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Right words and left words: electrophysiological evidence for hemispheric differences in meaning processing [1]

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Abstract

Both cerebral hemispheres are involved in language processing, each playing a unique role that may derive from differences in knowledge organization and on-line meaning integration. Here, we examine lateralized differences in knowledge representation and retrieval using event-related potentials (ERPs) elicited by words in sentences. Volunteers read pairs of sentences ending with three target types: (1) expected words, (2) unexpected words from the expected semantic category, and (3) unexpected words from an unexpected category. Context was presented word by word at fixation while targets were presented two degrees to the right or left of fixation. ERPs to unexpected endings were more negative than those to expected endings in both visual fields. However, when presented to the right visual field (left hemisphere), unexpected items from the expected category elicited smaller N400s than those from an unexpected category. In contrast, when presented to the left visual field (right hemisphere) all unexpected endings elicited N400s of similar amplitude. Thus, while both hemispheres are sensitive to context, only the left hemisphere is sensitive to semantic similarity between an unexpected ending and the expected completion. The results suggest lateralized differences in how new information is integrated into sentences. We propose that right hemisphere processing is best characterized as 'integrative'; new information is compared directly with context information. In contrast, left hemisphere processing is better characterized as 'predictive'; the processing of context leads to an expectation about the semantic features of upcoming items and new information is compared with that expectation rather than directly with the context. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The two cerebral hemispheres differ both physically and functionally. For example, the hemispheres differ in their sensitivity to hormones (see e.g., Ref. [56]) and pharmacological agents (see e.g., Ref. [38]) and apparently have different distributions of neuro-transmitters (e.g., review by Tucker [84]). Anatomically, the right and left hemisphere differ in the size and shape of a number of important landmarks (e.g., sylvian fissure, planum temporale, pars operculatis — see review by Galaburda [33]), as well as the ratio of grey to white matter [40], neuronal number [34], neuronal size [41], and extent of dendritic branching [78] in some areas.

Even more striking, however, are the functional differences in the nature of perceptual information processed, attended, and stored and in the type and quality of motor control (see e.g., Ref. [22]). For example, visual processing in the two hemispheres is differentially affected by retinal eccentricity, size, luminance, contrast, exposure duration, spatial frequency, and temporal frequency (reviewed in [19,20]). The hemispheres also seem to differ in the extent to which they (1) direct attention to global (whole object) or local (object feature) aspects of visual stimuli (see e.g., Refs. [23,32,85]), (2) process visuo-spatial relations in categorical (e.g., above/below) or metric (distance) terms [1,42,47,55,77], and (3) remember visual stimuli [58–61].

These physical and functional differences have implications for an understanding of each hemisphere's role in language comprehension. Because the right hemisphere seems to have little, if any, control over speech production in most people, it was also thought to lack language comprehension abilities. Studies, however, have shown

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that the right hemisphere is not only able to comprehend written and spoken language (though with slightly poorer word recognition [66] that may be based on serial processing [73]), but that it plays a unique and integral role in normal language processing. A distinct pattern of language-related deficits has been documented in conjunction with right hemisphere damage, including difficulties with producing and interpreting intonation contours (see e.g., Refs. [5,72,75]), extracting the main message from discourse, understanding and producing appropriate discourse structure (e.g., reviews by Hough [43] and Brownell [8]), and comprehending jokes and non-literal language (metaphor, indirect requests) (see e.g., Refs. [9,11]). Thus, each hemisphere seems to make a significant, albeit different, contribution to language processing.

1.1. Hemispheric differences in meaning processing: semantic priming studies

The fact that both hemispheres seem to be involved in language comprehension brings up interesting questions about what role each hemisphere plays in meaning processing (i.e., recruitment and integration of knowledge stored in long-term, semantic memory) and how it carries out that role. Does each hemisphere have its own record of world experience and, by extension, its own semantic memory store, or do the hemispheres share a unified store of knowledge? Do the right and left hemispheres recruit semantic information (whether independent or shared) similarly during normal sentence processing and what kind of representation does each form as the result of sentence or discourse processing? Behavioral results have implied substantial hemispheric differences in the nature and timecourse of information retrieval during word processing.

It has long been known that a word is recognized as such (lexical decision) or named more quickly when it is preceded by a semantically related word than alone or in the context of an unrelated word (see e.g., Ref. [68]). Such semantic priming results have been taken to reflect aspects of the organization of word meaning in semantic memory. Both hemispheres are subject to semantic priming effects in visual half-field designs [13,14,17,24,57,88], suggesting that each has access to a structured store of semantic knowledge. When strategic meaning comparison/integration is discouraged (e.g., though the use of brief, pattern-masked primes, low proportions of related stimuli, and/or brief stimulus-onset-asynchronies), the amount of facilitation in the two hemispheres is often equivalent [2].

However, Chiarello et al. [17] discovered that the hemispheres differ in their sensitivity to different types of semantic relationships. The hemispheres show equivalent levels of priming for lexically associated members of a semantic category (e.g., DOG–CAT) [3] and show no priming for lexical associates that do not share category membership (e.g., BEE–HONEY). However, only the right hemisphere shows significant priming for lexically unassociated category members (e.g., DOG–GOAT). When strategic factors are minimized and semantic feature overlap is reduced, priming is observed only in the right hemisphere. In contrast, when paradigms encouraging more intentional recruitment of semantic information (e.g., high relatedness proportions, long stimulus onset asynchronies) are used, inhibition for semantically unrelated [18,67] and more remotely associated word pairs [67] is observed primarily in the left hemisphere. This has been attributed to an active suppression mechanism in the left hemisphere. Together, these studies have been taken to mean that the left hemisphere is biased toward the processing of close lexical-semantic relationships, while the processing of more loosely-related semantic associations relies more heavily on the right hemisphere (see e.g., Refs. [15,16]).

Beeman et al. [4] extended these findings in a summation priming paradigm, wherein a lateralized target word (e.g., 'wedding') is preceded by a series of three weakly-related prime words (e.g., 'white', 'ceremony', 'tuxedo') whose contributions may sum. Facilitation from the summation primes was greater in the right than in the left hemisphere under conditions encouraging intentional meaning processing, and equivalent when strategic factors were minimized; however, the left hemisphere gained more benefit from a single, strongly related prime than from multiple weakly related primes, while the right hemisphere showed equal facilitation for both prime types. The authors conclude that the left hemisphere actively narrows its attentional focus to highly related words while the right hemisphere activates a broader range of words.

Hemispheric differences also have been reported in the timecourse of meaning activation. For example, Burgess and Simpson [13] observed facilitation for both meanings of homographic primes at short stimulus onset asynchrony or SOA (35 ms), and reduced facilitation for the infrequent meaning at the longer SOA (750 ms) in the right visual field (left hemisphere), reminiscent of central presentation results [81]. In contrast, in the left visual field (right hemisphere), facilitation for the frequent meaning decreased while facilitation for the less frequent meaning increased at long, as compared to short, SOAs. Based such results, they suggested that the right hemisphere activates semantic information more slowly and maintains it longer than the left, thereby making infrequent or distantly-related word meanings available for longer intervals in the right hemisphere (see e.g., Ref. [12]).

[2] Under more strategic conditions, it is not uncommon to observe greater priming in the left hemisphere.

[3] Note that such items typically contain a significant degree of semantic feature overlap. Chiarello and her colleagues take this, rather than the lexical association per se, to be the critical factor [16].

1.2. Hemispheric differences in meaning processing: behavioral studies with sentences

In sum, visual field word pair priming studies have led to the conclusion that meaning activation in the right hemisphere is relatively sustained and non-specific, whereas meaning activation in the left hemisphere is faster and subject to selection mechanisms that restrict activation to more frequent or closely-associated meanings. Extending such a model beyond the word level has led to the suggestion that the left hemisphere is more crucial for the rapid, focussed meaning activation necessary for comprehending 'everyday' language, whereas the right hemisphere's slower processing and more dispersed associations give it an critical role in the processing of non-literal language (as suggested from neuropsychological data) (see e.g., Refs. [12,15,16]).

To date, very few studies have directly examined hemispheric differences in sentence processing or beyond. Faust et al. [29,30] found that priming in the left hemisphere increased incrementally with the number of words (six word sentence > three word phrase > one word > no prime), while the right hemisphere showed equal facilitation in all three conditions. Likewise, in a subsequent study which directly manipulated sentence constraint, left hemisphere facilitation was graded by constraint, while right hemisphere facilitation effects were smaller and showed a significant difference only between the highest constraint condition and all others [28]. These results led to the hypothesis that while the left hemisphere can take advantage of message-level information in a sentence, the right hemisphere processes only at the level of intralexical associations. In support of this, Faust et al. [26] found that the right hemisphere showed equal facilitation from words whether they were in scrambled or syntactically and semantically congruent sentences, whereas the left hemisphere showed greater priming from structured sentences. Similarly, Faust et al. [26] observed that the right hemisphere gains equal facilitation from an incongruous sentence as from a congruous one as long as it contains strong lexical associates (e.g., 'The patient parked the medicine' vs. 'The patient swallowed the medicine'), while the left hemisphere benefits more from the congruent sentence. In sum, they argue that right hemisphere lexical processing takes place independently of message-level information while left hemisphere lexical processing is modulated by sentence level congruity, structure, and constraint.

