capture the amplitude of the visual N1 component. Visual N1 amplitude is known to be larger over scalp sites contralateral to the visual field of presentation; N1 amplitude analyses thus allowed us to investigate the effectiveness of lateralized presentation of target words in biasing initial processing to the contralateral hemisphere.

The next analysis window was 200–500ms, corresponding to the N400. This time window keeps with that used by Metusalem et al. (2012) in their analysis of N400 amplitude. All N400 amplitude analyses were conducted on the N400 effects: the mean amplitude 200–500ms of the Event-Related minus Expected and the Event-Unrelated minus Expected difference ERPs. Analysis directly comparing the N400 effects for the Event-Related and

Event-Unrelated targets in the two visual fields focused on a subset of channels that showed the greatest reduction in N400 effect amplitude for Event-Related versus Event-Unrelated targets in the Metusalem et al.'s Experiment 1. Taking the data from that experiment, we calculated mean amplitude from 200–500ms of the Event-Related minus Expected and Event-Unrelated minus Expected difference ERPs as a measure of the amplitude of N400 effects for the two anomalous conditions. At each of the 26 channels, we subtracted the amplitude of the N400 effect for Event-Related targets from that for the Event-Unrelated targets. All channels were then rank ordered according to this N400 amplitude difference, with channels showing more negative values (i.e., greater reduction of N400 effect for Event-Related relative to Event-Unrelated targets) ranked higher. The top half of channels were then chosen for analyses of N400 amplitude. The channels in this subset are underlined in the scalp diagram depicted in Figure 1. Analysis of N400 effect scalp topography was conducted on the same subset of 16 electrodes analyzed in Metusalem et al.'s scalp topography analysis. These electrodes are colored in on the scalp diagram in Figure 1.

Analyses in these time windows were conducted with repeated measures ANOVAs and t-tests as indicated in *Results*. For F-tests with more than one numerator degree of freedom, the Greenhouse-Geisser (1959) adjustment to degrees of freedom was used to correct for possible violations of sphericity. In these instances, reported F-test results include the uncorrected degrees of freedom, the Greenhouse-Geisser epsilon (ε_{GG}), and the p-value for the corrected degrees of freedom. For families of follow-up tests larger than two, Bonferroni corrected alpha values were used to control the family-wise error rate.

The final time window of analysis was from 500–900ms. Metusalem et al. observed effects in this time window; specifically, a frontal negativity for Event-Unrelated targets relative to the other two target types, and a posterior positivity for both anomalous target types relative to Expected targets, with a seemingly earlier onset for Event-Unrelated targets. As no specific hypotheses regarding late effects were made for that study or for the present experiment, exploratory analyses were conducted to assess the presence of any late effects here. These analyses utilized a mass univariate analysis technique implemented in MATLAB in the Mass Univariate ERP Toolbox (Groppe, Urbach, & Kutas, 2011a; http://openwetware.org/wiki/Mass_Univariate_ERP_Toolbox). Four separate analyses were conducted, one for each difference ERP resulting from subtraction of the ERPs to Expected targets from ERPs to each of the two anomalous target types, separately for each visual field. Each analysis consisted of a series of two-tailed t-tests on difference ERP amplitudes at every channel and time point from 500–900ms, resulting in 2,626 t-tests per analysis. For example, the analysis for Event-Related targets with RVF/LH presentation consisted of subtracting ERPs to Expected targets with RVF/LH presentation from those for Event-Related targets with RVF/LH presentation. At every channel and time point, a two-tailed single sample t-test with 47 degrees of freedom was conducted on the amplitude of this difference ERP to detect positive or negative deviations from zero. False discovery rate was controlled at the 0.05 level (see below). Statistically significant results in the family of tests were taken to indicate a reliable difference in ERP amplitude between the Event-Related and Expected targets for RVF/LH presentation.

To protect against a large proportion of Type I errors in these test families, an adaptive two-stage false discovery rate (FDR) control introduced by Benjamini, Krieger, and Yekutieli (2006) was employed to determine statistically significant deviations from zero while controlling FDR at the 0.05 level. While this FDR control procedure is guaranteed to work only when tests are independent, simulations have suggested that accurate FDR control is achieved even when tests are correlated (Groppe, Urbach, & Kutas, 2011b). This analysis method was chosen because it allows for exploring differences between conditions in the absence of a priori hypotheses regarding the direction, timing, or scalp distribution of differences, and because it achieves a desirable balance between statistical power and Type I error rate control.

3. Results

3.1. Comprehension question accuracy

Before analysis of ERP data, each participant's comprehension question accuracy on target trials was assessed to determine if the participant understood the target discourses. Across the 48 participants, mean percent of comprehension questions answered correctly was 96% (range: 85% to 100%); only two participants scored below 90% accuracy. Errors did not vary systematically by condition. Comprehension question accuracy was deemed acceptable for all participants, and no data were excluded based on comprehension question performance.

3.2. N1 amplitude

Figure 1 shows the ERPs for the three target types at all 26 channels, separately for left and right visual field presentation. For all targets in both visual fields, the N1 can be seen as a negative-going wave peaking around 150ms post-stimulus onset. The N1 appears largest over posterior sites over the hemisphere contralateral to the visual field of presentation, a pattern commonly found with lateralized presentation of visual stimuli. Analysis of N1 amplitude confirmed this pattern. Mean ERP amplitude from 75–175ms was entered into a Target (Expected vs. Event-Related vs. Event-Unrelated) x Visual Field (RVF/LH vs. LVF/RH) x Hemisphere (right vs. left hemisphere channels) x Channel (11 non-midline channels within each hemisphere) ANOVA. A statistically significant Visual Field x Hemisphere interaction ($F(1,47)=48.30$, $p<0.0001$) revealed that with RVF/LH presentation, N1 amplitude was larger at left than right hemisphere channels (−1.30 μV vs. −0.63 μV; $t(47)=-4.41$, $p<0.0001$), whereas with LVF/RH presentation, N1 amplitude was larger at right than left hemisphere channels (−1.20 μV vs. −0.62 μV; $t(47)=-4.05$, $p<0.001$). Analysis also revealed a Visual Field x Hemisphere x Channel interaction ($F(10,470)=16.19$, $\varepsilon_{GG}=0.1928$, $p<0.0001$), indicating that the Visual Field x Hemisphere interaction varied across the scalp. There was no main effect of or interactions involving Target (all $p>0.17$). In sum, N1 amplitude was larger at channels over the hemisphere contralateral to the visual field of presentation, providing evidence that lateralized presentation of target words was effective in biasing visual processing to the hemisphere contralateral to the visual field of presentation.

3.3. N400 effect amplitude

In the canonical time window and centro-parietal scalp region of the N400, Expected targets elicited more positive ERPs than the Event-Related and Event-Unrelated targets for both RVF/LH and LVF/RH presentation (Figure 1). Differences between the visual fields become apparent when comparing the Event-Related and Event-Unrelated target ERPs. With RVF/LH presentation, ERPs at centro-parietal channels appear to be of very similar amplitude for both anomalous target types in the 200–500ms analysis window. With LVF/RH presentation, however, the ERPs in this time window are more negative for Event-Unrelated targets than for Event-Related targets. Figure 2 shows close-ups of ERPs at the midline parietal electrode, where this difference between visual fields can be seen clearly. This pattern of results aligns with the prediction that the N400 effect for Event-Related targets would be reduced relative to that for Event-Unrelated targets with LVF/RH but not RVF/LH presentation.

