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Research Article

RIGHT-HEMISPHERE MEMORY SUPERIORITY: Studies of a Split-Brain Patient

Janet Metcalfe, Margaret Funnell, and Michael S. Gazzaniga²

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Abstract—Six experiments explored hemispheric memory differences in a patient who had undergone complete corpus callosum resection. The right hemisphere was better able than the left to reject new vents similar to originally presented materials of several types, including abstract visual forms, faces, and categorized lists of words. Although the left hemisphere is capable of mental manipulation, magnation, semantic priming, and complex language production, these functions are apparenently linked to memory confusions—confusions less apparent in the more literal right hemisphere. Differences between the left and right hemispheres in memory for new schematically consistent or categorically related events may provide a source of information allowing people to distinguish between what they actually witnessed and what they only inference.

People are indisputably able to interpolate, make inferences. and imagine plausible scenarios that fit with what they perceive However, they frequently commit false alarms on new schemaconsistent or categorically related events, thinking that they had actually been presented (Bartlett, 1932, Loftus, Donders, Hoffman, & Schooler, 1989, Mandler, 1984) Many studies have been directed at how people distinguish real events from those that were only inferred or imagined. This research (Johnson, Foley, Suengas, & Rave, 1988, Schooler, Gerhard, & Loftus, 1986) indicates the importance of the clarity of the retrieved representations, the amount of sensory information or detail present, and memory for the cognitive operations. Here we suggest that people may have an additional source of information-a hemispheric difference in memory for unpresented related material. Our hypothesis is that the left hemisphere encodes and stores not only the events that it experiences in the world, but also the interpolations, extrapolations, and inferences that it adds. Thus, it will "remember" items related to the presented events as well as the presented events themselves The right hemisphere, being less capable of generalization and inferences, tends not to store them and hence does not retrieve them. It will, therefore, exhibit more vendical memory, particularly within a certain range of relatedness to the presented events

Several studies lend credibility to our hypothesis Phelos and Gazzanga (1992) showed spill-brain patients a sequence of sides of a schematic event—of a woman baking cookies, for example: Twenty slides of this schema were shown, free field, for 3 s each. The recognition test probes included the 20 ids slides, 20 schema-consistent new slides (of the same woman baking cookies), and 20 new slides that were unrelated to the

schematic event. There were no hemispheric differences in responses to either the exact old items or the nonschematic new items. However, the left hemisphere tended to accept new schema-consistent slides, whereas the right hemisphere tended to reject them.

Although these results are suggestive, there are difficulties in interpretation. First, the patients may have treated the test as a classification task. Although the patients were asked for literal recognition-whether the slides were old or new-they may have thought they were being asked whether the shdes were schematically consistent with the material they had studied Under this assumption, saving "ves" to the new schemaconsistent slides was correct, and the left hemisphere was simply better than the right. Such results might have no bearing on memory differences. Second, the right-hemisphere superiority might have been attributable to the pictorial materials. Many studies have shown left-hemisphere specialization for language functions and right-hemisphere specialization for visual-spatial functions (Bogen & Gazzaniga, 1965, Gazzaniga, Bogen, & Sperry, 1962, 1965, Gazzaniga & Sperry, 1967, Kosslyn, 1987, LeDoux, Wilson, & Gazzaniga, 1977, McCarthy & Warrington, 1990, Milner, 1965). Our hypothesis about differential memory for events related to the target event is orthogonal to the visualverbal differences. In the experiments that follow, we address both of these interpretive difficulties in Phelos and Gazzaniga's (1992) seminal study