Overall, then, the picture emerging from the behavioral literature is that left hemisphere language processing is more controlled, more focused, and perhaps faster than right hemisphere language processing and takes place at higher (e.g., sentence message) levels of analysis. However, our understanding is far from complete. For example, Faust et al.'s results suggesting that the right hemisphere is insensitive to sentence-level information does not mesh with deficits in discourse processing following right hemisphere damage. And, it seems unlikely that broader word meaning activation alone will be able to account for the right hemisphere's role in the processing of jokes or metaphors (which critically involve higher order structures — see, e.g., Coulson [21] and Grady [39]). Reconciliation is difficult, in part, because the same issues have typically not been investigated at different levels of analysis. For instance, we do not know whether hemispheric differences for weakly related word pairs will generalize when these are embedded in sentences. We, therefore, set out to explore the processing of semantically related and unrelated items — similar to those used in semantic priming studies — in a sentence processing task.

1.3. The advantages of electrophysiological techniques

In doing so, we also hoped to avoid some of the limitations inherent in the techniques that have been brought to bear on the issue. Lexical decision and naming studies, for example, require a speeded decision, and it is known that the hemispheres are differentially able to perform such decisions. In naming tasks, for example, it is likely that collosal transfer must be involved for left but not right visual field presentations, since right hemisphere speech is relatively uncommon [36,37]. Studies in split brain patients have suggested a similar imbalance for the lexical decision task, which leads to an underestimation of the semantic abilities of the right hemisphere (see review by Baynes and Eliasson [2]). Although these methodological difficulties are ameliorated when conclusions are based on differences between conditions rather than absolute performance, task-engendered hemispheric differences still may contribute to the results observed (e.g., the influence of context may increase or decrease with task difficulty).

Speeded reaction time measures also are limited in the inferences they allow about hemispheric differences in the timing of word or sentence processing and meaning activation. The most common approach of manipulating SOA in RT studies merely allows one to examine how processes differ when information is spaced at various intervals, but does not provide a direct measure of the normal time course of response. For example, if an effect is found at both short and long SOAs for the left hemisphere but only at long SOAs for the right, it may that some process builds up more slowly in the right hemisphere, or, alternatively, that the right hemisphere is more susceptible (than the left) to interference at some stage of processing.

These problems can be circumvented by using the event-related brain potential (ERP) technique, as it does not require any task beyond reading for comprehension and allows direct inferences about the timing of processes with ms-level resolution [50,76]. ERPs provide an especially useful measure for examining hemispheric differences in processing meaning because a negative component of the ERP (N400) systematically varies with the processing of semantic information. The N400 seems to be the normal response to meaningful stimuli whether they are printed, spoken, or signed words (see e.g., Ref. [48]) or pictures (see e.g., Refs. [35,70]). The N400 is also sensitive to context, whether that context is a sentence or a single preceding word (see e.g., Refs. [6,7,49]). Kutas and Hillyard [51] first observed the N400 (a negative deflection between 250 to 600 ms) to words which were semantically anomalous with respect to the sentence context when sentences were read word by word for comprehension. Subsequent investigations have revealed that each word in a sentence elicits an N400, with an amplitude that is highly correlated with individuals' off-line expectations as measured by 'cloze probability [4]' [52] and that decreases as contextual information builds over the course of a sentence [87].

Only a few studies have used ERPs to examine hemispheric differences in word processing, and even fewer have examined hemispheric processing of word meaning per se. Neville, Kutas, and Schmidt [69] compared the ERP to individual words presented in the left and right visual fields and found differences in components elicited over more posterior sites but fairly similar patterns of response over more anterior electrode sites. McCarthy and Nobre [62] found similar patterns of N400 effects to semantically related and repeated target words in the two visual fields when they were attended, but observed no N400s whatsoever when the stimuli were not in the attended half of space. Recently, Swaab et al. [82] observed facilitation (in the form of reduced N400s) to associatively-related pairs in patients with right hemisphere damage and a group of age-matched controls, but facilitation for unassociated but semantically-related pairs only in the controls. These ERP results support Chiarello's suggestion of a special role for the right hemisphere in processing weaker semantic associations.

1.4. Predictions for the present study

To our knowledge, no ERP study has examined hemispheric differences in meaning activation during normal sentence processing. In general, qualitatively similar N400 amplitude modulations are observed in semantic priming studies, as a function of the semantic relationship between words, as during sentence processing, as a function of a word's fit to the sentence level meaning [49,86]. In previous work, we have shown that N400 amplitudes simultaneously reflect context-independent semantic knowledge structure and fit to sentence context [31]. Specifically, we observed that the N400 to an unexpected sentence-final word was reduced if that word shared a categorical relationship with the word most expected in the context. For example, given the context'They wanted to make the hotel look more like a tropical resort.So along the driveway they planted rows of....'we observed a smaller N400 to the unexpected but categorically related ending, 'pines', than to the also unexpected but not categorically related ending, 'tulips'. This difference between the two contextually-unexpected endings seems to specifically reflect the degree of semantic feature overlap between the contextually-expected item and the word that is actually presented, and not differences in lexical association or plausibility.

The model emerging from behavioral studies of hemispheric differences seems to make specific predictions about the contribution of each hemisphere to this pattern of results with central presentation. If the left hemisphere is assumed to have access to sentence-level meaning information, then we would expect it to respond differently to expected sentence completions than to unexpected ones. Moreover, if the left hemisphere is also assumed to be biased toward narrowly focusing on contextually-appropriate meaning(s), then we might predict no difference in its response to the two types of unexpected endings. In our stimulus set, these semantically-related unexpected endings were from the same category as the expected ending, but were not lexically associated with it. They are thus similar in kind to the categorically related primes used by Chiarello and colleagues, for which only the right hemisphere showed facilitation. Since sentence contexts provide even stronger constraints than single words, it would seem even more unlikely for the left hemisphere to be sensitive to this contextually- (and therefore task-)irrelevant relationship.

Faust and her colleague's results suggest that, unlike the left hemisphere, the right hemisphere is not sensitive to sentence message-level information, but rather to the lexical-associative structure provided by the individual words in the sentence. Accordingly, we would expect the right hemisphere to show a difference in response to expected and unexpected sentence completions, though perhaps not as great as the left hemisphere's differentiation if message-level constraints really are not used. Assuming that right hemisphere processing is less informed by message-level constraints and that it activates a broader set of meanings in response to words, we should predict it to show significantly greater facilitation for the semantically-related but contextually-unexpected endings than the left hemisphere, and thus differential processing of them relative to unexpected endings that are not categorically-related.

To test these predictions, we recorded ERPs as individuals read sentences with one of these three types of endings (expected exemplars, within category violations, and between category violations) for comprehension. Sentence-final targets were presented using a visual-half-field design, and ERP averages were computed for each ending type in each visual half-field. By comparing the response

[4] The cloze probability of a word in a given context refers to the proportion of people who would choose to complete that particular sentence fragment with that particular word [83].

to expected endings in each hemisphere, we can determine whether the hemispheres are equally able to use sentence context information to facilitate the processing of contextually congruent words. By comparing the pattern of responses to the two types of contextually unexpected items, we can further test the prediction that meaning activation is broader in scope in the right than in the left hemisphere. Finally, by comparing the latency of the N400 response to the various ending types, we can assess the hypothesis that meaning activation/integration proceeds more slowly in the right hemisphere than in the left.

2. Materials and methods

2.1. Materials

Stimuli were identical to those used in Federmeier and Kutas [31]. They consisted of 132 pairs of sentences, ending with three types of target words: (1) *Expected exemplars*, items with the highest cloze probability in the sentence contexts, (2) *Within category violations*, contextually unexpected items derived from the same taxonomic category as the expected exemplar, and (3) *Between category violations*, contextually unexpected items derived from a different category than the expected exemplar. The first sentence of each pair established the expectation for item and category [5]. In contrast, the second sentence, when separated from the first, could be plausibly completed by any of the three possible targets. There were no lexical associates of any of the possible endings within the sentence containing the target word. Although derived from the same category, expected exemplars and within category violations were, as a whole, not lexically associated (only 10 of 132 had a lexical association greater than 0.1 in the Edinburgh Associative Thesaurus).

Target items were pictureable objects from 66 categories (two items from each). Categories were chosen to be those at the lowest level of inclusion for which the average undergraduate student could be expected to readily differentiate several exemplars. For approximately half the categories used, this level was basic as determined by Rosch et al. [74] or by analogy. Other categories were based at what Rosch et al. would have defined as the next highest level (a superordinate of the basic level) because it was unclear that the average participant could clearly and consistently differentiate below this level (e.g., vegetable (different types of carrots?), sports equipment (different types of bats?)). To control for the general plausibility of the two types of violations, between-category targets for each sentence pair were chosen from a related category that shared key features (e.g., animacy, size, general function) with that from which the expected exemplar and within category violation were derived.

Target items were rotated across the stimulus set such that each item appeared six times, once as each kind of ending (3) in each visual field (2). Thus, across the experiment all conditions were perfectly controlled for length, frequency, imageability, and concreteness; context sentences in each ending type condition were also perfectly controlled for length and grammatical complexity. Stimuli subtended between 3.7 and 10.3 degrees of horizontal visual angle and approximately one degree of vertical visual angle (and when lateralized were presented with nearest edge two degrees from fixation). The experimental sentences were divided into six lists of 132 sentences each; each participant viewed one list. Sentence contexts and items were used only once per list; each list consisted of 44 of each type of target (expected exemplars, within category violations, between category violations), half presented in the right and half in the left visual field (22 per field). To balance the number of plausible and implausible sentences read by each participant, the same 44 plausible filler sentence pairs were added to each list, half in each visual field. Appendix A gives examples of the stimuli.