N400 effect amplitudes for Event-Related and Event-Unrelated targets were entered into a Difference (Event-Related N400 effect vs. Event-Unrelated N400 effect) x Visual Field x Channel (13 channels in the previously mentioned subset) ANOVA. The analysis did not reveal main effects of Difference ($F(1,47)=3.17$, $p=0.081$) or Visual Field ($F(1,47)=1.39$, $p=0.244$). It did reveal a main effect of Channel ($F(12,564)=9.54$, $\varepsilon_{GG}=0.2754$, $p<0.001$), simply indicating that the amplitude of N400 effects varies across channels, on average across all levels of Visual Field and Difference.

Critically, the analysis also revealed a Difference x Visual Field x Channel interaction ($F(12,564)=2.98$, $\varepsilon_{GG}=0.2867$, $p=0.027$), suggesting differences across the visual fields in how the relationship between Event-Related and Event-Unrelated N400 effects varies across the channels. (The Difference x Visual Field interaction was not statistically significant ($F(1,47=0.68$, $p=0.414$).) Follow-up Difference x Channel ANOVAs conducted separately for each Visual Field showed the N400 effect for Event-Related targets to be smaller than that for Event-Unrelated targets only with LVF/RH presentation. Analysis of data obtained with LVF/RH presentation revealed a main effect of Difference ($F(1,47)=4.66$, $p=0.036$), with the N400 effect for Event-Related targets smaller than that for Event-Unrelated targets (−1.71 μV vs. −2.52 μV). The Difference x Channel interaction did not reach significance ($F(12,564)=2.12$, $\varepsilon_{GG}=0.2763$, $p=0.094$). In contrast, analysis of data obtained with RVF/LH presentation did not show a main effect of Difference (Event-Related=−2.60 μV; Event-Unrelated=−2.95 μV) or a Difference x Channel interaction (both $p>0.25$).

The presence of a reduced N400 effect for Event-Related targets relative to Event-Unrelated targets for LVF/RH presentation but not RVF/LH presentation could be driven by changes in N400 effect amplitude across the visual fields for either condition. That is, the N400 effect for Event-Related targets could be reduced with LVF/RH presentation relative to RVF/LH presentation, the N400 effect for Event-Unrelated targets could be increased with LVF/RH presentation relative to RVF/LH presentation, or some combination of both. To investigate this, we conducted Visual Field x Channel ANOVAs separately for Event-Related and Event-Unrelated N400 effects. For the Event-Unrelated N400 effect, analysis did not reveal a main effect of Visual Field or a Visual Field x Channel interaction (both $p>0.50$). For the Event-Related N400 effect, analysis did not show a main effect of Visual Field but did reveal a Visual Field x Channel interaction (F(12, 564)=2.67, ε_{GG}=0.3223, p=0.036). While 12 of the 13 channels in this analysis showed a larger (i.e., more negative) Event-Related N400 effect for RVF/LH than LVF/RH presentation, lower-tailed t-tests comparing RVF/LH presentation to LVF/RH presentation at each channel did not reveal any statistically significant differences after Bonferroni correction; however, t-tests at five adjacent channels showed p-values of less than 0.05: LMCe (left medial central), RMCe (right medial central), MiPa (midline parietal), LDPa (left dorsal parietal), and LMOc (left medial occipital). No evidence of differences in N400 effect amplitude between visual fields was found for Event-Unrelated targets. This pattern of results suggests that the difference in N400 effect amplitude between Event-Related and Event-Unrelated targets observed for LVF/RH but not RVF/LH presentation was likely driven by a reduction in N400 effect amplitude for Event-Related targets for LVF/RH relative to RVF/LH presentation.

To assess the presence of differences across individuals in the degree of N400 reduction for Event-Related relative to Event-Unrelated targets, participants were divided into two groups based on a median split of performance on the Author and Magazine Recognition Tests (ART/MRT), and analyses of N400 effect amplitude paralleling those above were conducted for each group. Metusalem et al. (2012) found that for central target word presentation, the top half of ART/MRT performers showed evidence of N400 reduction for Event-Related targets, while the bottom half did not, and suggested that perhaps increased print exposure, or possible enrichment of general knowledge resulting from increased print exposure, was related to greater N400 reduction for Event-Related targets. In the present study, the low-scoring group (mean ART/MRT score=12.04, standard deviation=2.74) did not show any main effects or interactions involving Difference or Visual Field (all p>0.10). The high-scoring group (mean ART/MRT score=26.00, standard deviation=6.44) did not show a statistically significant Difference x Visual Field interaction (F(1,23)=0.42, p=0.524) but did show a Difference x Visual Field x Channel interaction (F(12, 276)=2.65, ε_{GG}=0.2876, p=0.047). Follow-up Difference x Channel ANOVAs within each Visual Field for this group did not reveal a significant main effect of Difference or a Difference x Channel interaction for either Visual Field (all p>0.14). Thus, evidence of ARM/MRT-based individual differences in this study is limited to the significant Difference x Visual Field x Channel interaction observed only for the top-scoring ART/MRT group. While Metusalem et al. tentatively argued that the high-scoring ART/MRT group drove N400 reduction for Event-Related targets with central presentation, we do not find conclusive evidence that this is the case with lateralized presentation. Further research is needed to determine if and how individuals differ with respect to activation of contextually anomalous event knowledge elements during incremental comprehension.

3.4. N400 effect scalp distribution

The N400 effects are broadly distributed, generally peaking over centro-parietal scalp regions, with a slight exception for the Event-Related N400 effect from LVF/RH presentation, which appears slightly frontally distributed relative to the others (Figure 3). The scalp distribution of N400 effects was analyzed according to the procedure used by Metusalem et al. (2012). N400 effects for the channel subset mentioned in *Methods* above and indicated in the scalp diagram in Figure 1 were entered into a Difference x Visual Field x Hemisphere (right vs. left hemisphere channels) x Laterality (medial vs. lateral channels) x Anteriority (prefrontal vs. frontal vs. parietal vs. occipital channels) ANOVA.

A main effect of Laterality revealed larger N400 effects over medial than lateral sites (−2.58 μV vs. −1.20 μV; $F(1,47)=51.26$, $p<0.0001$). A Laterality x Hemisphere interaction ($F(1,47)=4.48$, $p=0.04$) and follow-up two-tailed t-tests revealed a drop-off in N400 effect amplitude from medial to lateral channels for both the right (−2.62 μV vs. −1.40; $t(47)=-6.31$, $p<0.0001$) and left hemisphere channels (−2.54 μV vs. −1.00 μV; t(−7.03), $p<0.0001$), though the drop-off was greater in the left hemisphere. A Laterality x Anteriority interaction ($F(3,141)=10.56$, $\varepsilon_{GG}=0.7080$, $p<0.0001$) and follow-up tests revealed that lateral channels did not show any differences between levels of Anteriority (all $p>0.25$), while medial channels showed larger N400 effects at frontal than prefrontal sites (−2.70 μV vs. −2.15 μV, $t(47)=-3.49$, $p=0.001$). Taken together with the Laterality x Hemisphere interaction, this pattern of effects generally indicates that the largest N400 effects are observed medially over the frontal, temporal/parietal, and occipital sites.

