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Hemispheric differences in the activation of perceptual information during sentence comprehension

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Abstract

Previous research has suggested that perceptual information about objects is activated during sentence comprehension [Zwaan, R. A., Stanfield, R. A., & Yaxley, R. H. (2002). Language comprehenders mentally represent the shapes of objects. *Psychological Science*, *13*(2), 168–171]. The goal in the current study was to examine the role of the two hemispheres in the activation of such information. Participants read sentences that conveyed information about the shape of an object (e.g., the egg was in the pan versus the egg was in the carton) and then received a picture of the object that was either consistent or inconsistent with the shape implied by the sentence (e.g., a fried egg versus a whole egg). In Experiment 1, pictures were presented briefly in either the left-visual field or the right-visual field. Participants showed a mismatch effect, slower responses when the picture was inconsistent with the shape of the object implied by the sentence than when it was consistent, but only when the pictures appeared in the right-visual field (left hemisphere). In Experiment 2, the sentences were revised such that the shape of the object was described explicitly. Participants showed a mismatch effect in both visual fields. These findings suggest that the right hemisphere activates shape information during sentence comprehension when a shape description is explicit, whereas the left hemisphere activates such information both when the shape is described explicitly and when it is implied.

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Language comprehension, like most cognitive abilities, involves the coordination of multiple distinct processes that occur in both cerebral hemispheres. Comprehension requires the decoding of words and propositions in a sentence as well as the use of world knowledge retrieved from long-term memory. Consider the concept *lemon* in the sentence "The lemon was in the iced tea". The meaning of *lemon* in this context is likely to refer to a slice or a wedge of lemon, rather than a whole lemon. The activation of contextually relevant word meanings is a fundamental aspect of language comprehension.

A growing body of evidence suggests that understanding the meaning of a sentence involves the activation of contextually relevant, perceptual information (Fincher-Kiefer, 2001; Pecher,

Zeelenberg, & Barsalou, 2003; Solomon & Barsalou, 2001; Spivey, Tyler, Richardson, & Young, 2000). Zwaan, Stanfield, and Yaxley (2002) demonstrated this in a picture-matching paradigm. They had participants read sentences that implied the shape of an object. For example, the sentence "There was an eagle in the sky" implies the shape of an eagle with wings outstretched rather than the shape of a perched eagle with tucked wings. After reading the sentence, a picture of the object was presented. The picture was either consistent or inconsistent with the shape implied by the sentence (e.g., a flying eagle versus a perched eagle) and participants judged whether the pictured object had been mentioned in the sentence. Zwaan et al. (2002) found that participants' responses were faster when the pictured object's shape matched the shape implied by the sentence than when the picture was inconsistent with the implied shape. They argued that these results are evidence for the routine activation of perceptual information during language comprehension.

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Similar results were found in a study by Stanfield and Zwaan (2001). They had participants view sentences and decide whether a pictured object had been mentioned in the preceding sentence. Each sentence implicitly suggested a particular orientation for an object (e.g., "John put the pencil in the cup." <vertical> versus "John put the pencil in the drawer." <horizontal>). The orientation of the picture was varied such that it was either consistent or inconsistent with the orientation implied by the sentence. Stanfield and Zwaan found that participants responded faster to pictures matching the implied orientation of the object than to pictures that did not match the orientation. The authors concluded that these findings provide support for theories proposing perceptual activation during language comprehension.

The activation of perceptual information during comprehension does not appear to be explained by semantic relations among individual words in a sentence. Glenberg and Robertson (2000) had participants read scenarios describing novel situations. These situations were sensible (e.g., using a newspaper to protect one's face from the wind) or nonsensical (e.g., using a matchbook to protect one's face from the wind) and participants made sensibility judgments (scale of 1 "virtual nonsense" to 7 "completely sensible") and envisioning ratings (scale of 1 "impossible to imagine" to 7 "easy to imagine"). Glenberg and Robertson computed indices of semantic association using high-dimensional vector representations (e.g., latent semantic analysis, LSA) in order to determine the extent to which meaning was conveyed by preexisting semantic relations among words in the sentences. They found that participants rated the sensible and nonsensical scenarios differently, whereas LSA cosines for the two types of scenarios did not differ. The LSA analyses suggest that the scenarios were equivalent with respect to semantic relatedness. The cosines did not predict the 'sensibility' of the scenarios. In contrast, participants' perceptual 'envisioning ratings' reliably predicted how they rated the sensibility of the scenarios. Glenberg and Robertson argued that readers computed the functional affordances of objects based on perceptual information that was activated during language comprehension.