2.2. Cloze procedure and expectancy ratings

Cloze probabilities were obtained for the 132 sentence pair contexts (sentence pairs missing the final word of the second sentence). These were divided into two lists, such that the two sentence contexts presumed to be predictive of items coming from the same category did not both appear on the same list. Student volunteers were asked to complete each sentence pair with 'the first word that comes to mind'. List 1 was completed by 56 students and list 2 was completed by a different set of 59 students. A subset of the original stimuli were rewritten and clozed separately by a third group of 55 students. Cloze probability for a given word in a given context was calculated as the proportion of individuals choosing to complete that particular context with that particular word. Expected exemplars were always the item with the highest cloze probability for a given context (mean = 0.74). All violations had cloze probabilities of less than 0.05, yielding a mean cloze probability of 0.004 for the within category violations and 0.001 for the between category violations.

In order to determine the extent to which within and between category violations (which, with rare exceptions, were not generated in the cloze task) were expected in the sentence contexts, we obtained expectancy ratings of all items in their sentence contexts from a different group of student volunteers. The sentences were split into the same three lists used in the actual ERP experiment, such that no item or context was repeated within a list. Volunteers were

[5] Forty-two out of 132 of these first sentence contexts contained a word lexically associated at a level of 0.1 or greater (Edinburgh Associative Thesaurus) with the expected exemplar.

asked to rate, using a percentage scale, how 'surprising' they found each target in its context (where 0% meant the target item 'is not at all what I expected (is very surprising)' and 100% meant the item 'is the one and only word I expected (is not surprising at all)'). Lists one, two, and three were rated, respectively, by 18, 21, and 18 student volunteers. Mean rated expectancy, calculated by averaging the expectancy ratings for all items of a given condition within each subject and then averaging the scores across subjects, was 90.5% for expected exemplars, 14.4% for within category violations, and 5.9% for between category violations. Thus, not only were the violations not produced in the sentence contexts, they were also regarded as surprising/difficult to integrate when placed into them.

2.3. Participants

Eighteen UCSD undergraduate volunteers (9 women, 18 to 28 years of age, mean age 21) participated in the experiment (none of these took part in any of the norming procedures). All were right-handed (as assessed by the Edinburgh Inventory [71]) monolingual English speakers with normal vision and no history of reading difficulties or neurological/psychiatric disorders; none had a left-handed immediate relative. All participants gave written, informed consent as per institutional guidelines and were compensated for their participation with course credit or cash. Three participants were randomly assigned to each of the six stimulus lists.

2.4. Experimental procedure

Volunteers were tested in a single experimental session conducted in a soundproof, electrically-shielded chamber. They were seated in a comfortable chair 40 inches in front of a monitor and instructed to read the stimulus sentences for comprehension. They also were informed that they would be given a recognition memory test over the stimuli at the conclusion of recording. The session began with a short practice run.

Each trial began with the first sentence of a pair appearing in full on a CRT. Volunteers read this sentence at their own pace and pushed a button to view the second sentence. Presentation of the second sentence was preceded by a series of crosses to orient the volunteer toward the center of the screen. The second sentence was then presented one word at a time horizontally for a duration of 200 ms with a stimulus-onset-asynchrony of 500 ms. Non-sentence final words were presented in the center of the screen while sentence final words were presented pseudorandomly [6] in the left or right visual hemifield with inner edge two degrees of visual angle from fixation [7]. A central fixation point remained visible throughout the trial, positioned $\frac{1}{2}$ degree below the bottom-most edge of the centrally presented words. Volunteers were asked not to blink or move their eyes during the second sentence. The final, target word was followed by a blank screen for 3000 ms, after which the next sentence appeared automatically.

Volunteers were given a short break after every 17 pairs of sentences. At the conclusion of the recording session, participants were given a recognition memory test consisting of 50 sets of sentence pairs: 10 new, 20 unchanged experimental pairs (of which 10 ended with expected exemplars, 5 ended with within category violations, and 5 ended with between category violations), and 20 modified sentence pairs in which the final word had been changed from that originally viewed by the volunteer (10 in which violations had been changed to expected exemplars and 10 in which expected exemplars had been changed to violations). Volunteers were instructed to classify the sentences as new, old, or similar (changed).

2.5. EEG recording parameters

The electroencephalogram (EEG) was recorded from twenty-six tin electrodes embedded in an Electro-cap, referenced to the left mastoid (see Fig. 1). These sites included Midline Prefrontal (MiPf), Left and Right Medial Prefrontal (LMPf and RMPf), Left and Right Lateral Prefrontal (LLPf and RLPf), Left and Right Medial Frontal (LMFr and RMFr), Left and Right Mediolateral Frontal (LDFr and RDFr), Left and Right Lateral Frontal (LLFr and RLFr), Midline Central (MiCe), Left and Right Medial Central (LMCe and RMCe), Left and Right Mediolateral Central (LDCe and RDCe), Midline Parietal (MiPa), Left and Right Mediolateral Parietal (LDPa and RDPa), Left and Right Lateral Temporal (LLTe and RLTe), Midline Occipital (MiOc), Left and Right Medial Occipital (LMOc and RMOc), and Left and Right Lateral Occipital (LLOc and RLOc). Blinks and eye movements were monitored via electrodes placed on the outer canthus (left electrode serving as reference) and infraorbital ridge of each eye (referenced to the left mastoid). Electrode impedances were kept below 5 Kohms. EEG was processed through Grass amplifiers set at a bandpass of 0.01–100 Hz. EEG was continuously digitized at 250 Hz and stored on hard disk for later analysis.

[6] Equal numbers of each ending type (expected exemplar, within category violation, and between category violation) were shown to each hemisphere in an experimental session. Order of presentation was randomized with the stipulation that no more than three stimuli in a row be presented to the same hemifield.

[7] There are well-known issues with lateralized presentations of words, since the information closest to foveal vision is the beginning of the word for RVF presentations and the end of the word for LVF presentations (see e.g., Ref. [44]). In the present study, however, the primary comparison is that of the response to the three ending types within a given hemifield where this factor is held constant.

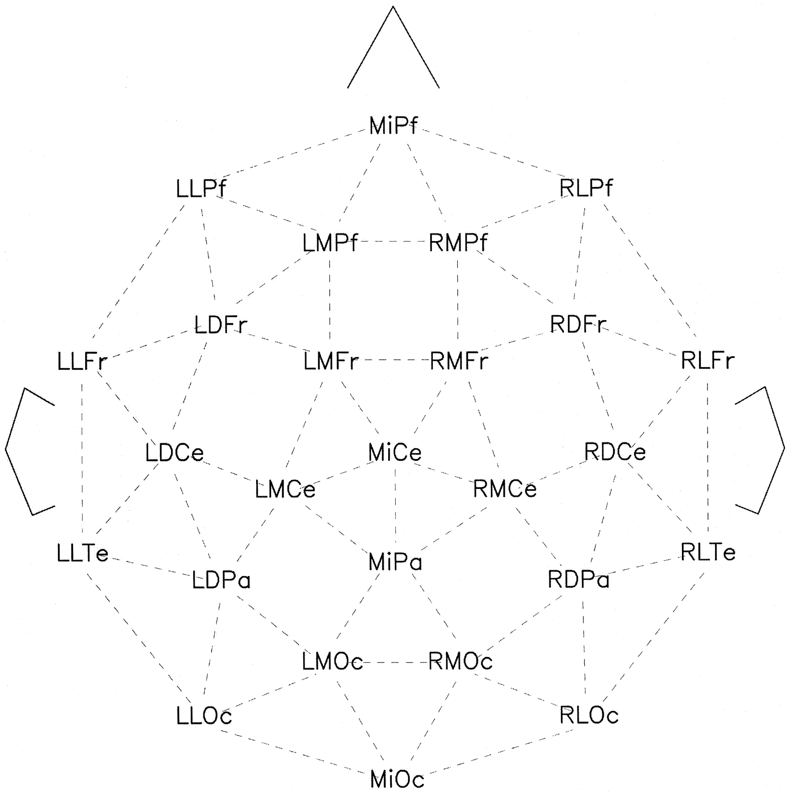

Fig. 1. Schematic of the electrode array used in the experiment. In all, 26 scalp electrodes were employed, arranged in a series of four equally spaced concentric rings.

2.6. Data analysis

Data was re-referenced off-line to the algebraic sum of the left and right mastoids. Trials contaminated by eye movements, blinks, excessive muscle activity, or amplifier blocking were rejected off-line before averaging; approximately 15% of trials in each hemifield were lost due to such artifacts. ERPs were computed for epochs extending from 100 ms before stimulus onset to 920 ms after stimulus onset. Averages of artifact-free ERP trials were calculated for each type of target word (expected exemplars, within category violations, between category violations) in each hemifield (right and left) after subtraction of the 100 ms pre-stimulus baseline.

3. Results

3.1. Behavior

Volunteers correctly classified an average of 78% of the items on the recognition memory test. The most common type of error was a misclassification of 'similar' sentences (those in which only the final word had been altered from that actually shown in the experiment) as 'old', followed by a misclassification of 'old' sentences (those seen in the same form during the recording session) as 'similar'. Together, these two error types account for 64% of all errors observed. Most of the remaining errors consisted in volunteers classifying 'old' or 'similar' sentences as 'new'; these two error types account for 30% of all observed. Only eleven errors in which 'new' sentences were classified as 'old' or 'similar' were observed across the 18 participants. Overall, the behavioral results indicate that participants were attending the experimental sentences during the recording session.