Additionally, the analysis revealed a Difference x Visual Field x Anteriority interaction ($F(3,141)=4.38$, $\varepsilon_{GG}= 0.4034$, $p=0.0338$). To follow-up this three-way interaction, separate Difference x Anteriority ANOVAs were conducted for each visual field of presentation. No statistically significant effects were found for RVF/LH presentation (all $p>0.22$), while a Difference x Anteriority interaction was found for LVF/RH presentation ($F(3,141)=4.14$, $\varepsilon_{GG}=0.4060$, $p=0.039$). Twelve two-tailed t-tests were conducted comparing the levels of Anteriority separately within each level of Difference for LVF/RH presentation. For the Event-Related condition, no comparisons reached statistical significance (all $p>0.30$). For the Event-Unrelated N400 effect, the difference between frontal and prefrontal sites approached significance after Bonferroni correction, suggesting larger N400 effects at frontal than prefrontal sites (−1.71 μV vs. −1.03 μV, $t(47)=-2.86$, $p=0.0063$). No other comparisons approached statistical significance after correction (all $p>0.025$). This pattern of effects suggests that the Difference x Visual Field x Anteriority interaction was driven by a difference in the effect of Anteriority between the Event-Unrelated and Event-Related N400 effects obtained with LVF/RH presentation. Specifically, the Event-Unrelated N400 effect exhibits a centro-parietal peak that drops off significantly at more anterior channels, while the Event-Related N400 effect shows a broader and slightly more frontal distribution (as can be seen in Figure 3).

3.5. Late window (600–900ms)

In general, both anomalous conditions in both visual fields appear to elicit sustained negativities relative to the Expected condition from 500–900ms post-stimulus, albeit with variability in amplitude and scalp distribution. With RVF/LH presentation, centro-parietal channels appear to show negativities of similar amplitudes for both anomalous target types. These negativities appear to become smaller at occipital channels, while at frontal and prefrontal channels the negativity for Event-Related targets seemingly fades while that for Event-Unrelated targets remains. With LVF/RH presentation, centro-parietal channels appear to show a three-way split, with both anomalous target types going more negative than Expected targets, and with this relative negativity appearing larger for Event-Unrelated targets. These differences appear to become smaller both at occipital and frontal and prefrontal channels.

The mass univaritate analyses confirmed that both anomalous conditions in both visual fields elicited negativities relative to the Expected targets (Figure 4, darkened cells indicate a statistically significant negative deviation from zero after FDR control). In general, the negativity was statistically reliable at more channels and time points for Event-Unrelated than Event-Related targets and for LVF/RH than RVF/LH presentation. For Event-Unrelated targets with LVF/RH presentation, the negativity is reliable at a large majority of time points and channels throughout the 500–900ms window. With RVF/LH presentation, the negativity to Event-Unrelated targets is reliable widely across the scalp from 500ms to ~650ms. After that, the effect ceases to be reliable at temporal and occipital channels, while generally remaining reliable over other scalp regions. Event-Related targets show a negativity from 500–600ms at central and posterior channels for both visual fields of presentation. LVF/RH presentation also shows the negativity to be reliable at frontal channels in this time window. Unlike the Event-Unrelated targets, the Event-Related targets in both visual fields show little evidence of a negativity at frontal channels after ~650ms, although occasional clusters of significant tests suggest that the negativity to Event-Related targets may be sustained throughout the 500–900ms window, only with a smaller amplitude than the negativity to the Event-Unrelated targets, making it harder to detect statistically.

Perhaps most interestingly, the data show no evidence of a positivity relative to the Expected targets for either anomalous target type in either visual field. This contrasts with Metusalem et al.’s report of a posterior positivity to both anomalous target types, with a seemingly earlier onset for Event-Unrelated targets. Metusalem et al. also reported a frontal negativity to Event-Unrelated targets relative to the other two target types. Analyses here also reveal a negativity to Event-Unrelated targets at frontal sites, although the connection with the frontal negativity observed by Metusalem et al., if any, is unclear.

Analyses in the 500–900ms window thus lead to two conclusions: First, the late positivity observed by Metusalem et al. was not found here. Second, both anomalous target types in both visual fields elicit negativities relative to the Expected condition following the N400 time window, with the negativities being reliable at a greater number of channels and time points for Event-Unrelated targets and for LVF/RH presentation.

4. Discussion

The present study sought to advance our understanding of how the brain activates contextually anomalous but event-related information during incremental language comprehension, specifically through investigation of asymmetries across the cerebral hemispheres in this process. Participants’ EEG were recorded as they read short stories in which a sentence-medial word in the final sentence was either highly expected (Expected), semantically anomalous in the linguistic context but related to the described event (Event-Related), or semantically anomalous but unrelated to the described event (Event-Unrelated). Visual half-field presentation of target words was utilized to assess hemispheric asymmetries in the brain’s responses to these target words. With both RVF/LH and LVF/RH presentation, both anomalous Event-Related and Event-Unrelated targets elicited larger N400s than Expected targets. This finding aligns with previous research suggesting that sentence and discourse processing in both hemispheres is affected by message-level context (Coulson et al., 2005; Federmeier & Kutas, 1999b; Wlotko & Federmeier, 2007). Importantly, the N400 effect for Event-Related targets was reduced relative to that for Event-Unrelated targets with LVF/RH presentation, while no difference was found between Event-Related and Event-Unrelated N400 effect amplitudes obtained with RVF/LH presentation. This finding suggests an asymmetry across the hemispheres in the activation of contextually anomalous but event-relevant information; specifically, such activation appears to rely strongly on right hemisphere processes. This finding additionally informs our understanding of the functional properties of event knowledge activation with respect to expectancy generation and inference. With the Event-Related targets being semantically anomalous in sentence context, it is unlikely that they were expected to appear, and because the Event-Related targets did not probe concepts necessary to maintain discourse coherence (i.e., coherence inferences), they can be argued to probe elaborative inferences. The present findings thus align with previous research suggesting that the generation of linguistic expectancies and of elaborative inferences, both of which draw upon event knowledge, are crucially supported by the left (Federmeier & Kutas, 1999b) and right (Beeman et al., 2000) hemispheres, respectively. The present study thus provides evidence suggesting a functional distinction between event knowledge activation for elaborative inference and for expectancy generation.

4.1. Inference

Comprehending discourse often involves inferring unstated information, and numerous studies have suggested that right hemisphere processes are important for inference generation (Beeman, 1993; Beeman et al., 2000; Brownell et al., 1986; Mason & Just, 2004; Virtue et al., 2006). At a broad level, a distinction is generally drawn between coherence inferences (i.e., those necessary to maintain connections between sentences in a discourse) and elaborative inferences (i.e., those that capture likely outcomes of stated events or fill in additional information regarding a described event). Beeman et al. (2000) present evidence that elaborative inference generation relies on the right hemisphere, and when discourse coherences breaks down and inference is required to re-establish coherence, concepts activated through elaborative inference are selected by the left hemisphere for further processing.