The activation of perceptual information during language comprehension appears to influence the interaction between language and motor processing. In one study, participants judged the sensibility of an action (e.g., close/open the drawer) when the response modality was in the same direction as the described action (toward/away from the body). The dependent measure was "action-sentence compatibility" (i.e., the interaction between implied sentence direction and the direction of the actual, physical response). Participants were slower to make a sensibility judgment when it required a response in the opposite direction of the one implied in the sentence than when it required a response in the same direction. This occurred for action-based sentences (open/close drawer) and for sentences that referred to physical transfer (e.g., You handed Courtney the notebook). Remarkably, the effect was also observed for the transfer of abstract entities (e.g., "Liz told you the story"/"You told Liz the story"). These data suggest that at least some linguistic constructions are grounded in an action-based system (Glenberg & Kaschak, 2002).

1. The activation of perceptual information in the two hemispheres

The goal of the current study was to examine how the two hemispheres contribute to the activation and maintenance of perceptual information during language comprehension. Research suggests that the two hemispheres have different processing strengths. The left hemisphere (LH) is dominant for language processing, whereas the right hemisphere (RH) has strengths in visual perception and imagery. Thus, the two hemispheres may play different roles in the activation and integration of perceptual information during comprehension.

Numerous studies have documented a RH advantage in shape recognition, picture processing, and visual imagery. For example, Marsolek (1995, 1999) showed hemispheric differences when the perceptual form of objects was altered on repeated presentation using a visual half-field technique in combination with a repetition priming procedure. In one study (Marsolek, 1999), participants viewed objects presented centrally in a study phase and then named objects presented in the left-visual field/right hemisphere (LVF/RH) or right-visual field/left hemisphere (RVF/LH) at test. The test objects were (a) the same as the ones presented at study (e.g., a grand piano at study and the same grand piano at test), (b) different from the studied objects but were exemplars of the same category (e.g., an upright piano at study and a grand piano at test), and (c) words that referred to the studied objects (e.g., piano). Marsolek hypothesized that an abstract-category subsystem operates in the LH. Thus, naming latencies in the same and different condition should be equivalent and faster than latencies in the word condition when objects are presented in the RVF/LH. In contrast, he hypothesized that the RH has "exemplar specific" processing mechanisms. Thus, latencies to stimuli in the same condition should be faster than to those in the different or word conditions. The results were consistent with Marsolek's hypotheses. The RH appeared to be more sensitive to differences among exemplars than was the LH, suggesting that it was involved in processing specific visual information about the objects. In contrast, the LH appeared to generalize across different exemplars, supporting a more abstract or lexical-semantic contribution to visual object processing.

Behavioral findings, like those described above, have been supported and extended in both neuroimaging and neuropsychological studies. Koutstaal et al. (2001) investigated hemispheric differences to novel and repeated objects in the fusiform cortex. They hypothesized that the right fusiform cortex processes comparatively more specific visual form information about previously encountered objects. Thus, the usual reduction in neural activity that is observed when participants view repeated objects should be less pronounced in the right fusiform than in the left when different exemplars from the same category are presented at test. The results were consistent with their hypothesis. They found significantly less repetition-induced reduction in the right fusiform than in the left fusiform in response to different relative to same exemplars (Koutstaal et al., 2001; Vuilleumier, Henson, Driver, & Dolan, 2002).

Neuropsychological studies of patients with damage to RH cortices also support the claim that the RH is more sensitive to exemplar form than is the LH. The RH contribution to visual form-specific priming has been documented in case studies of patients with: (a) right occipital resections (Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995; Vaidya, Gabrieli, Verfaellie, Fleischman, & Askari, 1998), (b) damage to right occipitotemporal cortex leading to prosopagnosia (an impaired ability to recognize faces), and (c) damage to right occipitotemporal cortices (Farah, 1991; Gauthier, Behrmann, & Tarr, 1999; see also Yonelinas et al., 2001).