Converging evidence bearing on our hypothesis comes from a study of the N400 event-related potential in split-brain patients (Kutas, Hillyard, & Gazzaniga, 1988) The N400 does not occur when two highly related words occur together, but is produced, in a graded manner, with decreasing degrees of relatedness. Kutas et al. (1988) found that provided the patient had no language production from the right hemisphere, the left hemisphere but not the right hemisphere produced N400 responses. The authors interpreted this finding as indicating that the left hemisphere but not the right hemisphere is sensitive to differences in semantic similarity. If so, then the left hemisphere should show semantic priming with related stimuli to a greater extent than should the right hemisphere, and it does (Beeman et al., 1994, Experiment 2) If activation by similarity is triggered more strongly in the left hemisphere than the right. then the left but not the right hemisphere might tend to treat events that are similar to presented events as if they had actually occurred Furthermore, Marsolek, Kosslyn, and Squire (1992) showed a right-hemisphere priming advantage based on exact physical matches. These results are consistent with our hypothesis that the right hemisphere may be better than the left on vendical information, whereas the left hemisphere generalizes over and (incorrectly) remembers related information Some researchers however, have suggested that the right

Address correspondence to Janet Metcalfe. Department of Psychol. 1255 over and (Incorrectly) remembers related information ogy. Dartmouth College. Hanotyphyllb 8356-167991-8955816901. con 1991 1891-96487-1992, pays by the seat of inferential processing. Berman dartmouth edu

(1993) tested reaction time to unpresented words that would | have been reasonable inferences in stones. Normal subjects exhibited equal priming to inference words and presented words Patients with right-hemisphere damage showed less priming to the inference words than to the presented words Similarly, Brownell, Michel, Powelson, and Gardner (1983) showed that right-hemisphere-damaged patients chose mappropriate punch lines for jokes, suggesting an affective impairment and possibly a decreased ability to appreciate violations of expectations. In both of these studies, though, damage to the right hemisphere may have had its deleterious effects by distorting the input to the left hemisphere and hence altering its performance. The split-brain nations studied here has completely disconnected hemispheres and does not have such potentially distorted input. In addition, little can be concluded from experiments not including a matched left-hemisphere-damaged group, such a group might have shown even more severely impaired processing. Indeed, Bihrle, Brownell, Powelson, and Gardner (1986) showed that left-hemisphere-damaged patients also responded inappropriately (excessively literally) to jokes Similarly, Chiarello and Church (1986) studied similarity judgments in both left- and right-hemisphere-damaged patients on rhyme, visual similarity, and meaning tasks. Although the righthemisphere-damaged patients showed some impairment on the semantic task, they were less impaired on all tasks, including the semantic task, than were the left-hemisphere-damaged patients

Chiarello, Burgess, Richards, and Pollock (1990) found that closely related pairs of words, such as bee-honey or doctornurse, produced more priming in the left hemisphere than in the right However, marginally similar word pairs, such as deerpony, tested at 500 ms revealed no priming in the left hemisphere and a small priming effect in the right hemisphere. Similarly, Beeman et al. (1994) found a small right-hemisphere priming advantage for remotely related words. The result was fragile, though, and was not replicated in their second experiment Burgess and Simpson (1988) found that although both hemispheres revealed automatic priming to the dominant meaning of a word (with the left hemisphere showing more priming than the right), only the left hemisphere produced controlled priming indicated by first facilitation but then (by 750 ms) inhibition of the nondominant meaning. This inhibition is considered to be fundamental for the lexical disambiguation needed for comprehension. The possibility that the inhibition process occurs only or primarily in the left hemisphere deserves further investigation. We are not suggesting that the right hemisphere does no priming and makes no inferences, only that it may do less than does the left hemisphere

Either because the left hemisphere stores inferences but the right tends not to, or because the left hemisphere keeps some record of primed related events but the right tends not to, we expected the left hemisphere to show less veridical memory for events than the right. In particular, we expected that the right hemisphere, to a greater extent than the left, would correctly reject lures that were highly similar to presented events

THE PATIENT

JW is a 41-year-old, right-handed male who underwent a

endensy 10 testing in 1989 showed a verbal score of 97, nerformance IQ of 95, and Memory Quotient of 102 (Tramo & Bharucha, 1991) Midsaggital magnetic resonance imaging has confirmed surgical report and the psychological evidence indicating complete callosal section. This patient has been the subject of extensive and demanding studies, and his results on a variety of tasks have been reported (Gazzaniga, Holtzman, Deck, & Lee, 1984, Gazzaniga & Smylie, 1984, Luck, Hillvard, Mangun, & Gazzaniga 1989, 1994, Reeves, 1991, Sidtis, Volne, Holtzman, Wilson, & Gazzaniga, 1981)