The discourses in the present study involved no coherence breaks, and with the Event-Related targets obtained by asking people to visualize and elaborate on described events, the Event-Related targets can be considered to probe elaborative inferences. The present results thus are consistent with the notion that elaborative inference generation relies upon the right hemisphere. N400 reduction for Event-Related targets observed with central presentation (Metusalem et al., 2012) may indeed reflect elaborative inference generation, suggesting that elaborative inference affects the processes indexed by the N400 elicited by a word that is semantically anomalous in sentence context. This interpretation is consistent with previous research showing that the N400 elicited by a centrally presented, semantically congruous word is reduced when that word corresponds to an elaborative inference relative to when it does not (St. George, Mannes, & Hoffman, 1997).

4.2. Expectancy generation

In addition to inference, incremental language comprehension involves the generation of expectations for words or concepts likely to appear in the upcoming input (Altmann & Mirković, 2009; DeLong, Troyer, & Kutas, 2014; Federmeier, 2007), and research has suggested that expectancy generation is biased toward the left hemisphere (Federmeier et al., 2005; Wlotko & Federmeier, 2007; see Federmeier (2007) for discussion). Federmeier and Kutas (1999a,b) provide evidence that left hemisphere processes support pre-activation of the semantic features of likely upcoming words. Like semantic feature information, event knowledge is believed to guide expectancy generation (Altmann & Mirković, 2009; Elman, 2009; McRae & Matsuki, 2009). Metusalem et al. (2012) argued that their finding of N400 reduction for Event-Related targets with central presentation provides further evidence of the role of event knowledge in expectancy generation. They proposed that during incremental comprehension, the brain activates concepts that align with the general type of event being described, and those concepts that meet additional constraints, such as those on semantic features (e.g. the patient of the verb *build* should possess the features of objects that are commonly built), are likely to receive further activation and therefore be more strongly expected to appear. Under the notion that the left hemisphere is critically involved in expectancy generation, the present finding of N400 reduction for Event-Related targets with LVF/RH but not RVF/LH presentation raises an important question: Does N400 reduction for Event-Related targets observed here and by Metusalem et al. (2012) relate to expectancy generation, and if so, how?

There are at least two possibilities. First, N400 reduction for Event-Related targets observed here and in Metusalem et al. (2012) may be unrelated to expectancy generation. Under this account, both hemispheres engage event knowledge independently during incremental comprehension, with the right activating a range of event knowledge elements and the left activating only those elements that would be expected to appear in the unfolding sentence. This view would suggest a functional dissociation between event knowledge activation for expectancy generation and for elaborative inference. Another possibility is that left hemisphere processes draw upon right hemisphere event knowledge activation to generate expectancies. Under this view, the left hemisphere does not itself engage event knowledge, but rather selects activated event knowledge elements in the right hemisphere that also meet additional constraints on expectancy generation imposed by the linguistic context. Beeman et al. (2000) found that coherence inference is supported by left hemisphere selection of concepts activated in the right hemisphere, and such a mechanism might also support expectancy generation. Further research is necessary to determine if right hemisphere event knowledge activation plays a role in expectancy generation.

4.3. Complementary hemispheric asymmetries in language processing

Beyond the issues of inference and expectancy generation, the present findings generally inform theories of hemispheric asymmetries in language comprehension. One such theory, termed *coarse semantic coding*, has been put forth by Beeman (Beeman, 1998; Jung-Beeman, 2005). Coarse semantic coding posits that the hemispheres differ primarily in the strength and breadth of semantic activation in response to meaningful inputs: The left hemisphere strongly activates narrow semantic fields, limiting activation only to those concepts that are closely linked to the inputs, while the right hemisphere weakly activates a broad semantic field that includes more distantly related concepts. The present findings align in principle with coarse semantic coding. The left hemisphere might activate only conceptual information that closely aligns with the sentence context at a particular point, precluding the activation of contextually anomalous words regardless of relation to the described event. If the right hemisphere activates concepts more broadly related to the input, a word generally related to the described event should be activated to a greater degree than a word that does not relate to the event, even if that event-related word is anomalous the sentence context.

What remains unclear with respect to a coarse semantic coding account of these results is the level at which semantic activation patterns are driven. Activation of concepts through coarse semantic coding is often explained at the lexical level (e.g., Beeman, 1998; Jung-Beeman & Chiarello, 1998). In the present study it is possible, for example, that words like *blizzard*, *kids*, and *outside* could each weakly activate the Event-Related target *jacket*. However, Metusalem et al. (2012) attempted to rule out this possibility. First, they analyzed a subset of items for which the average Latent Semantic Analysis (LSA; Landauer, Foltz, & Laham, 1998) association scores between the discourse context and the Event-Related and Event-Unrelated targets were equal and still found N400 reduction for Event-Related targets. Second, they ran an additional study in which they removed the first two sentences from the context and did not find N400 reduction for Event-Related targets, indicating that any effect of lexical association would have to be limited to the first two sentences and persist over a full sentence lag. Therefore, a lexical-level account of coarse semantic coding may be insufficient here. Coarse semantic coding at a sentence or discourse level of meaning would better explain the present results.

Another general account of hemispheric asymmetries of semantic activation in language processing is that the right and left hemispheres differ in the top-down versus bottom-up use of context (Faust, 1998; Federmeier, 2007). Federmeier (2007) has argued that the left hemisphere quickly generalizes away from input to construct a message-level meaning representation, which it then applies in top-down fashion to predict upcoming input. Right hemisphere processing, on the other hand, is argued to be bottom-up and integrative, with processing affected mainly by the degree to which the incoming word can be integrated into the message-level meaning at that point.

The present findings align with the notion of left hemisphere processing as supporting expectancy generation. Both Event-Related and Event-Unrelated targets in this study were highly unexpected in context, and we did not observe a difference in N400 amplitude between these target types with RVF/LH presentation. The present findings have interesting implications for the view of the right hemisphere as integrative. N400 reduction was found for Event-Related targets relative to Event-Unrelated targets in the right hemisphere, despite both being semantically anomalous in context and presumably equally difficult to integrate into the unfolding sentence at the point in which they appeared. This may challenge the notion of the right hemisphere as engaging in integrative processing; yet, if integration is defined not only by the fit between a word and the message-level meaning of the unfolding sentence, but also by the fit between a word and the mental or situation model under construction more generally, then perhaps the notion of the right hemisphere as integrative can account for the present findings.

4.4. Late positivities with central but not lateralized presentation

It is worth noting that the pattern of effects in the 500–900ms window observed in this study differs qualitatively from those observed in Metusalem et al.'s Experiment 1 with central presentation. In that experiment, a posterior positivity was observed for the two anomalous target types, with an earlier onset for the Event-Unrelated targets. No positivity was observed in this study for either anomalous target type in either visual field. Instead, both anomalous target types appeared to elicit negativities relative to the Expected targets in both visual fields, with strongest evidence of this effect for Event-Unrelated targets presented to the left visual field. While the absence of a posterior positivity could be due to the slower presentation rate used here, it might reflect that the positivity appears only when words are presented centrally. In fact, Federmeier and colleagues report a similar finding: a late frontal positivity elicited with central presentation (Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007) that disappears when the same stimuli are presented laterally (Wlotko & Federmeier, 2007). Furthermore, extension of negativities in the N400 time window into the post-N400 time window have been observed in other visual half-field ERP studies (Coulson & Wu, 2005; Coulson et al., 2005; Federmeier & Kutas, 1999b; Wlotko & Federmeier, 2013), further suggesting that the late effects seen here result from visual half-field presentation of the stimuli. It may be the case that certain late processes in response to unexpected words, observed at the scalp as positivities relative to expected words, are disrupted when initial visual processing is biased to one hemisphere.