Other unique visual processing characteristics have been ascribed to the RH. The RH appears to have an aptitude for visual–spatial relations. It processes metric (distance) relations more quickly and accurately than categorical (e.g., above/below) relations. The opposite pattern is found in the LH (Kosslyn, Maljkovic, Hamilton, Horwitz, & Thompson, 1995; Kounios & Holcomb, 1994; Laeng, Zarrinpar, & Kosslyn, 2003). Moreover, hemispheric asymmetries are found in attention to global (whole object) or local (object part/feature) properties of visual stimuli. The RH generally favors global stimulus properties (Delis, Robertson, & Efron, 1986; Fink et al., 1996; Van Kleeck, 1989), whereas the opposite is true of the LH. It is clear that the RH makes a unique contribution to visual, spatial processing.

While the RH maintains sensitivity to exemplar form and demonstrates unique visual processing characteristics, the activation of object shape information at the category level as a consequence of lexical processing has been ascribed to the LH in several behavioral and imaging studies. Damasio, Tranel, Grabowski, Adolphs, and Damasio (2004) reviewed lesion studies and positron-emission tomography (PET) evidence and proposed a model for understanding the links between lexical and visual representation in the LH. The model accounts for naming concrete objects at the category level (i.e., a picture of a cup). It is comprised of a processing stream that activates bilateral primary visual cortices, concept retrieval areas of parieto-occipital cortices, followed by reconstruction of explicit sensorimotor information pertaining to the referent in areas of the inferior temporal left cortex, and finally classical language areas to produce a naming response. This processing stream runs in reverse when subjects receive a word (or sentence) referring to a concrete object. The left hemisphere language areas activate LH temporal regions where word meaning, including shape information at the category level, becomes active as a consequence of lexical processing. In support of the model, a study in which participants judged whether a target word was related to a prime word showed that unassociated prime-target pairs that shared similar shapes (e.g., LADDER-RAILROAD) yielded longer "no" responses than unassociated prime-target pairs. Using visualfield techniques, this effect was localized in the LH (Zwaan & Yaxley, 2004). Thus, substantial evidence supports a role for the LH in category level activation of shape information, in relation to the exemplar specific designations in the RH.

Is the RH also involved in processing perceptual/spatial information when the input to the system is linguistic? Recent evidence suggests that it may. Zwaan and Yaxley (2003) investigated whether semantic judgments about words were influ-

enced by the spatial relations among their referents. Participants made semantic relatedness judgments to word pairs that were presented in an iconic relation to their referents (e.g., ATTIC <above>—BASEMENT
below>) or to word pairs that did not match their typical spatial relationship (i.e., ATTIC
below>—BASEMENT<above>). The authors hypothesized a hemispheric asymmetry in semantic relatedness judgments, based on the assumption that visual—spatial relations are stored and processed in the RH. Participants were faster to make judgments in the iconic condition than in the mismatch condition, but only when word pairs were presented in the LVF/RH. Zwaan and Yaxley argued that the word stimuli activated perceptual information about their referents.

The goal of Experiment 1 was to examine hemispheric differences in the activation of perceptual information during sentence processing. As recent literature has shown, sentence presentation in the context of an object processing task can be useful in examining the interaction between language processing and the activation of perceptual information (Kaschak et al., 2005; Larsen, Wilkins, Yang, & Swick, 2004; Stanfield & Zwaan, 2001; Zwaan et al., 2002). In the following experiments, participants read sentences that conveyed information about the shape of an object and then received a picture of the object that was either consistent or inconsistent with the shape implied by the sentence. Pictures were presented to the LVF/RH or to the RVF/LH and reaction times (RTs) were recorded. If the RH uniquely activates and maintains perceptual information sensitive to the specific object exemplar, then participants should respond faster to pictures in the match condition than in the mismatch condition, but only when pictures are presented to the LVF/RH. Alternatively, the link between lexical representations and resulting activation of objects shape information may be lateralized to the LH as a consequence of the lexical processing required by the sentence stimulus and would be revealed by faster RTs in the match versus the mismatch condition when pictures are presented to the RVF/LH.

2. Experiment 1

In Experiment 1, we used materials and adapted procedures from a previous experiment by Zwaan et al. (2002) for use in a divided visual-field study. Participants read sentences and then responded to pictures presented to the LVF/RH or the RVF/LH. If the RH plays a unique role in activating perceptual information sensitive to specific object exemplars during comprehension, then we should see faster responses to pictures in the match than in the mismatch condition. Based on research showing the activation of object shape information in the LH (Damasio et al., 2004; Zwaan & Yaxley, 2004), we predicted faster responses to pictures in the match than mismatch condition when items were presented to the RVF/LH. Our specific interest in this experiment concerned performance when pictures were presented to the LVF/RH. The RH is better than the LH at shape recognition, picture processing, and visual imagery; thus, we also predicted a match effect in the LVF/RH, faster responses to pictures that matched the shape implied in the sentence than to pictures that mismatched the implied shape.