3.2. ERPs

Grand average ERPs to sentence final words in each visual field are shown in Fig. 2. Early components in all conditions and hemifields include, at posterior sites, a positivity peaking around 100 ms (P1), a negativity peaking around 150 ms (N1), and a positivity peaking around 280 ms (P2). As expected, these effects are strongly lateralized, being most prominent over posterior sites contralateral to the visual half-field of presentation. At frontal sites all conditions included a negativity peaking around 130 ms (N1) and a positivity peaking around 230 ms (P2). Early components are followed, in the expected exemplar conditions, by a broad late positivity, largest over central and posterior sites, and, in the violation conditions, by a broadly-distributed negativity peaking around 400 ms (N400). The N400 in the violation conditions is followed

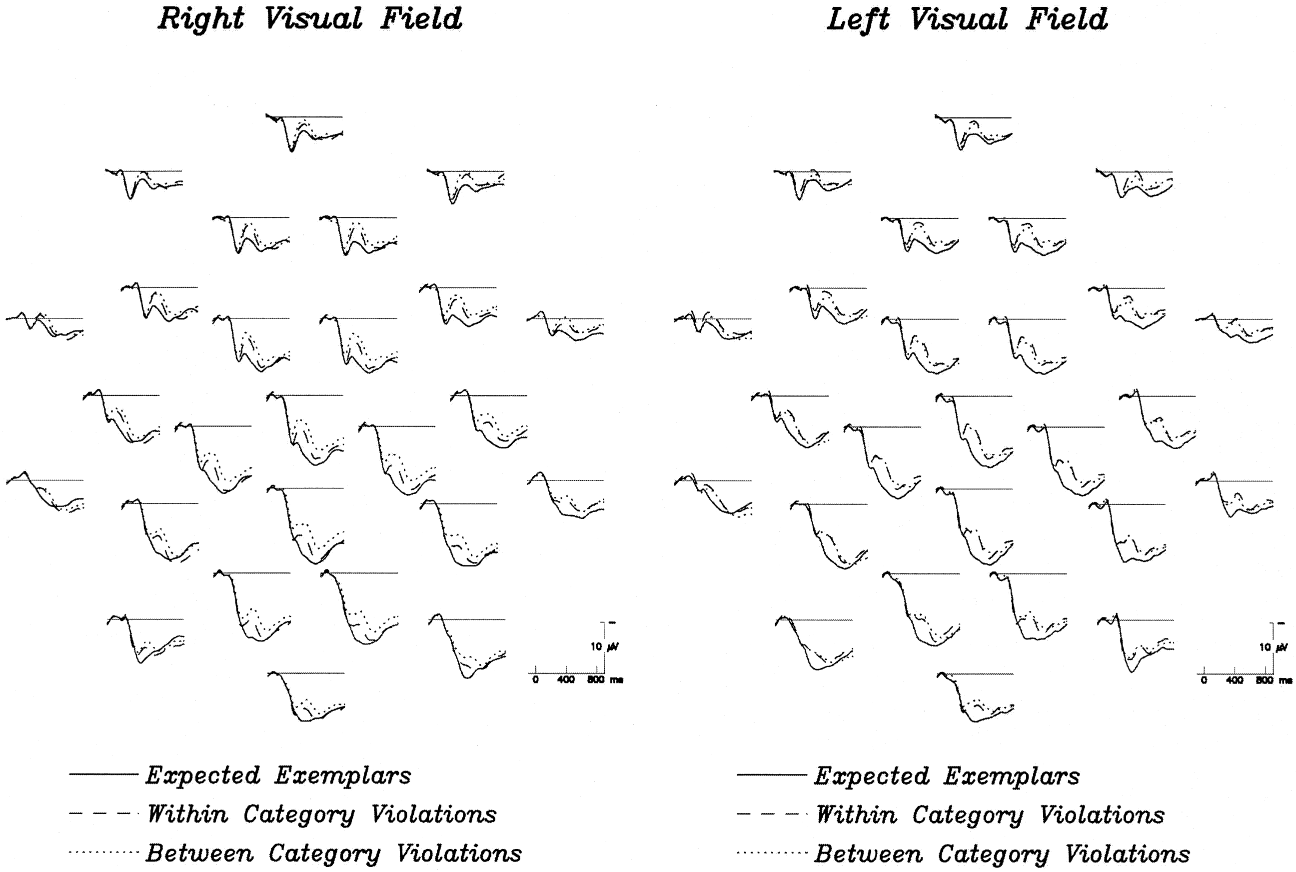

Fig. 2. Grand average ($N = 18$) ERP waveforms for the three ending types at all 26 electrode sites. ERPs elicited during left hemisphere (right visual field) presentation are shown on the left and ERPs elicited during right hemisphere (left visual field) presentation are shown on the right. Negative is plotted up. The ending types in both visual fields are characterized by the same set of early components; N1 amplitudes are lateralized as expected for lateralized stimulus presentation. Regardless of visual field, in the 350–450 ms time window expected exemplars (solid line) showed a sustained positivity while both within category violations (dashed line) and between category violations (dotted line) showed a negativity, the N400. With presentation to the left hemisphere, this N400 amplitude was reduced for within, relative to between, category violations. In contrast, with presentation to the right hemisphere, responses to the two violations were of similar amplitude.

by an extended late positivity of roughly similar amplitude to that observed for the expected exemplars.

3.3. Response to expected exemplars

Similar to the effect observed with central presentation [31], the response to expected items in both hemifields was characterized by a broad late positivity, prominent over more posterior electrodes. We compared the latency, amplitude, and distribution of this positivity as a function of hemifield of presentation.

3.4. Latency

Latency of the largest positive peak between 300–600 ms post-stimulus-onset was measured for each hemifield condition in each subject and subjected to an omnibus analysis of variance (ANOVA). Repeated measures included 2 levels of Hemifield (right vs. left) and 26 levels of Electrode. All p-values in this and all subsequent analyses are reported after Epsilon correction (Greenhouse–Geisser) for repeated measures with greater than one degree of freedom.

Mean peak latency (in ms) was 462 ms in the right visual field (LH) and 474 ms in the left visual field (RH). The effect of Hemifield was not statistically significant [$F(1,17) = 1.01$; $p =$ n.s.] and did not interact with Electrode [$F(25,425) = 1.63$; $p =$ n.s.].

3.5. Amplitude

Based on the peak latency analysis, mean voltage measures of the positivity elicited by expected exemplars were taken in a 200 ms window around 450 ms (i.e., 350–550 ms post-stimulus-onset). These measures were subjected to an omnibus analysis of variance (ANOVA) on 2 levels of Hemifield (right vs. left) and 26 levels of Electrode.

Mean amplitude was 8.24 microvolts in the right visual field (LH) and 8.21 microvolts in the left visual field (RH); there was no main effect of Hemifield [$F(1,17) = 0.00$; $p =$ n.s.]. The interaction of Hemifield with Electrode was marginal [$F(25,425) = 2.15$; $p = 0.10$], indicating a possi-

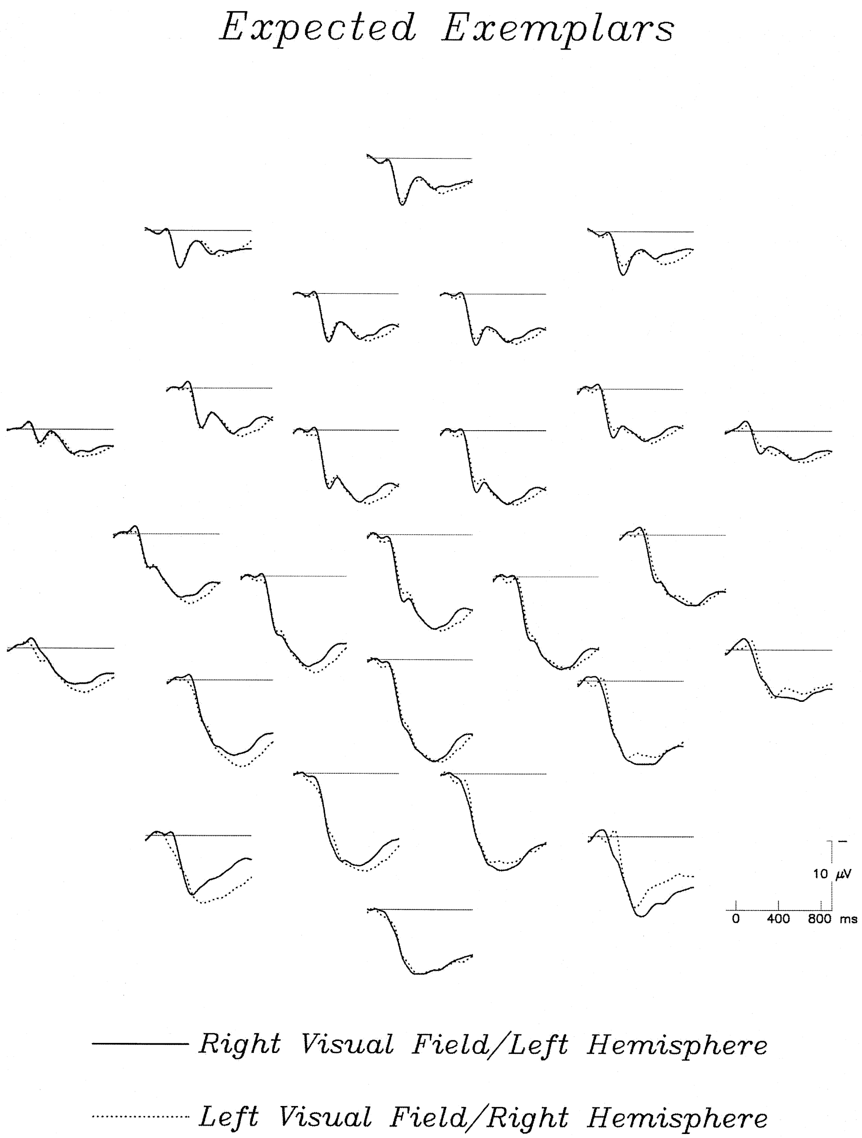

Fig. 3. Response to expected exemplars as a function of visual field of presentation. Over most of the scalp, responses to stimuli presented to the right and left visual fields were quantitatively and qualitatively similar. Over lateral occipital sites, beginning around 400 ms post-stimulus-onset, more positive responses are observed over sites ipsilateral to the visual field of presentation.

ble distributional difference in the response to expected items as a function of hemifield of presentation.