5. Conclusion

Event knowledge activation is a central component of the real-time processes involved in incremental language comprehension. During comprehension, the brain activates event knowledge elements that are semantically anomalous in context. The present study found that this process appears to be supported crucially by the right cerebral hemisphere. This finding furthers our understanding of the neural basis of event knowledge activation and more generally advances our understanding of how event knowledge is activated during generation of expectancies and elaborative inferences during the course of incremental comprehension.

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Appendix

The 72 experimental items. Target word position in the context is underscored. Target words are listed in the following order: Expected (top), Event-Related (middle), Event-Unrelated (bottom). The comprehension question answers are provided in parentheses.

Comprehension questions targeted recognition of explicit statements made in the discourse or of unambiguous implications of those statements. Across all items, questions were equally likely to target statements made in either the first, second, or third sentences. No question's answer required consideration of the target word in the final sentence. This restriction allowed the same comprehension questions to be used across all conditions.

Context	Targets	Comprehension Question
Elizabeth was standing at the intersection waiting for the light to change. All of a sudden she saw a car barrel through the red light. A moment later, she heard a terrible ______ come from down the street.	crash policeman priest	Was somebody driving recklessly? (Yes)
For several months, there had been burglaries in the neighborhood. Many people thought they knew who the crook was. Finally, he was caught when he set off somebody's ______ one night.	alarm police dealer	Was the crook eventually caught? (Yes)
I think it's important to start the day right. Every morning, I make sure to eat a hearty breakfast. Sometimes there's almost no room left on my ______ once I finish dishing up.	plate eggs ring	Do I usually eat a modest breakfast? (No)
The band was very popular, and Joe was sure the concert would be sold out. Amazingly, he was able to get a seat down in front. He couldn't believe how close he was when he saw the group walk out onto the ______ and start playing.	stage guitar poles	Did Joe get stuck with a bad seat? (No)
My Aunt Bettie was very popular in our family. When she died, lots of people gathered to pay their respects. Her three brothers and three sisters all gave very moving ______ during the service.	speeches coffins cages	Was Aunt Bettie liked by the rest of the family? (Yes)
Traveling these days is much less fun than it used to be. Now you have to deal with worries about terrorism. It can take several hours to make it through ______ and find your gate.	security luggage helmet	Has the threat of terrorism made travel more difficult? (Yes)
I'm very sluggish when I wake up. Sometimes it takes me an hour to get ready in the bathroom. I often end up staring blankly at myself in the ______ for a while.	mirror toothbrush book	Am I usually energetic in the morning? (No)
Debbie is more of a risk taker than she should be. She loves to gamble but really isn't very good at card games. Last night, she had a rough time playing ______ at the casino.	poker dealer receptionist	Is Debbie a good card player? (No)
Many people think living in the country is easy. But I grew up on a farm and I know there are some downsides. What I hated most was being woken up early each morning by the ______ outside my window.	rooster barn grills	Did I grow up on a farm? (Yes)
My friend Julie spends all her time exercising. The machine she likes the most is the treadmill. By the time she's done, she's drenched in ______ and breathing very heavily.	sweat towel brush	Does Julie exercise frequently? (Yes)
Going to the movies is great fun. Before the show starts, I like to get a snack. There's nothing like watching the show while eating a big box of ______ covered with butter.	popcorn soda toothbrush	Is chocolate my favorite snack? (No)
Bob and Linda celebrated their 25th anniversary recently. Their kids wanted to do something nice for them. So they all got together and threw a big ______ at the beach.	party family parachute	Did Bob and Linda get married last year? (No)

Context	Targets	Comprehension Question
Michelle had a toothache for several months. She knew she should do something about it, but held off. She finally got checked out when she was told she could get some anesthetic to reduce the ______ and ease her discomfort.	pain dentist runners	Did Michelle eventually see somebody about her toothache? (Yes)
The parents were very excited about their new baby girl. One of the first things they did was to get her baptized in their church. The baby liked baths, so she smiled when she was sprinkled with ______ on her forehead.	water priest conductor	Did the baby enjoy getting baptized? (Yes)
During the summer, many people like to cook outdoors. Everybody has different preferences for what to make. My father likes both hot dogs and ______ but his favorite is bratwurst.	hamburgers grills dress	Do people like to cook indoors during the summer? (No)
Getting divorced is always difficult. Even when people get along, there are many details to work out. If there are children, the hardest part is the question of who gets ______ of them.	custody lawyer teacher	Is getting divorced a simple matter? (No)
The summer is a great time to go the beach. It's true you have to bring a lot of things with you, but that's OK. The only thing I don't really like is that your food gets full of ______ and attracts lots of ants.	sand towel puck	Do you need to bring a lot of things with you when you s pend the day at the beach? (Yes)
If you live in a city, the best way to see unusual animals is to go to the zoo. There are all kinds of exotic animals that children don't normally see. Sometimes, however, the kids are scared by the roar of the ______ and scream in terror.	lion cages license	Do kids sometimes get scared at the zoo? (Yes)
A favorite American pastime during the summer is going to a ballgame. Of course, people occasionally get rowdy. My sister gets really upset when people drink too many ______ and start acting crazy.	beers hotdogs luggage	Does my sister like it when people drink a lot at the ballgame? (No)
After a day of off-roading, my truck was covered in mud. I parked it out on the driveway to give it a wash. When I started, I realized that I had forgotten to turn on the ______ on the side of the house.	hose soap hammer	Did I take my truck to the car wash? (No)
The case of Bill the Butcher was the largest that this court had ever tried. The entire town came out to hear the opening statements. Once they were finished, the prosecution called its first ______ to the stand.	witness lawyer actors	Did the opening statements draw a large crowd? (Yes)
This spring, I decided to start growing my own vegetables. I bought a variety of seeds and planted them in my backyard. I made sure to choose a spot that got plenty of ______ during the day.	sun dirt money	Did I start a vegetable garden? (Yes)
My parents were very happy when my sister finally got married. At the ceremony, my father looked so proud. My mother started crying when the couple recited their ______ and proclaimed their love.	vows ring water	Were my parents worried about my sister getting married? (No)