2.1. Method

2.1.1. Participants

Participants were 64 undergraduate students at the University of California, Davis (42 females/22 males, 17–25 years of age, mean age 20) who received course credit for their participation. All were right-handed, native English

speakers with normal or corrected-to-normal vision and no history of learning disabilities or neurological/psychiatric disorders.

2.1.2. Materials

The experimental sentences and pictures were used previously by Zwaan et al. (2002). The reader is referred to the original paper for further information on stimuli, methods, and design, as only a brief description is provided here. Each sentence conformed to a scripted grammatical structure "There was a/an <object>
in the nest."). The sentences were constructed in pairs. Each introduced an object and included a prepositional phrase that implied the shape (or state) of the object ("There was a lemon in the tree." or "There was a lemon in the drink."). Each subject saw 28 experimental items and an additional 24 filler items. Filler items were constructed using the same grammatical structure as the experimental sentences but were paired with an unrelated object (e.g., "There was a suitcase at the airport."

barn>).

The pictures were black and white depictions of objects. Each object was associated with a pair of pictures, each representing a different shape of the object, see examples in Fig. 1. Some of the pairs included a balloon (inflated versus deflated), an apple (sliced versus whole), spaghetti (uncooked versus cooked) and a chicken (alive versus roasted). Additional pictures were used to construct filler items. They were scaled to occupy a square of approximately 3 in. (7.6 cm).

Sentence version (There was a mushroom in the forest, There was a mushroom in the salad), picture version (whole mushroom, sliced mushroom) and VF condition were counterbalanced across eight lists. Each participant saw only one list.

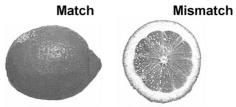
2.1.3. Procedure

Participants were instructed to read each sentence and to make a yes/no judgment as to whether the pictured object had been mentioned in the preceding sentence. Participants were further informed that their RT was being measured and that they should make their judgments as quickly and as accurately as possible. Participants pressed a key labeled "yes" if the picture matched an object mentioned in the preceding sentence and a key labeled "no" if the picture did not match. Participants were encouraged to keep their fingers on the yes/no keys at all times. Response hand was counterbalanced across participants such that half of the participants responded only with the right hand and the remaining used only their left hand. Responses and response latencies were recorded for each picture. Subjects were presented with on-screen instructions and four practice items, with feedback, to familiarize them with the task. The experimental items and fillers were presented randomly.

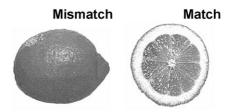
Participants were seated 57 cm from a computer screen and maintained head position in a chin rest throughout the experiment. Stimuli were presented by a PC on a 17 in. display using Direct RT stimulus presentation software (http://www.empirisoft.com/directrt/). The sentences were presented in the center of the screen for 4000 ms, allowing adequate time for processing the sentence. All sentences were presented in a white, 32 pt. font on a black screen. Each sentence was followed by a fixation point (250 ms) and then a picture. The picture was presented to either the RVF/LH or the LVF/RH. The center of each picture was presented at 6° of visual angle to the left or to the right of the fixation point such that the medial edge was never closer than 2.2° of visual angle from the midline. The picture remained on screen for 150 ms, after which the participant viewed a black screen until a response was made.

2.2. Results and discussion

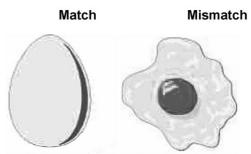
We performed 2(match condition) \times 2(VF) \times 2(response hand) ANOVAs on accuracy rates and RTs to pictures. Match condition (sentence and picture matched versus sentence and picture mismatched) and VF (LVF versus RVF) were within-participant factors; response hand (R-hand versus L-hand) was a between-participant factor. Incorrect responses were removed from the analyses. All errors and latencies greater than or less than three standard deviations from a participant's mean were replaced with a value equal to the participant's mean reaction time plus or minus three standard deviations, respectively (altogether 176 errors and 33 outliers were replaced). Long and short response latencies which were replaced represented less than one percent of the data. All effects



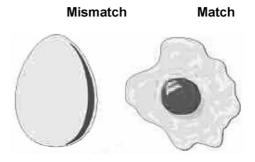
"There was a lemon in the tree."