3.6. Distribution

The scalp distribution of the positivity elicited with right vs. left hemifield presentation was examined by taking mean voltage measures 350–550 post-stimulus-onset. These measures were normalized according to the procedure described in McCarthy and Wood [63] and then subjected to an analysis of variance (ANOVA) on four repeated measures, 2 levels of Hemifield (right vs. left), 2 levels of Hemisphere (left vs. right) [8], 2 levels of Laterality (lateral vs. medial), and 4 levels of Anterior/Posterior (prefrontal vs. frontal vs. parietal vs. occipital) [9].

Overall, the positivity elicited by expected exemplars is bigger over right than left hemisphere electrodes [$F(1,17) = 5.63$; $p = 0.03$], is bigger over medial than lateral electrodes [$F(1,17) = 157.05$; $p < 0.01$], and is bigger over posterior than anterior sites [$F(3,51) = 37.71$; $p < 0.01$]. The difference between medial and lateral was greater over

[8] To avoid confusion, in our analyses we use the term 'Hemifield' to refer to the location of the stimulus on the screen and use the term 'Hemisphere' to refer to the location of electrodes on the head.

[9] In order to examine scalp distribution, in this and subsequent distributional analyses we use the standard procedure of dividing scalp electrodes into regions (left/right, medial/lateral, anterior/posterior). Not all electrode sites can be used (e.g., our four central electrodes cannot be classified with respect to hemisphere); here, we use 16. Left lateral sites are (from front to back): LLPf, LLFr, LLTe, LLOc. Left medial sites are: LMPf, LMFr, LMCe, LMOc. Right medial sites are: RMPf, RMFr, RMCe, RMOc. Right lateral sites are: RLPf, RLFr, RLTe, RLOC.

left than right hemisphere electrode sites (significant Hemisphere by Laterality interaction [$F(1,17) = 12.07$; $p < 0.01$]), and the difference between posterior and anterior was greater over lateral electrodes (significant Laterality by Anteriority interaction [$F(3,51) = 24.50$; $p < 0.01$]). Finally, a significant Hemisphere by Laterality by Anteriority interaction [$F(3,51) = 3.32$; $p = 0.05$] indicates that the Laterality by Anteriority interaction just mentioned is more prominent over left than right hemisphere electrode sites. In other words, the distribution of the positivity is broader over right hemisphere sites and more focused to medial-central/posterior sites over the left hemisphere.

We found a marginally significant interaction of Hemifield with Hemisphere [$F(1,17) = 3.83$; $p = 0.07$], which was modulated by a significant Hemifield by Hemisphere by Laterality interaction [$F(1,17) = 4.34$; $p = 0.05$] and a significant Hemifield by Hemisphere by Anteriority interaction [$F(1,17) = 15.36$; $p < 0.01$]. These three-way interactions were in turn modulated by a significant Hemifield by Hemisphere by Laterality by Anteriority interaction [$F(3,51) = 11.43$; $p < 0.01$]. All other distributional effects were non-significant. The pattern of the effects can be seen in Fig. 3. Over medial, posterior sites stimuli presented to the right visual field elicit a larger positivity over the right than left hemisphere while stimuli presented to the left visual field elicit the opposite pattern (i.e., larger positivity over left than right hemisphere electrodes). This pattern is very similar to that previously observed by Neville et al. [69] in response to lateralized single words.

3.7. Summary

Overall, responses to contextually expected targets in the 350–550 ms window (i.e., the window in which ERP responses related to word meaning and contextual integration are typically observed) were equivalent in the two hemifields in their latency, amplitude, and distribution. The only significant effect was a distributional interaction in which stimuli presented to a single visual field elicit larger positivities at ipsilateral (as compared to contralateral) posterior electrode sites.

3.8. Response to violations

Again, similar to the effect observed with central presentation [31], within and between category contextual violations elicited a broadly-distributed negative-going potential peaking around 400 ms post-stimulus-onset (N400) when presented in either hemifield.

3.9. Latency

To examine the latency of the N400 effect across hemifield and violation type, we first computed the ERP difference between each violation type and the expected exemplar from the same hemifield condition. We then measured the latency of the largest negative peak in the 300–600 ms time window for each difference wave (within category violation RVF minus expected exemplar RVF ERP; between category violation RVF minus expected exemplar RVF ERP; within category violation LVF minus expected exemplar LVF ERP; between category violation LVF minus expected exemplar LVF ERP). These measures were subjected to an analysis of variance (ANOVA) on three repeated measures, 2 levels of Hemifield (right vs. left), 2 levels of Ending Type Difference (within category violation vs. between category violation), and 26 levels of Electrode.

N400 latency was 421 ms for within category violations in the right visual field, 423 ms for within category violations in the left visual field, 412 ms for between category violations in the right visual field and 439 ms for between category violations in the left visual field. Neither the main effect of Hemifield [$F(1,17) = 2.18$; $p =$ n.s.] nor the main effect of Ending Type [$F(1,17) = 0.09$; $p =$ n.s.] was significant, and there were no significant interaction effects.

3.10. Amplitude

Based on the peak latency analysis, mean voltage analyses were conducted on the N400 effects (difference waves) in a 200 ms window around 400 ms (i.e., 300–500 ms post-stimulus onset). These measures were subjected to an omnibus analysis of variance (ANOVA) on three repeated measures, 2 levels of Hemifield (right vs. left), 2 levels of Ending Type Difference (within category violation vs. between category violation), and 26 levels of Electrode.

Mean amplitude of the N400 effect was -2.33 and -3.42 microvolts for within category violations in the right and left visual fields, respectively, and was -3.81 and -2.98 microvolts for between category violations in the right and left visual fields, respectively. There was no main effect of Hemifield [$F(1,17) = 0.04$; $p = 0.85$] and no main effect of Ending Type [$F(1,17) = 2.56$; $p = 0.13$]. However, there was a significant Hemifield by Ending Type interaction [$F(1,17) = 4.26$; $p = 0.05$], indicating a different pattern of response to the two violation types in the two hemifields. The Ending Type by Electrode interaction was also significant [$F(25,425) = 4.69$; $p < 0.01$], indicating that the response to the two types of violations may have a different distribution over the scalp; this will be explored in the next section. The same pattern of results emerges for analyses performed on the raw N400 response as for those performed on the N400 effect (difference waves).

To understand the nature of the Hemifield by Ending Type interaction, we performed four planned comparisons on the mean voltage measures. First, we compared within and between category violations in each hemifield individually, using an omnibus analysis of variance (ANOVA) on 2 levels of Ending Type (between category violation vs.

within category violation) and 26 levels of Electrode. In the right visual field (LH), between category violations were significantly more negative than within category violations across the scalp [$F(1,17) = 7.11$; $p = 0.02$]. This effect of Ending Type interacted with the effect of Electrode [$F(25,425) = 2.93$; $p = 0.03$], indicating a distributional difference in the response to the two violation types in this hemifield. In contrast, in the left visual field (RH), there was no main effect of Ending Type [$F(1,17) = 0.57$; $p =$ n.s.]. The interaction of Ending Type with Electrode was marginally significant [$F(25, 42) = 2.23$; $p = 0.09$]. Thus, as can be seen in Fig. 4, while all violation conditions elicit an N400, these responses are of the same amplitude to both violation types in the left visual field (RH), but larger to between than within category violations in the right visual field (LH).

We next compared the response to each violation type individually as a function of visual field of presentation, using an omnibus analysis of variance (ANOVA) on 2 levels of Hemifield (right vs. left) and 26 levels of Electrode. Within category violations presented in the right visual field (LH) elicited an N400 of significantly smaller magnitude than these same violations presented in the left visual field (RH) [$F(1,17) = 5.73$; $p = 0.03$]. The Hemifield by Electrode interaction was not significant for this comparison [$F(25,425) = 1.69$; $p =$ n.s.]. In contrast, the response to between category violations did not differ as a function of hemifield [$F(1,17) = 0.85$; $p =$ n.s.]. Again, the Hemifield by Electrode interaction was not significant [$F(25,425) = 0.88$; $p =$ n.s.]. A difference in the amplitude of the N400 response to the within category violations in the two hemifields thus seems to be the primary force driving the observed Hemifield by Ending Type interaction.

3.11. Distribution

The distribution of the N400 effect (difference wave) for each violation type in each hemifield was examined in the 300–500 ms time window. Difference waves were normalized according to the procedure described in McCarthy and Wood [63] and were then subjected to an analysis of variance (ANOVA) on five repeated measures, 2 levels of Hemifield (right vs. left), 2 levels of Ending Type Difference (within category violation vs. between category violation), 2 levels of Hemisphere (left vs. right), 2 levels of Laterality (lateral vs. medial), and 4 levels of Anterior/Posterior (prefrontal vs. frontal vs. parietal vs. occipital).