Context	Targets	Comprehension Question
I usually take the bus to work in the morning. It was over twenty minutes late on Friday. To top it off, when it finally came I realized that I didn't have any ______ to pay the fare.	money driver salesman	Did the bus arrive on time on Friday? (No)
The restaurant down the street is known for its lousy service. One time, I actually caught a waiter taking a bite of someone's dinner. I immediately asked to speak with the ______ about the waiter's conduct.	manager food barn	Is it common to have bad service at the restaurant? (Yes)
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 ______ in the front yard.	snowman jacket couch	Did my kids play outside on their day off from school? (Yes)
My dad had a lot of trouble when I took him skiing for the first time. It took him forever just to figure out how to stand up. Then he fell when he tried to get onto the ______ with his skis crossed.	lift poles guitar	Is my dad a good skier? (No)
Jackie is a very methodical poker player. During the high-stakes tournament, she was even more careful than usual. Every few hands, she made sure to count her ______ silently to herself.	chips table jacket	Was Jackie playing carelessly during the poker tournament? (No)
My friend Mike went mountain biking recently. He lost control for a moment and ran right into a tree. It's a good thing he was wearing his ______ or he could have been seriously hurt.	helmet dirt coral	Did Mike crash on his bike? (Yes)
It's generally a good idea to drive slowly and obey traffic laws. If you don't, you're likely to get pulled over. It's always a terrible feeling when the officer issues you a ______ and sends you on your way.	ticket license box	Is it a good idea to obey traffic laws? (Yes)
I used to love taking field trips with my elementary school. We got out of class for the day, and we usually went someplace fun. I would always get excited when we were about to board the ______and head off.	bus teacher lawyer	Were my field trips usually boring? (No)
We're lucky to live in a town with such a great art museum. Last week I went to see a special exhibit. I finally got in after waiting in a long ______ and paying an entrance fee.	line painting surfboard	Did I see a special exhibit at the aquarium? (No)
I took my friends to the desert for a few days of camping. After a couple hours of hiking, we found a good spot to spend the night. The weather was so nice that we didn't even pitch a ______ or use our sleeping bags.	tent fire family	Did we have nice weather on our camping trip? (Yes)
Jenny had a really difficult math exam earlier this week. She was so worried about being late that she arrived twenty minutes early. As soon as she arrived, she made sure to sharpen her ______ and find a seat.	pencil calculator vegetables	Did Jenny arrive early to the test? (Yes)
My friends and I played a game of pond hockey over the weekend. It was clear from the beginning that one of my friends had never played before. The poor guy couldn't even lace up his ______ or hold his stick properly.	skates puck hotdogs	Are all my friends experienced hockey players? (No)

Context	Targets	Comprehension Question
Filming for the new movie was getting underway, and the crew was ready to shoot the first scene. One of the cameramen mentioned that she was getting some really bad glare in the shot. Somebody quickly dimmed the ______ and the director called action.	lights actors police	Did the cameraman complain about the lights being too dim? (No)
A high profile bank was robbed yesterday afternoon. The robbers entered through the back and made their way to the lobby. All the customers froze when they saw several masked men pointing ______ and threatening to shoot.	guns money dirt	Were there customers present during the bank robbery? (Yes)
It's a good idea to get some reading material before going on a long trip. I tend to go to the library the day before I leave. Last time I went, I was shocked to find out that I owed a huge ______ for something I had already returned.	fine book soda	Do I usually go to the library before going on a trip? (Yes)
Shopping at the used car lot can be a stressful ordeal. Even if you find a car you like, you never know if it has any problems. Just make sure to have a good look under the ______ before buying anything.	hood salesman clowns	Can you be certain whether or not a used car has problems? (No)
My little brother doesn't know how to swim, but we still bring him along when we go to the pool. One time, he fell into the deep end while no one was looking. He was quickly brought to safety by the ______ and given to our mother.	lifeguard water fire	Is my brother a good swimmer? (No)
Last Saturday I laid around watching television into the middle of the night. I eventually found myself watching an infomercial for some new cleaning product. I wanted to change the channel, but I couldn't find the ______ anywhere.	remote couch car	Was I watching TV late at night? (Yes)
Even the laziest people clean up around the house every once in a while. The worst part is always the bathroom. When you tackle the toilet, it's good to wear some ______ to guard against bacteria.	gloves bleach booths	Is the bathroom the worst part of cleaning the house? (Yes)
The airlines are getting so stingy that they don't even provide free food anymore. A lot of people complain that they no longer get a complimentary meal on long flights. I'd be happy just to get a bag of ______ or some crackers.	peanuts drinks bleach	Do all the airlines still provide complementary meals? (No)
We had our entire family over to our house for Thanksgiving this year. My mother set the table as if the President were coming for dinner. She laid out a nice tablecloth and even lit a couple ______ for effect.	candles turkeys boots	Did we set the table for an ordinary dinner? (No)
The last presidential election drew an incredible number of voters. My polling place had a line out the door when I arrived on election day. I waited three hours before I was finally able to cast my ______ and head to work.	vote booths coffins	Did a lot of people vote in the election? (Yes)
My sister was only twenty when she won a Grammy for her first album. She seemed so nervous as she gave her acceptance speech. Her voice was shaky as she spoke into the ______ and thanked everyone.	microphone dress painting	Was my sister young when she won her Grammy? (Yes)

Context	Targets	Comprehension Question
Jeremy is a great athlete despite being prone to injury. During his last high school football game, he was knocked unconscious twice. That still didn't stop him from scoring the winning ______ with only seconds remaining.	touchdown helmet glass	Did Jeremy sprain his ankle during the football game? (No)
Living in San Diego is great if you love to surf. The downside is that the water can be freezing during the winter. You'll be sorry if you go out without wearing your ______ or at least a shirt.	wetsuit surfboard food	Is the winter water warm enough to surf in just your bathing suit? (No)
Raja likes to go to the supermarket early in the morning to avoid the crowds. He usually brings his daughter along. She always insists on riding in the ______ while Raja pushes.	cart vegetables bed	Does Raja try to do his shopping when the store isn't crowded? (Yes)
My husband and I had some nice red wine with dinner last night. He's so clumsy that he ended up spilling some all over me. At least my shirt was dark enough to partially hide the ______ for the rest of the evening.	stain glass medal	Was I wearing a dark shirt? (Yes)
Andy was excited to get his driver's license, but he was afraid he wouldn't pass the parallel parking section of the test. He tried to remain calm as he checked his mirrors and began. Unfortunately, he ended up failing for knocking over too many ______ and had to retake the test.	cones instructors doctors	Did Andy pass his driver's test? (No)
Having major surgery is never a pleasant experience. You lie in a sterile room next to an operating table full of scary tools and devices. As if the anxiety isn't enough, you usually have to deal with a cold draft up your ______ while you wait to begin.	gown doctor instructors	Can major surgery be a pleasant experience? (No)
I used to love getting my hair cut when I was a kid. I got so excited every time I walked into barbershop. I would giggle with joy as I hopped into the ______ and greeted the barber.	chair scissors turkeys	Did I enjoy haircuts as a child? (Yes)
Tanya was totally pumped to be skydiving for the first time. When it was her turn to jump, she got a huge smile on her face. She didn't hesitate at all before leaping out of the ______ head first.	plane parachute eggs	Was Tanya excited to be skydiving? (Yes)
When Maya's laptop was stolen, she went to the Apple store to buy a replacement. She wanted to make sure to get one with a fast processor. She also had tons of files to store, so she wanted a lot of ______ as well.	memory salesman driver	Did Maya do her computer shopping online? (No)
My friends and I took a cross-country road trip after graduating from college. We ended up getting lost somewhere in the middle of Nevada. We eventually decided to stop and ask for some ______ at a gas station.	directions car table	Did we stop because we were out of gas? (No)
I helped my neighbor build a shed recently, and we managed to run into a few problems. First, we realized that we didn't make the doorway the right size. Then we didn't have enough shingles to finish the ______ so we returned to the store.	roof hammer drinks	Did we run out of shingles? (Yes)