"There was a lemon in the drink."



"There was an egg in the refrigerator."



"There was an egg in the skillet."

Fig. 1. Examples of match and mismatch stimuli from Experiment 1.

were tested at a significance level of p < .05, unless otherwise indicated. Accuracy data and mean RTs in the match and mismatch condition appear in Table 1 and Fig. 2.

The analyses revealed a marginal effect of match condition, F(1, 63) = 3.50, MSE = 23,292, p = .07. The critical match × VF interaction was not reliable, F(1, 63) = 1.3. Nonetheless, we had specific hypotheses about the magnitude of

Table 1 Accuracy data for Experiment 1

Hemisphere/visual field	Percent accurate		
	Match condition	Mismatch condition	
LH/RVF	92	91	
RH/LVF	94	92	

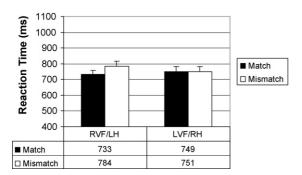


Fig. 2. Mean response times in the match and mismatch condition for Experiment 1.

the match condition in each VF; therefore, we conducted a follow-up analysis to determine whether the match effect was larger in the LVF/RH than in the RVF/LH. The pattern of RTs, however, was inconsistent with our predictions. Participants responded faster to pictures when they matched the shape implied by the sentence than when they did not match, but only when the pictures were presented in the RVF/LH, F(1, 63) = 4.50, MSE = 27,329. We found no reliable effect of match condition in the LVF/RH, F < 1. The accuracy data was analyzed similarly. We found no reliable effects (all Fs < 1).

We had predicted a match effect in the RVF/LH based on previous research suggesting that shape information is activated in the LH when readers comprehend sentences (Damasio et al., 2004; Zwaan and Yaxley, 2004) and our results were consistent with this prediction. We had also predicted a match effect in the RH as well. Previous research has documented a strong RH advantage in shape recognition and picture processing. Nonetheless, our results were not consistent with this prediction. One explanation for our pattern of results may be that the RH does not activate perceptual information about shape in response to linguistic stimuli. This conclusion may be premature, however. In the sentences used in this experiment, the shape information was implied by the sentence content; it was not explicit. That is, the shape information required an inference based on world knowledge about the situations depicted in the sentences. For example, the sentence "There was a balloon in the pack" requires that the reader infer that the balloon is deflated; similarly, the sentence "There was an egg in the pan" requires knowledge that, in this situation, an egg is usually cracked and not whole in the shell. Thus, one explanation for the results in Experiment 1 is that the LH activated perceptual information by making an inference in response to the sentence. The RH may routinely activate perceptual information, but it may not do so by means of inferential processing. There is currently debate in the literature about the role of the hemispheres in making inferences (Bihrle, Brownell, Powelson, & Gardner, 1986; Brownell, Potter, Bihrle, & Gardner, 1986; Hough, 1990; Metcalfe, Funnell, & Gazzaniga, 1995; Phelps & Gazzaniga, 1992; Rehak et al., 1992; Van Lancker & Kempler, 1987; Wapner, Hamby, & Gardner, 1981; Winner & Gardner, 1977). This debate is addressed in Section 4.

3. Experiment 2

The goal of this experiment was to examine the activation of shape information when such information is described explicitly in a sentence. The sentences from Experiment 1 were modified such that each sentence included explicit information about the shape of the object it described (e.g., "A *slice* of lemon was in the drink.").

If the RH fails to activate shape information from linguistic input, then we should replicate the pattern of results that we observed in Experiment 1. We should find a match effect only when pictures are presented in the RVF/LH. If, however, the RH activates shape information, but only when shape is described explicitly, then we should see a match effect in both VF conditions.

3.1. Method

3.1.1. Participants

Participants were 32 undergraduate students (18 females/14 males, 17–22 years of age, mean age 19) at the University of California, Davis, who partic-

Table 2 Accuracy data for Experiment 2

Hemisphere/visual field	Percent accurate		
	Match condition	Mismatch condition	
LH/RVF	92	82	
RH/LVF	95	87	

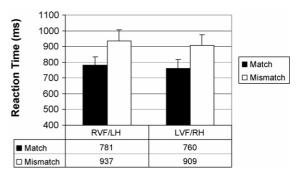


Fig. 3. Mean response times in the match and mismatch condition for Experiment 2.

ipated for course credit. All were right-handed, native English speakers with normal or corrected to normal vision and no history of learning disabilities or neurological/psychiatric disorders.