EXPERIMENT 1 RECOGNITION MEMORY AND CATEGORIZATION OF ABSTRACT PATTERNS

In Experiment 1, we used the classic classification paradigm of Posner and Keele (1968), which has formed the basis for several decades of experimental research and modeling efforts on categorization and its relation to recognition memory (e.g., Homa, Goldhart, Burrel-Homa, & Smith, 1993, Metcalfe & Fisher, 1986, Nosofsky, 1988) Testing classification as well as recognition was important because a classification strategy had been a possible mitigating factor in Phelos and Gazzaniga's (1992) results

Method

Materials

A prototype was formed by having the computer randomly determine six dot locations that were joined by straight line segments. Category exemplars were generated by describing a Gaussian distribution of standard deviation 15 pixels around the vertices of the prototype, and joining these displaced dots. Different categories were constructed by allowing the central tendency prototypes to be randomly assigned afresh. New out-ofcategory lures were formed by assigning six dot locations at random and joining the dots

Procedure

In the study phase, the patient was shown, via computerized display, four exemplars from Category A and four from Category B (with "A" or "B" drawn on the computer screen under each) Each to-be-remembered pattern was displayed center field for 10 s, and the nationt was free to move his eyes about so that the stimuli were registered in both hemispheres. In the test phase, he fixated a central dot, and the test patterns-eight old exemplars, four new category exemplars (not presented at study), two prototypes, and two extracategorical lures---were flashed to the left or right visual field, randomly chosen, for 150 ms each. With the hand insulateral to the test pattern, the patient pointed to "old" or "new" on the computer screen to indicate recognition and to "A," "B," or "neither" to indicate classification After a practice session, the patient completed five 2-hr testing sessions with 10 such trials in each, for a total of 50 trials

Design

The experiment was a higher sphere) × 4 (probe type protwo-stage callosotomy 12 years ago for treat any feet and the company of the comp (sessions) × 10 (trials) design with two main dependent measures, recognition and classification Proportions entered into the analyses of variance were computed by calculating a proportion correct across macroblocks consisting of five trials each

Pretesting of normal subjects

To determine whether the similarities of the exemplars were in a range to allow discrimination between the old and new exemplars, we pretested 38 right-handed Dartmouth College students on 10 trials of this task. Though the procedure was identical to that used with JW. they showed no lateralization deficials. They called the old exemplars old 60% of the time, and the new exemplars old 42% of the time.

Results

Recognition

Although there was tittle hemispheric difference in recognition on either the old or the new exemplars, there was a night-hemisphere advantage on the extracategory litres (see Fig. 1). The interaction between hemisphere and probe type was significant, F(3,27)=10.027, $MS_c=0.007$, $\rho=0.00$. A Tukey test showed right-hemisphere superiority on correctly rejecting the extracategory litres. The right hemisphere was 18% more accurate than the left on these probes. The effect of probe was also significant, F(3,2.77)=10.4991, $MS_c=0.018$, $\rho=0.000$.

Categorization

If the patient called a probe new, he always said it belonged to "neither" category on the classification task. We considered

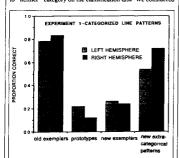


Fig 1 Results of the recognition memory test in Experiment 1 Exemplars from two categories of abstract patterns were presented in the study phase Proportion correct on the recognition test is plotted for old category exemplars, prototypes, new carecopy exemplars, and extracate/gov/dat/patto/fig/ID SS_SSAGED