N400 effects were generally larger over right than over left hemisphere electrode sites (marginally significant Hemisphere main effect [$F(1,17) = 3.77$; $p = 0.07$]), and were larger over medial than over lateral electrodes [$F(1,17) = 32.29$; $p < 0.01$]. Although the effect was not significant, there was a trend for effects to be larger over central and posterior sites than over frontal sites [$F(3,51) = 2.13$; $p = 0.16$]. A Hemisphere by Laterality interaction [$F(1,17) = 5.46$; $p = 0.03$] indicates a greater difference between medial and lateral sites over the left than over the right hemisphere, while a significant Hemisphere by Anteriority interaction [$F(3,51) = 3.20$; $p = 0.05$] indicates that over the left hemisphere effects were biggest at the most posterior electrode sites while over the right hemisphere effects were biggest more centrally. The observed distribu-

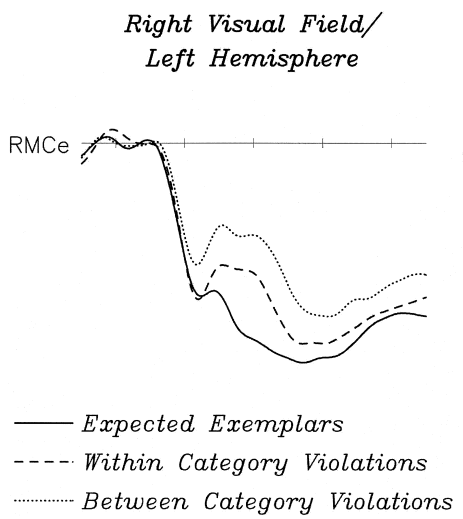

Fig. 4. Effect of ending type. Effect is shown at the right medial central site where N400 effects are most prominent. For right visual field (left hemisphere) presentations (left side of the figure), a three-way split can be observed in the amplitude of the N400 response. N400 amplitude was significantly larger for between category violations (dotted line) than within category violations (dashed line) and significantly larger for within category violations than expected exemplars (solid line). This pattern is similar to that observed when stimuli are presented at the center of gaze (Federmeier and Kutas [31] in press). For left visual field (right hemisphere) presentations (right side of the figure), in contrast, N400s of similar amplitude were elicited by within and between category violations, both of which were more negative than the response to expected exemplars. Responses to both violation types in the right hemisphere were similar in amplitude to responses to between category violations in the left hemisphere.

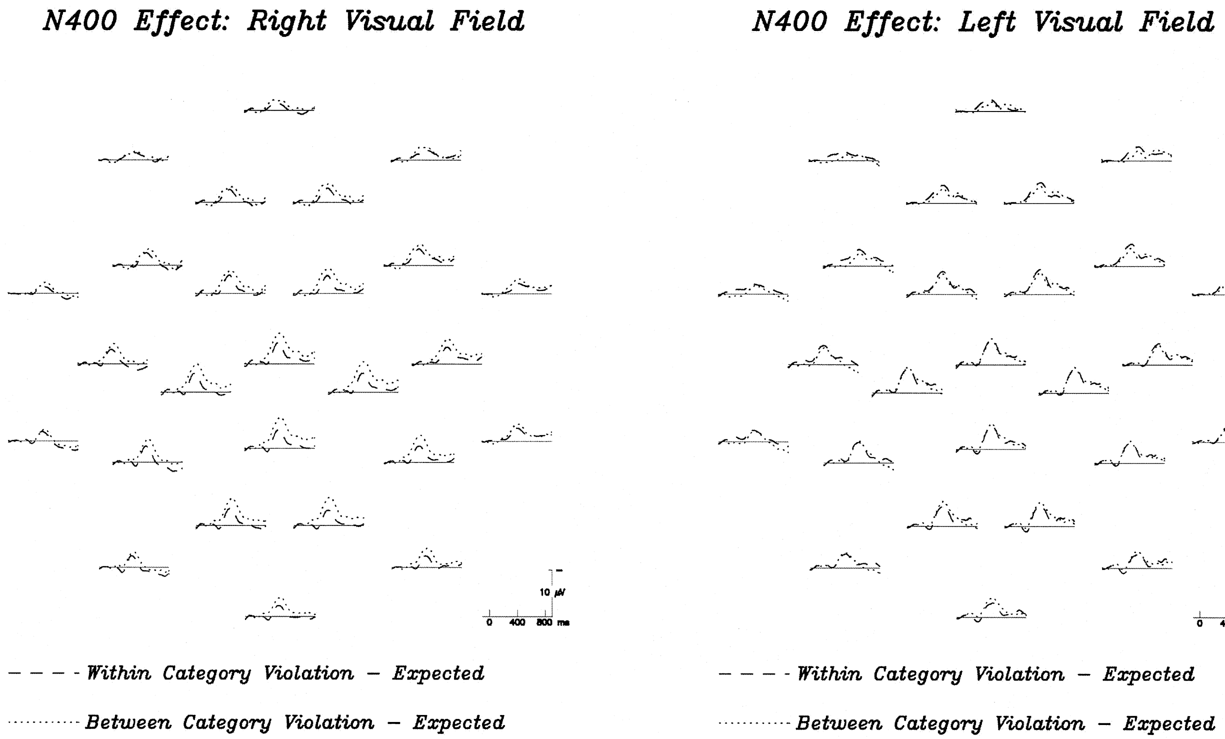

Fig. 5. Distribution of the N400 effect. Difference waves showing the N400 effect to within category violations (dashed line) and between category violations (dotted line) are given at all 26 electrode sites for presentations to the right and left visual field respectively. For both conditions and both visual fields, the N400 effect was larger over medial posterior sites and slightly larger at sites over the right side of the scalp than over the left. Both ending types in both visual field conditions elicited an N400 of similar latency.

tion of the N400 effect (biggest over right, medial, central-posterior electrodes) is typical of that seen during word by word reading [54], and, in this experiment, tended to be somewhat broader over the right half of the scalp and more focused at posterior, medial sites over the left half of the scalp.

Hemifield did not interact (significantly or even marginally so) with any distributional variable, suggesting that very similar patterns of response over the scalp were elicited to stimuli presented to the right and left visual fields. A significant Ending Type by Anteriority interaction [$F(3,51) = 7.39$; $p = 0.01$] and a marginally significant Ending Type by Laterality [$F(1,17) = 2.97$; $p = 0.10$] were observed. In general, the response to within category violations was broader in its distribution than that to between category violations. A larger anterior to posterior and a larger medial to lateral difference was observed for between category violations than for within category violations. Fig. 5 shows the pattern of N400 effects over the scalp for the two violation types as a function of hemifield of presentation.

3.12. Summary

While the latency and distribution of the N400 response to sentence-final violations did not differ as a function of presentation hemifield, the pattern of N400 amplitudes elicited by violation types did. With right visual field (LH) presentation, N400s to within category violations were significantly smaller than those to between category violations, as they were with central presentation of the same stimuli [31]. However, with left visual field (RH) presentation, the response to the two violation types did not differ; both were equivalent in amplitude to the response to between category violations with right visual field presentation. In other words, the response to within category violations in the left hemisphere was significantly reduced relative to the other three conditions (RH within category, LH between category, and RH between category violations), which did not differ from one another.

4. Discussion

Both the cerebral hemispheres seem to play an important, even unique, role in normal language processing. It is thus important to understand what type of semantic knowledge is available to each and how each brings semantic knowledge to bear during normal language processing. Investigations of these issues with reaction time measures have yielded consistent hemispheric differences in the processing of meaning and the use of contextual information to guide knowledge activation and integration. These findings have led to more general hypotheses about each hemisphere's role in normal language processing (see e.g., Refs. [3,16,25]), aspects of which relating to fine timing and qualitative processing differences have thus far proven difficult to test. We examine these here, in what, to our knowledge, is the first study that brings electrophysiological measures to bear on these issues.

In previous work [31], we used ERPs to show that both sentence context information and more general (context-independent) semantic information (i.e., structure of knowledge in long-term memory) modulate the ease with which a word in a sentence is processed online and, further, that they do so in a qualitatively similar manner (i.e., both affecting N400 amplitude). This same paradigm, wherein sentential and general semantic information are set in competition, provides a means for testing the idea that the two hemispheres differentially activate general semantic information and use sentence context information during sentence reading.

4.1. Testing the predictions

In the introduction, we outlined a set of predictions derived from the current literature regarding how the right and left cerebral hemispheres might be expected to respond to sentence-final words that are (1) contextually expected, (2) contextually unexpected but semantically related to the expected ending, and (3) contextually unexpected and not particularly related to the expecting ending. We tested these predictions by comparing the pattern of ERP responses to these target types when they were presented in the left versus the right visual hemifield.

Previous work suggests that word processing in both cerebral hemispheres is facilitated when that word is consistent with contextual information, albeit via different aspects of the context in each case. For example, Faust and her colleagues maintain that only the left hemisphere is sensitive to message-level contextual constraints (see e.g., Refs. [26,28]) whereas the right hemisphere makes greater use of the lexical associative information from the sentence instead. We predicted, therefore, that while both hemispheres would distinguish expected from unexpected endings, they would do so on the basis of different information, thereby yielding different ERPs to expected endings in the two visual field conditions.

As predicted, both hemispheres differentiate expected exemplars from contextual violations as reflected in qualitatively different ERPs [10]. Regardless of presentation hemifield, violations elicit a negativity peaking around 400 ms (N400) while responses to expected items are characterized by a broadly-distributed, sustained positivity. Thus, in line with the predictions, both hemispheres do show processing benefits for target words that are consistent with information in the preceding sentence context. In contrast to the prediction, however, the ERP to expected items is unaffected by the hemifield of presentation in latency or amplitude and is identical in distribution as a function of hemifield over most of the scalp (mirror image effects as a function of hemifield are seen over medial, posterior electrodes (see Fig. 3)). Although Kutas et al. [53] did not report a direct comparison of the ERPs to congruent sentence completions presented in the two hemifields, their data also reveal no apparent field-based differences in either the commissurotomized or control individuals.