3.1.2. Materials and procedure

The sentences from Experiment 1 were altered to include explicit information about shape. This was accomplished by adding adjectives ("A *deflated* balloon was in the package"), more specific noun phrases ("A *wedge of cheese* was on the tray"), or a more specific verb ("An airplane *flew* through the sky"). The stimuli sentences were paired with the same objects as in Experiment 1. The procedure was the same as that used in Experiment 1.

3.2. Results and discussion

The accuracy and RT data were analyzed as described in Experiment 1. All errors were removed from the analyses. All errors and latencies greater than or less than three standard deviations from a participant's mean were replaced with a value equal to the participant's mean reaction time plus or minus three standard deviations, respectively (altogether 98 errors and 23 outliers were replaced). Outliers represented 1.4% of the data. Accuracy rates and mean RTs appear in Table 2 and Fig. 3.

Our analyses of the RTs revealed a reliable effect of match, F(1, 31) = 19.74, MSE = 744,200, but no effect of visual field, F < 1. Participants responded faster to pictures in the match condition than in the mismatch condition. This occurred in both VF conditions. The accuracy data was analyzed similarly. We found reliable effects of both match condition, F(1, 31) = 26, MSE = .26, and VF, F(1, 31) = 4, MSE = .04. Subjects were less accurate to mismatch items than to match items in both the RVF/LH and the LVF/RH.

The findings from Experiment 2 suggest that perceptual information about the shape of an object is activated in the RH when shape information is explicit in a sentence. It should be noted, however, that the RH was not unique in activating this information. We found a reliable match effect to stimuli presented in the RVF/LH as well.

¹ We conducted an additional analysis to determine whether slow responses in the mismatch condition was a group effect rather than the result of a few subjects with slow RTs. The five subjects with the slowest RTs were removed from the analysis. We again found a reliable effect of match condition, F(1, 26) = 20.6, MSE = 17,592.

4. General discussion

Our goal in this study was to investigate the extent to which the two cerebral hemispheres activated perceptual information during language comprehension. Our experiments yielded three findings. First, RH was sensitive to shape information as a consequence of language comprehension. Second, the activation of shape information in the RH occurred only when the sentence described an object's shape explicitly. When the shape of an object had to be inferred, only the LH showed activation of shape information. Finally, the activation of shape information was not unique to the RH. The LH activated such information both when shape was described explicitly and when shape information was implied.

Our findings in this study can be interpreted in light of claims by Faust and Chiarello (1998) with reference to message-level and lexical-level processing differences in the two hemispheres. Lexical-level processing refers to the effects of context that are a function of the associations among single words, whereas message-level processing describes the effects of context that arise from the conceptual representations of sentences based on a combination of syntactic, semantic, and world knowledge (Morris, 1994; Simpson, Peterson, Casteel, & Burgess, 1989). The LH is believed to be especially proficient in message-level processing, whereas both hemispheres are proficient at intralexical processing (Faust, Babkoff, & Kravetz, 1995; Faust, Kravetz, & Babkoff, 1993). The RH may be better at intralexical processing than message-level processing because it lacks mechanisms for utilizing syntactic knowledge and structure or because it possesses mechanisms for processing words that are different than those in the LH. Regardless of the reason, the RH is proficient at processing single words and may even treat sentences as a string of words. The LH, in contrast, is proficient at both single-word and message-level processing. It employs syntactic, semantic, and world knowledge from long-term memory to select the meaning of a word (or the implied shape of an object) that is most appropriate to the sentence context.