Context	Targets	Comprehension Question
The doctor was running very late, which was not uncommon. Mary couldn't wait any longer and decided to reschedule her check-up. So she asked if she could make another ______ for the following week.	appointment receptionist lawyer	Did Mary try to reschedule her appointment? (Yes)
Marathons take a lot out of you, and it's important not to get dehydrated. Ralph had been doing OK up until mile twenty-six. As he rounded the final bend, someone gave him some ______ and cheered him on.	water runners dentist	Did Ralph compete in a triathlon? (No)
Having serious car trouble is the worst. Aside from being unable to drive, it's hard to find a mechanic you can trust. You never know if you're being charged a fair ______ or not.	price tire towel	Is it easy to find a trustworthy mechanic? (No)
Little kids love to go to the circus. There are always exotic animals, and children find the acts very exciting. The scariest act is of course when the lion tamer puts his head inside the lion's ______ while the crowd gasps in horror.	mouth clowns salesman	Are there any scary acts at the circus? (Yes)
The Olympic ice skating competition is always well attended. Last year, the winner was the favorite, who was extremely popular. The crowd roared with delight as she took her place on the ______ and waved to her fans.	podium medal blood	Was the winner of the competition popular? (Yes)
The boxing match had gone on for seven rounds, and both contestants were exhausted. One of them had sustained serious injuries and finally fell to the mat. Worried about his condition, the referee declared the other fighter the ______ and ended the match.	winner blood rod	Did the referee end the match because one of the fighters cheated? (No)
I started taking an introductory painting course a few weeks ago. During the first class, the instructor had a very hard time giving even a simple demonstration. It was clear that he didn't have much teaching ______ and wouldn't be a good instructor.	experience brush towel	Did my painting class start out well? (No)
Nadia went snorkeling in the Great Barrier Reef while on vacation in Australia. She found it to be more beautiful than she had ever imagined. After several hours of swimming around, she still couldn't bring herself to climb back in the ______ and head to shore.	boat coral dirt	Did Nadia enjoy her time at the Great Barrier Reef? (Yes)
Music fans have a lot of different tastes when it comes to live performances. A lot of people like to go to rock concerts, but I prefer a symphony. My favorite part is the string ______ because I love the violin.	quartet conductor policeman	Do I prefer a symphony over a rock concert? (Yes)
Moving to a new house is always a huge hassle. If you do it yourself, the whole ordeal can last several days. Things go much faster if you hire a moving ______ to help you.	company box gun	Is moving to a new house an easy job to do alone? (No)
The climb up Mount Whitney is beautiful but very challenging. Manny and Julia were tired but looking forward to what they knew awaited them at the top. Finally, they rounded the last bend and were awed by the magnificent ______ of Owens Valley below.	view boots scissors	Did Manny and Julia go hiking down by the river? (No)

Context	Targets	Comprehension Question
The last time Tommy went hunting, he was nearly shot by another hunter. He was creeping quietly through the woods when the other hunter almost mistook him for a deer. It’s a good thing he was wearing his orange ______ over his camouflage.	vest gun soap	Was Tommy almost shot by another hunter? (Yes)
I used to spend a lot of Saturday mornings fishing with my dad. We would wake up early and load the car with all of the equipment. We always brought a bucket of worms to use as the ______ even though worms grossed me out.	bait rod tire	Did I used to go fishing with my dad? (Yes)
I usually fall asleep pretty quickly. Sometimes, though, if I’ve had a busy day I find it hard to wind down. Then I find the best thing is to read a good ______ or magazine.	book bed car	Do I like to watch TV when I can’t fall asleep? (No)
It can be difficult to find a decent parking spot downtown. A lot of the time you have to park on the street. That’s why it’s always good to have some change to feed the ______ or you might get a ticket.	meter car calculator	Is it easy to find good parking downtown? (No)

- Hemispheric asymmetry in event knowledge activation during language comprehension
- Visual half-field ERP experiment
- N400 reduction for unexpected but event-related word with LFV/RH presentation only
- Right hemisphere plays important role in activating event knowledge

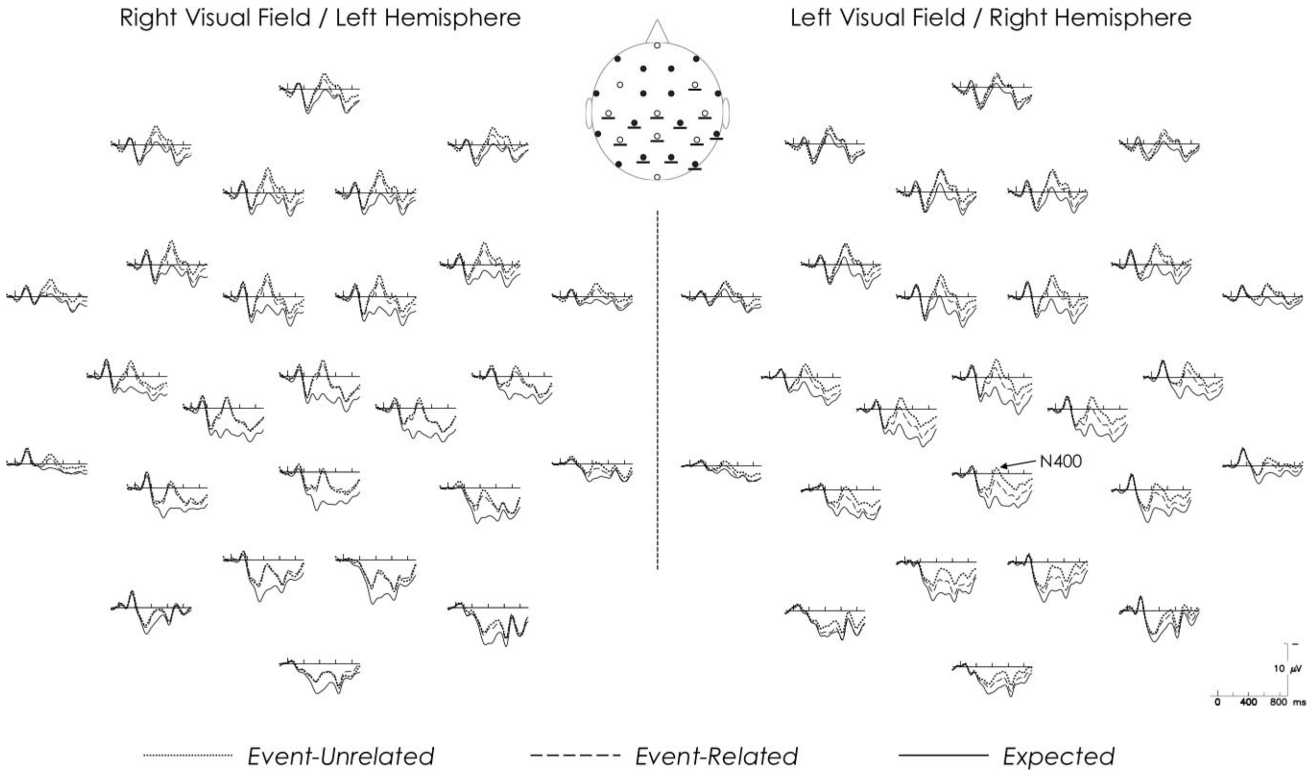

Figure 1.

Grand average ERPs at the 26 scalp electrodes for the three target word types, for both right visual field / left hemisphere (RVF/LH) and left visual field / right hemisphere (LVF/RH) presentation. Ticks on the x-axis represent 200ms intervals. Negative voltage is plotted up. A diagram of scalp electrode placement is provided. Channels included in analysis of N400 effect amplitudes are underlined. Channels included in the analysis of N400 effect scalp distribution are darkened.