Of course, the qualitative and quantitative similarity of the ERPs to contextually expected items in the two visual fields does not rule out the possibility that the two hemispheres extract different information from the context and/or integrate across sentence words in a different manner. For example, the absence of an N400 to an expected exemplar may be due to its fit to the message level meaning when presented in the RVF but due to its consistency with multiple, fairly weakly-related lexical items in the sentence pair [11] when presented in the LVF (as suggested in Ref. [25]). If, however, the hemispheres process context differently, as we will show, then it is all the more striking that these different processing strategies nevertheless seem to facilitate word processing in a very similar manner. In particular, in this case we would have to conclude that integrating a word with message-level sentence context information and integrating a word with lexical associative information are qualitatively similar processes. This idea is supported by ERP findings more generally, though it remains somewhat contentious (see e.g., Refs. [49,86]).

We had predicted that both types of contextual violations would elicit an N400 when presented in either visual half-field. However, the extant literature suggested that the two hemispheres would be differentially sensitive to the degree of semantic relationship between the violation and the item most consistent with the sentence context and would show different time courses of activation. Based on the hypothesis that the left hemisphere has a limited facilitative scope, zeroing in on the meaning or meanings most consistent with a language context (whether single word or sentence), we would not expect to see any differ-

[10] Here and throughout the discussion we refer to 'right/left hemisphere responses' as a shorthand for 'responses to items that are initially presented to the right/left hemisphere'. In intact individuals it is virtually certain that callosal transfer allows at least some information to be available to both hemispheres on all trials (though what information is transferred and when and where that transfer takes place remains unclear). In fact, given the possibility for callosal transfer, it is actually quite striking that significantly different patterns of responses are nonetheless observed to left and right visual field presentations of words in this and previous visual half-field studies.

[11] Note that, as a whole, our stimuli did not contain strong lexical associates of the target and that our sentence pairs were constructed such that any medium or strong lexical associates that might be present were separated from the target word by at least one sentence.

ence in response to the two violation types, neither of which is contextually appropriate, when these are presented to the right visual field. On the other hand, the response to contextual violations that bear some relationship to the expected endings versus those that do not would differ in the left visual field, according to the hypothesis that right hemisphere language processing is less informed by message-level constraints and broader in its priming scope, thereby activating more distantly related concepts. Moreover, based on studies suggesting that semantic information builds more slowly in the right hemisphere than in the left [12,13], we expected the N400 to violations in the left visual field, especially to distantly related words (i.e., within category), to be delayed relative to those in the right visual field.

The relative pattern of N400 amplitudes to within versus between category violations does differ with visual field of presentation, but not in the predicted direction; it is the left and not the right hemisphere that distinguishes between the two violation types. That is, within and between category violations elicit equivalent N400s when presented to the left visual field (right hemisphere) but a smaller N400 to within than between category violations is observed when these are presented to the right visual field (left hemisphere). This pattern of N400 amplitudes for right visual field (left hemisphere) presentation replicates that observed with central visual presentation [31]. In sum, right hemisphere processing seems to be affected only by contextual congruency while left hemisphere processing shows influences of both contextual congruency and the context-independent semantic relatedness between the within category violations and the expected sentence completions.

This hemispheric difference in the pattern of N400 responses seems to be driven by the response to within category violations, as N400 amplitudes to between category violations do not differ with hemifield. In fact, according to the ERPs both contextually predicted and contextually unexpected items from a different semantic category (i.e., that are only distantly related) are processed similarly regardless of the visual field of presentation. At least for these stimuli, then, the 'range' of each hemisphere"s response to words in context seems to be similar. The visual field of presentation, however, apparently does affect the processing of items that are contextually inappropriate but from the same semantic category as the contextually-predicted item (and thus sharing significant semantic feature overlap with it), i.e., within category violations. For right hemisphere-initiated processing, the responses to both violation types are the same, whereas for left hemisphere-initiated processing the N400 to within category violations is significantly smaller than for between category violations.

In contrast to the various effects on N400 amplitude, there is no difference in either the latency or the distribution of any condition as a function of hemifield of presentation. In short, using a measure with high temporal resolution, we do not find support for proposed timing differences in the hemispheres' processing of word meaning. Although this does not rule out the possibility that there are hemispheric timing differences that are invisible to the ERP measure [12], it does indicate that there are no timing differences for the aspects of meaning processing that are indexed by the N400, namely, those involved in integrating word meaning into context. If, then, there are earlier timing differences in meaning activation that are invisible to scalp ERP measures, these do not seem to impact the timing of later, integrative processes.

Thus, we do not observe the pattern of results that the behavioral literature — and in particular the results of single word priming studies — would lead us to predict either with respect to the timing or the nature of the hemispheres' responses to the two violation types. It is the right hemisphere processing that seems to be driven solely by fit to the sentence context, and it is the left hemisphere's processing which indicates an influence of the context-independent categorical relation that holds between the within category violations and the expected exemplars. Recall that in semantic priming studies, items with this type of relationship (members of a semantic category that are not lexically associated with one another) prime reaction times only with left visual field (right hemisphere) presentations (see e.g., Refs. [15–17]). As the most straightforward extrapolation from semantic priming studies to sentence processing thus does not appear to hold, we must look for other factors to explain the differences we observe.

4.2. Hemispheric differences in meaning integration

In discussing the results with central visual field presentation, we distinguished between two accounts of how processing a sentence might influence the processing of a word within it [31]. In what we termed an 'integration' account, the features of the target word are compared directly with those of the context (e.g., those associated with words in the sentence and/or the sentence message level). On this account within category and between category violations should elicit equivalent responses, as both contain features that clearly do not cohere well with context features. For example, within the context, 'They wanted to make the hotel look more like a tropical resort. So along the driveway, they planted rows of....' both the within category violation ('pines') and the between category violation ('tulips') have features that are incompatible with the features of context words, such as 'tropical', 'resort', etc., and that are difficult to reconcile with the sentence level meaning. Accordingly, both are unexpected

[12] See, e.g., [50] for a description of the types of electrical activity that will and will not be observed with scalp ERP measures.

and relatively implausible (as seen in the norming) and should elicit an N400 of similar amplitude. The integration account would further seem to predict (in line with behavioral results — see e.g., Refs. [79,80]) that a violation should be even more difficult to integrate as the context becomes more constraining (i.e., contains more specific features).

With central presentation, however, N400s to within category violations were smaller than those to between category violations, and smaller to within category violations in highly than in weakly constraining sentences. While inconsistent with an 'integration' account, this pattern of results is consistent with an 'expectancy' account of contextual facilitation. In this account, processing context is presumed to (pre)activate the semantic features of the item most consistent with (i.e., more predicted in) the context. It is these predicted features, rather than those of the context itself, that are then compared with the features of the presented item, with the amount of facilitation a function of the extent of semantic overlap between the item predicted and the item presented. In this account, within category violations would elicit a smaller N400 than between category violations because of their greater feature overlap with the item that is predicted by the context but that is never actually presented. As the prediction can be more specific in constraining context, the N400 reduction would be even greater.

Perhaps not coincidentally, the different patterns observed with presentations to the two visual fields in this study mirror the differences in the predictions of these two accounts. The right hemisphere distinguishes contextually expected and unexpected items but not the two different violation types. This is consistent with the predictions of an integration account, suggesting that the right hemisphere may be comparing the features of the target word directly with the features of context. The left hemisphere not only distinguishes contextually expected and unexpected items, but also between the various unexpected items, leading to reduced N400s across the scalp to those that share semantic features with the expected exemplar. This pattern is better explained by assuming that the left hemisphere's processing of context pre-activates features associated with the concept most likely to come next — namely, an expectancy account.

4.3. Integrating electrophysiological, behavioral, and neuropsychological findings

Our characterization of hemispheric differences also provides an alternative, but viable, account of many behavioral findings. Faust et al. [28–30], for example, observed that the left hemisphere was more sensitive than the right to contextual constraint, whether defined by amount of context (single word vs. phrase vs. sentence) or by strength of context as indexed by the cloze probability of the best completion. They interpreted these results as indicating that the left hemisphere is more sensitive than the right to the message-level representation of the context. Our view, however, suggests that the left hemisphere is more sensitive to contextual constraint because constraint specifically reflects the extent to which context information allows specific predictions to be made. Because only the left hemisphere seems to be generating expectations, only its processing reflects a strong influence of constraint. In fact, the right hemisphere seems to outperform the left precisely under conditions where prediction is difficult. Summation primes like those used by Beeman [4] are only weakly related to one another and therefore would not readily lead to any consistent predictions. Accordingly, we would expect the left hemisphere to gain little, if any, facilitation from this type of prime, and certainly less facilitation than from a single, strong associate; this is exactly what has been observed. By contrast, we would expect to observe facilitation when a target word can be integrated with each prime word directly, as we suggest is characteristic of right hemisphere processing.