If we view our results from Experiment 1 in light of Faust et al. claims about processing differences in the two hemispheres, the LH may have constructed a conceptual representation of the meaning of the sentences based on syntactic, semantic, and world knowledge, and used this information to infer the state of the objects. The RH, in contrast, used only lexical-level associations (e.g., lemon-tree; lemon-drink) to construct a sentence representation. Such information may not have been sufficient to infer the state of the object implied by the sentence. Instead, the RH may have activated multiple exemplars of the object (e.g., whole and sliced lemons) in response to the words in the sentence. If this were the case, the RH would accept any depiction of object shape (e.g., whole or sliced lemon) as consistent with the context of the sentence because any object shape would be consistent with individual words in the sentence. This would lead to no difference in RTs as a function of match condition. By introducing an explicit reference to the state of the object in Experiment 2, the individual words in the sentence provided constraints on the states of objects that would be consistent with the lexical information (e.g., slice-lemon-drink). Thus, the RH

had stronger activation for the object representations that were consistent with the sentence than those that were inconsistent with the sentence.

Our findings in this study raise at least two important issues about the role of the RH in language processing. The first concerns differences in our results and those reported previously by Zwaan and Yaxley (2003). They found that the RH was sensitive to perceptual information (spatial relations), whereas the LH was insensitive to such information. In contrast, we found that the LH was sensitive to perceptual information in both of our experiments. There are a number of factors that may account for this discrepancy. In the Zwaan and Yaxley experiment, participants responded to word pairs (e.g., LEAVES/ROOTS) that were presented in a manner that matched the relative spatial relation of their referents (e.g., LEAVES above ROOTS) or mismatched the typical relation (e.g., ROOTS above LEAVES). Participants were asked to determine whether the pair of words was semantically related. Zwaan and Yaxley argued that perceptual representations were activated when participants made semantic decisions and that the decisions were made more rapidly when the position of the words matched the perceptual representation. This task however differs from the one reported here in several important ways. First, in Zwaan and Yaxley, the decision was based only on presentation of word stimuli. The words referred to objects, but not to an event. In the current experiment, the additional steps involved in sentence comprehension and comparison of a visually presented target with an internal perceptual representation of an event make the task markedly more complex and may favor LH capacities. Second, Zwaan and Yaxley manipulated relative spatial position, whereas we manipulated shape information. There is evidence that the RH is uniquely involved in memory for spatial location (Kessels, de Haan, Kappelle, & Postma, 2002; Kohler, Kapur, Moscovitch, Winocur, & Houle, 1995; Kosslyn et al., 1995), but we have less evidence that shape information is specific to the RH. Zwaan and Yaxley (2004) conducted an experiment using a design similar to ours and found activation of shape information in the LH only.

A second issue raised by our findings concerns the role of the RH in making inferences. We found that the RH was sensitive to shape information, but only when it was explicitly described in the sentence. When an inference was required, we found no mismatch effect. If the RH plays an important role in making inferences to establish a coherent discourse representation, as many neuropsychologists have claimed, why did we find sensitivity to perceptual information only when an inference was not required (Bihrle et al., 1986; Brownell et al., 1986; Hough, 1990; Rehak et al., 1992; Van Lancker & Kempler, 1987; Winner & Gardner, 1977)? It is important to note that many of the neuropsychological findings with respect to the role of the RH in making inferences come from investigations of RH lesioned patients. The findings in these studies have been somewhat inconsistent. Some studies have found that RH damaged patients exhibit inference problems in a variety of comprehension tasks, including generating inferences to integrate ideas across sentences (Brownell et al., 1986), to identify main ideas and themes (Hough, 1990; Rehak et al., 1992), and to understand figurative language and humor (Bihrle et al., 1986; Van Lancker

& Kempler, 1987; Winner & Gardner, 1977). Other researchers, however, have not found inference deficits in RH damaged patients (Brookshire & Nicholas, 1984; Harden, Cannito, & Dagenais, 1995; Lehman-Blake & Tompkins, 2001; McDonald & Wales, 1986; Tompkins, Bloise, Timko, & Baumgaertner, 1994; Tompkins, Lehman-Blake, Baumgaertner, & Fassbinder, 2001). Moreover, experiments with split brain patients have indicated that the isolated RH responds veridically and does not incorporate schemas or inferences in decision making (Metcalfe et al., 1995; Phelps & Gazzaniga, 1992). Inconsistent findings across neuropsychological studies of RH damaged patients fail provide a clear picture of the role of the RH in inference processing.

Recent neuroimaging studies have also failed to clarify the role of the RH in making inferences. Some studies have shown RH involvement in making inferences (Nichelli et al., 1995; Robertson et al., 2000; St George, Kutas, Martinez, & Sereno, 1999) whereas other studies have found inference processing bilaterally or only in the LH (Ferstl & von Cramon, 2001; Mason & Just, 2004). Considerably more research will be necessary to determine when and how the RH contributes to inference generation during comprehension.