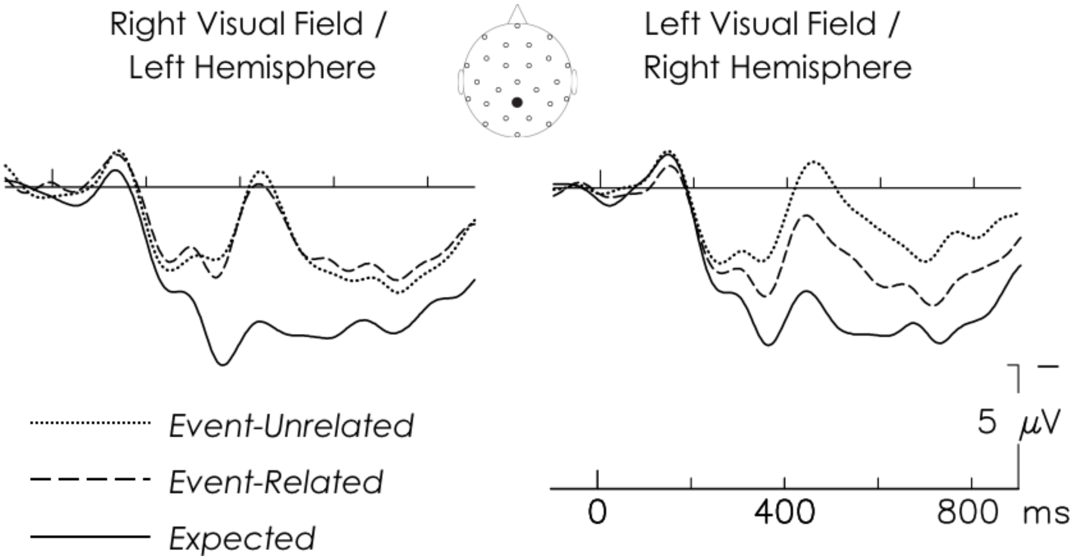

Figure 2.

Grand average ERPs at the midline parietal electrode for the three target word types, for both RVF/LH and LVF/RH presentation.

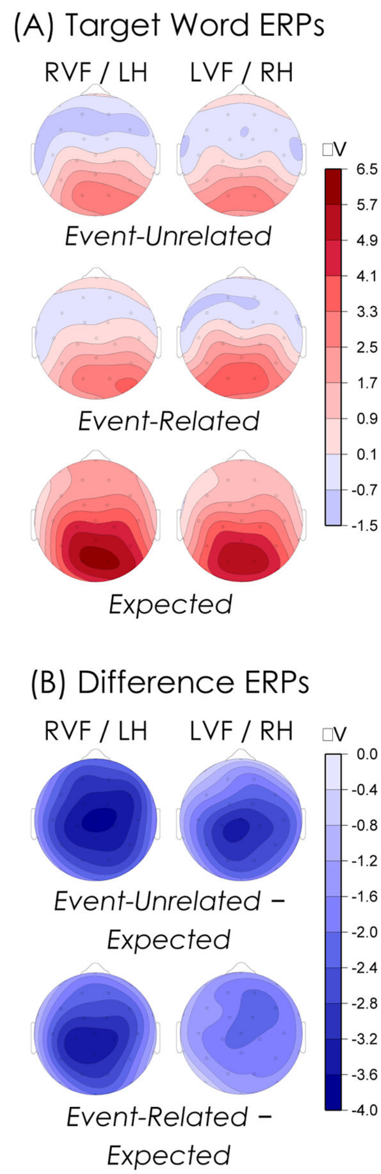

Figure 3.

Scalp topographies of mean ERP amplitude from 200–500ms post-stimulus onset. (A) Topographies for target word ERPs. (B) Topographies for the difference ERPs representing the N400 effects for Event-Related and Event-Unrelated target words.

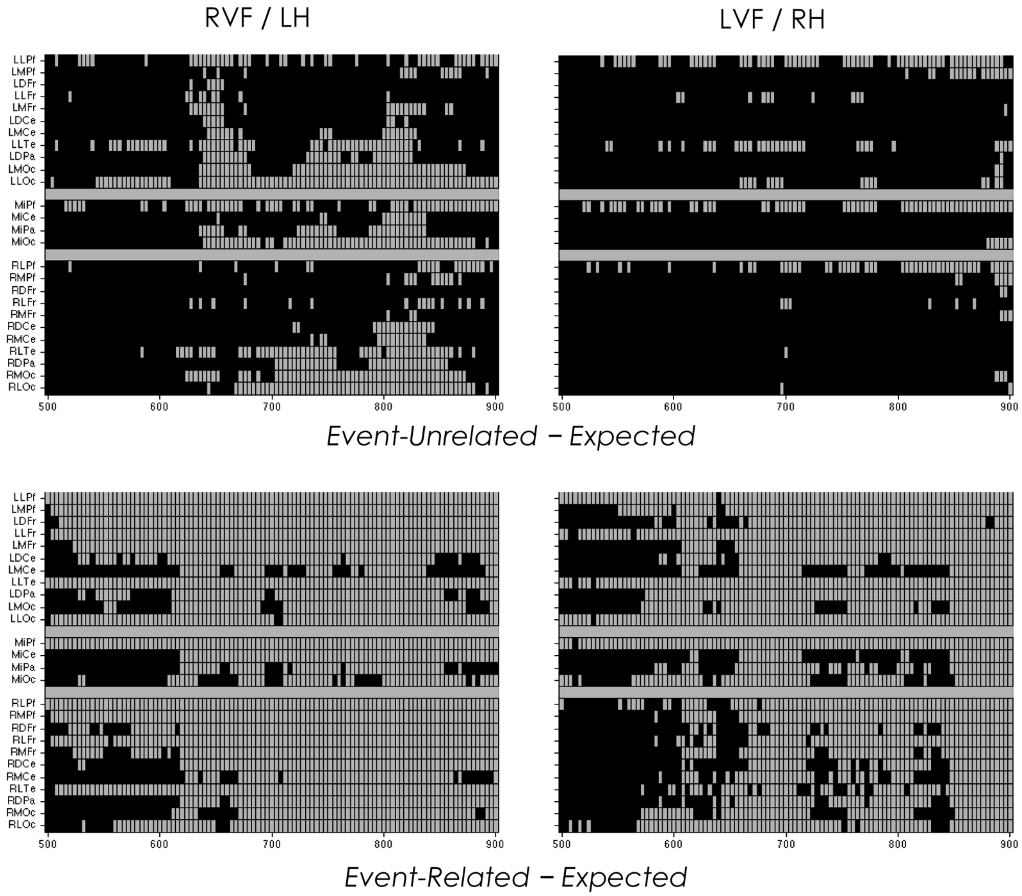

Figure 4.

Raster plots representing the results of the mass univariate tests conducted in the 500–900ms window. Time is represented on the x-axis with ticks at 100ms intervals. Electrodes are split into three groups along the y-axis: left hemisphere (top group), midline (middle group) and right hemisphere (bottom group). Electrodes in each group are listed in order of anteriority, with prefrontal at group top and occipital at group bottom. Darkened cells indicate a statistically significant negative deviation from zero in the indicated difference ERP, after FDR control.