Similarly, our left hemisphere expectancy/right hemisphere integration (LHE/RHI) account predicts that both hemispheres may show facilitation for contextually unexpected items, albeit under difference circumstances. The right hemisphere should show facilitation for a target word that is similar to another in the context, as their semantic features can be integrated. Indeed, Faust et al. [26] observed that reaction times were facilitated for contextually incongruous targets that were lexically associated with other words in the context (e.g., 'The patient parked the medicine'), but only for right hemisphere presentation. They attributed this to the right hemisphere's insensitivity to the message-level meaning of the sentence, a sensitivity the left hemisphere is proposed to have. This explanation, however, does not account for our finding of facilitation for contextually unexpected items that are related to the expected endings when these are presented to the left but not the right hemisphere. On the LHE/RHI view, left hemisphere processing of the context anticipates the features of the item most predicted in the context, thereby facilitating words sharing features with that item even if they themselves are not good fits to the sentence message level. This is exactly what we found for within category violations with right visual field (left hemisphere) presentation. Chiarello [15] has found that the right hemisphere is sensitive to the kind of semantic similarity that holds between our expected exemplars and within category violations when exposed directly to both. However, since the right hemisphere's processing of sentences does not involve expectation, it cannot appreciate this same relationship when it holds between a word actually presented (the within category violation) and one that is not presented but only predicted in the context.

In general, then, our data call for a different characterization of hemispheric differences in meaning processing than has been put forward to date. Our data do not support a description of right hemisphere meaning activation as just broader in scope as compared with a more focused, context-driven approach to processing in the left hemisphere [3,16]. We find not only that both hemispheres handle semantic information at a specific level within sentence, but that the right hemisphere — even more so than the left — distinguished between the particular category member predicted by the context (expected exemplar) and a related item, suggesting it is, in fact, processing context information in an explicit, detailed manner. The right hemisphere's processing strategy, however, might be characterized as broader in scope — or more 'global' — in a different sense. An integrative strategy, in which new items are compared directly with previously encountered items, necessarily entails that the information extracted from those items (i.e., context) be maintained over time. In fact, information maintenance seems to characterize right hemisphere processing more generally; for example, several studies have shown right hemisphere dominance for maintaining larger amounts of information [45], over longer periods of time [45,46], and with greater specificity [60,61] and therefore less susceptibility to memory confusions (e.g., tendency to judge new, but related items, as old) [64]. In contrast, in the left hemisphere specific lexical information seems to preactivate semantic feature information relating to the item most likely to appear next, perhaps guided by top-down information in the form of frames or schemas. This makes left hemisphere processing more efficient under most everyday language processing conditions when an expected item or one similar to it then occurs, but less efficient and more error-prone when initial assumptions must be revised (see e.g., Refs. [10,65]) or when old information must be distinguished from new but schematically consistent material [64]. In this sense, the left hemisphere might be said to have a more narrow, short-term — 'local' — view of context.

Thus, we do not think that only the left hemisphere processes the message level meaning [27]. We find, instead, that both do, albeit under different circumstances. More precisely, the two hemispheres use qualitatively different processing strategies, both of which are likely to be important for extracting 'message-level' information during normal language processing. In processing a discourse, for example, one must follow the local message-level (e.g., a description of an individual helping another to change a flat tire) while simultaneously maintaining more global information about who or what is being discussed and for what purpose (e.g., remember that I am talking about my colleague, giving examples of why I think she is a good person). Maintaining this more global, topic information, we suggest, may rely on right hemisphere processing strategies. Without them, one can follow the immediate flow of the discourse but may lose sight of the overall discourse meaning. Similarly, the processing of metaphors and jokes often requires reanalysis of or comparisons with items encountered earlier in the context. For example, correctly interpreting the statement: 'I hate that butcher; I can't believe he is her surgeon!' requires a frame-shift [21], a reinterpretation of the critical word 'butcher' that may be impossible without the right hemisphere's more global memory for the context items.

In conclusion, then, the pattern of electrophysiological responses we observed in each visual hemifield to contextually expected, contextually unexpected but semantically related, and contextually unexpected and unrelated words in sentence contexts did not fully accord with predictions derived from current accounts of hemispheric differences in meaning processing. In line with neuropsychological and behavioral findings, our results suggest that there are important differences in how the two hemispheres process sentence contexts and use contextual information to process words. However, these do not seem to be best characterized as differences in the scope of meaning activation or in the ability to use 'message-level' information. Rather, we propose that the left hemisphere's processing of context is predictive (resulting in the activation of features associated with the item most likely to be encountered in the future), while the right hemisphere processing is integrative (involving direct comparisons between the features of items in the context and those of the current word). Characterizing hemispheric processing along these lines leads to a more unified picture of the various patterns of lateralized differences and deficits that have been observed. This account also provides a more complete understanding of how, in extracting and maintaining different types of information from language contexts, the hemispheres each make their unique and critical contribution to normal language comprehension.

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Appendix A. Examples of Stimuli Used in the Experiment

One hundred thirty-two sentence contexts were used in the experiment, each ending with one of the three possible ending types (expected exemplars, within category violations, between category violations). Below are given forty representative examples of these stimuli. Ending types are expected exemplar, within category violation, and between category violation, respectively.

''Checkmate,'' Rosaline announced with glee.
She was getting to be really good at chess / monopoly / football.

Justin put a second house on Park Place.
He and his sister often spent hours playing monopoly / chess / baseball.
He caught the pass and scored another touchdown.
There was nothing he enjoyed more than a good game of football / baseball / monopoly.
Rich couldn't count the number of Yankees games he had seen with his father.
They both shared a lifelong interest in baseball / football / chess.
She felt that she couldn't leave Venice without the experience.
It might be a touristy thing to do, but she wanted to ride in a gondola / ferry / helicopter.
Getting both himself and his car to work on the neighboring island was time-consuming.
Every morning he drove for a few minutes and then boarded the ferry / gondola / plane.
The patient was in critical condition and the ambulance wouldn't be fast enough.
They decided they would have to use the helicopter / plane / ferry.
Amy was very anxious about traveling abroad for the first time.
She felt surprisingly better, however, when she actually boarded the plane / helicopter / gondola.
The day before the wedding, the kitchen was just covered with frosting.
Annette's sister was responsible for making the cake / cookies / toast.
The little girl was happy that Santa Claus left nothing but crumbs on the plate.
She decided he must have really enjoyed the cookies / cake / bagel.
Chris moped around all morning when he discovered there was no cream cheese.
He complained that without it he couldn't eat his bagel / toast / cake.
He wanted to make his wife breakfast, but he burned piece after piece.
I couldn't believe he was ruining even the toast / bagel / cookies.
I guess his girlfriend really encouraged him to get it pierced.
But his father sure blew up when he came home wearing that earring / necklace / lipstick.
She keeps twirling it around and around under her collar.
Stephanie seems really happy that Dan gave her that necklace / earring / mascara.
She wanted to make her eyelashes look really black and thick.
So she asked to borrow her older friend's mascara / lipstick / necklace.
He complained that after she kissed him, he couldn't get the red color off his face.
He finally just asked her to stop wearing that lipstick / mascara / earring.
Eleanor offered to fix her visitor some coffee.
Then she realized she didn't have a clean cup / bowl / spoon.
My aunt fixed my brother some cereal using her best china.
Of course, the first thing he did was drop the bowl / cup / knife.
At the dinner party, I wondered why my mother wasn't eating her soup.
Then I noticed that she didn't have a spoon / knife / bowl.
In the dorms, cutting your steak can be a huge struggle.
They always give you such a poor quality knife / spoon / cup.
He journeyed to the African plains, hoping to get a photograph of the king of the beasts.
Unfortunately, the whole time he was there he never saw a lion / tiger / panda.
George was hiking in India when he saw the orange and black striped animal leap out at him.
He sustained serious injuries before he managed to kill the tiger / lion / polar bear.
Hitting the huge animal with a tranquilizer dart was difficult in the Arctic winds.
Eventually, however, they were able to approach and tag the polar bear / panda / lion.
Wendy wondered how they had managed to ship such a large animal all the way from China.
She waited in line to see the newly acquired panda / polar bear / tiger.
Barb loved the feel of the waves on her feet, but she hated to walk barefoot.
As a compromise, she usually wore a pair of sandals / boots / shorts.
By the end of the day, the hiker's feet were extremely cold and wet.
It was the last time he would ever buy a cheap pair of boots / sandals / jeans.
Everyone agreed that the stone-washed kind were out of style.
But he continued to wear the same old pair of jeans / shorts / sandals.
As the afternoon progressed, it became hotter and hotter.
Keith finally decided to put on a pair of shorts / jeans / boots.
Pablo wanted to cut the lumber he had bought to make some shelves.
He asked his neighbor if he could borrow her saw / hammer / rake.
Tina lined up where she thought the nail should go.
When she was satisfied, she asked Bruce to hand her the hammer / saw / shovel.
The snow had piled up on the drive so high that they couldn't get the car out.

When Albert woke up, his father handed him a shovel / rake / saw.

The yard was completely covered with a thick layer of dead leaves.

Erica decided it was time to get out the rake / shovel / hammer.

Fred went to the pantry and got out the homemade jelly his grandmother had brought.

Fifteen minutes later, however, he was still struggling to open the jar / box / zipper.

After they unpacked the new refrigerator, they let Billy have his fun.

He played for days afterwards with the big box / jar / button.

It seemed to catch every time she opened or closed her backpack.

She decided she would have to replace the zipper / button / box.

One fell off her blouse and got lost, and she didn't have any extras.

She ended up searching all over town to find a matching button / zipper / jar.

The firefighters wanted to have a mascot to live with them at the firehouse.

Naturally, they decided it would have to be a dalmatian / poodle / zebra.

Muffie, old Mrs. Smith's pet, wears a bow on the puff of fur on its head.

I don't know how anyone could want to own a poodle / dalmatian / donkey.

''I'm an animal like Eeyore!'' the child exclaimed.

His mother wondered why he was pretending to be a donkey / zebra / dalmatian.

At the zoo, my sister asked if they painted the black and white stripes on the animal.

I explained to her that they were natural features of a zebra / donkey / poodle.

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