In summary, we found that perceptual information about the shape of objects was activated when participants read sentences, consistent with previous research suggesting that perceptual representations of linguistic content are reliably constructed during language comprehension (Fincher-Kiefer, 2001; Pecher et al., 2003; Solomon & Barsalou, 2001; Spivey et al., 2000; Zwaan et al., 2002; Zwaan & Yaxley, 2003). Our findings extend this research by demonstrating that both hemispheres activate shape information on the basis of explicit content in sentences. Only the LH, however, appears to do so when shape information must be inferred from world knowledge about the situations described by sentences.

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Appendix A. Stimuli

List A	List B
Experiment 1	
There was a balloon in the pack	There was a balloon in the air
There was a bat in the cave	There was a bat in the air
There was a book on the shelf	There was a book on the photocopier
There was an airplane in the hangar	There was an airplane in the sky
There was an apple in the bag	There was an apple in the salad
There was bread in the bakery window	There was bread in the toaster
There was cheese on the mousetrap	There was cheese on the sandwich
There was a lemon in the tree	There was a lemon in the drink
There was a lime in the produce section	There was a lime in the Corona
There was a lobster in the salad	There was a lobster in the sea

Appendix A (Continued)

List A	List B
There was a mushroom in the forest	There was a mushroom in the
There was a newspaper on the rack	soup There was a newspaper on the
m	driveway
There was pineapple on the skewer	There was a pineapple on the tree
There was an onion in the basket	There was an onion in the batter
There was a chicken in the oven	There was a chicken in the coop
There was a cigarette in the box	There was a cigarette in the ashtray
There was a fish in the pond	There was a fish in the oven
There was a hockey player on the ice	There was a hockey player on the bench
There was an eagle in the sky	There was an eagle in the nest
There was an egg in the refrigerator	There was an egg in the skillet
There was corn in the field	There was corn in the cooking
There was a sailboat on the trailer	pot There was a sailboat on the lake
There was a shirt on the hanger	There was a shirt on the shelf
There was a tissue in the box	There was a tissue in the
	trashcan
There was a tomato on the pizza	There was a tomato on the vine
There was a towel on the rack	There was a towel on the floor
There was watermelon in the bowl	There was a watermelon in the
There was smachatti in the how	garden
There was spaghetti in the box	There was spaghetti in the bowl
Literal sentences, list A	Literal sentences, list B
Experiment 2	
A deflated balloon was in the package	A balloon hovered in the air
A sleeping bat was hanging upside down	A bat flew through the air
A closed book was on the desk	A book lay open on the desk
An old airplane was on the ground	An airplane flew through the sky
An apple hung from the tree	A slice of apple was in the salad
A loaf of bread was in the bakery window	A slice of bread was in the toaster
A wedge of cheese was on the tray	A slice of cheese was on the sandwich
A lemon was on the tree	A slice of lemon was in the drink
A whole lime was on the counter	A wedge of lime was in the Corona
A lobster tail was served for dinner	A lobster swam through the sea
A mushroom grew in the forest	A slice of mushroom was in the sou
A newspaper was laying flat on the table	A rolled newspaper was on the driveway
A slice of pineapple was in the salad	A whole pineapple was at the marke
A whole onion was brought from the garden	A slice of onion was on the burger
A roasted chicken was cooked for dinner	A chicken was kept in the coop
An unlit cigarette was on the table	A cigarette butt was on the ground
A fish jumped from the stream	A fillet of fish was in the oven
A hockey player hit the puck	A hockey player sat on the bench
An eagle flew through the sky	An eagle sat on the branch
A whole egg was in the refrigerator An ear of corn was in its husk	A fried egg was in the skillet A cob of corn was in the boiling

A sailboat was missing its sails A button-down shirt hung on a

A tissue popped out of the box

hanger

A sailboat skimmed across the lake

A wad of tissue was in the trashcan

A folded shirt was on the shelf

Appendix A (Continued)

Literal sentences, list A	Literal sentences, list B
A slice of tomato topped the salad	A whole tomato was brought from the garden
A towel hung neatly on the rack A wedge of watermelon was served	A crumpled towel was on the floor A big watermelon grew in the garden
Uncooked spaghetti noodles were near the stove	A mound of cooked spaghetti was on the plate

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