It mappropriate to analyze classification probabilities including the items that were called new because he never true to classify them, and because differences in classification performance might be distorted by different probabilities of calling the items new We therefore analyzed categorization performance only on category members that were called old in recognition. There were too few data points for analysis of the prototypes and unrelated lures, so only old and new exemplars were used. The right hemisphere showed better performance on the classification task than did the left, F(1,9) = 10 986, $MS_x = 0$ 017, p = 009 In the right hemisphere, the probabilities of correctly classifying the old exemplars and new exemplars were, respectively, 753 and 749, in the left hemisphere, the probabilities were 595 and 630

Discussion

The night hemisphere was better than the left at rejecting lures similar to the presented maternals. Because classification was better in the right hemisphere than the left, the experiment is not open to the criticism that the apparent lieft-hemisphere memory inferiority was really derived from a left-hemisphere classification superiority. However, we had expected that the effect would show up with the new within-category exempliars rather than with the unrelated lures. Unlike the pretested students, J. W showed poor discrimination between the old and the new exempliars. We thought that this difficulty might account for the difference in which lures revealed the right-hemisphere superiority in our experiment as compared with that of Phelps and Gazzaniga (1992).

EXPERIMENT 2 RECOGNITION MEMORY OF A SINGLE CATEGORY

To attam better discrimination between the old and new exemplars, we assigned patterns five vertices instead of six and increased the spread on the distortions from 15 to 20 pixels. We also tried to reduce variability by including more observations per trial on the critical probes, and to reduce test interference by including only one category at time of study and conducting only the yes/no recognition test.

Method

On each of the 19 Irrals (conducted over three sessions), J W studied six random pattern stimuli from a single category, they were presented center field for 3 s each. He was then tested for recognition in each hemisphere with the six old patterns, six new within-category patterns, and six new five-vertex patterns.

Results and Discussion

The right hemisphere showed superior recognition memory to the left, $F(1,18) = 6\ 241$, $MS_0 = 0\ 028$, p = 022 The effect prototypes, new called from pss. sagepub 0.03739 UNBOC ALFG0R*9/hows, the superior performance SANTA BARBARA on March 16, 2012

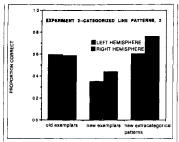


Fig 2 Results of the recognition memory test in Experiment 2 Exemplars from one category of abstract patterns were presented in the study phase Proportion correct on the recognition test is plotted for old category exemplars, new category exemplars, and extracategorical patterns

of the right hemisphere was apparent with both the new withincategory exemplars and the new lures. Thus, decreasing the within-category similarity resulted in a right-hemisphere advantage on the new exemplars, and the new "unrelated" patterns were apparently still similar enough to the presented patterns to produce the right-hemisphere memory superiority.

EXPERIMENT 3: RECOGNITION MEMORY FOR FACES

In Experiment 3, we investigated memory with a different class of materials—photographs of faces. The hypothesis was that the left hemisphere would have a high rate of false alarms to faces that were highly similar to the presented faces, and the right hemisphere, having a more vendical memory, would correctly reject the highly similar new faces. There is a considerable literature showing a general superiority of the right hemisphere on face perception (e.g., Schweinberger & Sommer, 1991, Weddell, 1989), but it is not directed at this particular aspect of the memory effect.

Method

The stimuli were images of children's faces. Half were pictures of individual faces (singles), whereas half were composites, that is, superimposed images of two faces. Having studied a list of single faces, students called old singles old 80 2% of the time, composites constructed from old singles ("old" composites) old 33 2% of the time, new singles old 3 6% of the time, and composites constructed from new singles old 47% of the time (Metcalfe, 1993). Thus, we thought that the old composites might be in the range of similarity with the old composites might be in the range of similarity. Single the composites might be in the range of similarity.

On each trial, J W studied four faces for 5 s each. He then fixated a central dot, and the test probes—old singles, old composites, new singles, and new composites—were flashed for 200 ms each, the time it took the computer to paint the image on the screen. Proportions were based on the four probes in each condition, and there were seven trials.

Results and Discussion

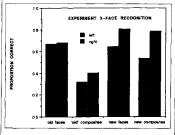
The right hemisphere showed superior memory performance, F(1,6) = 5.487, $MS_e = 0.042$, p = 0.26 Figure 3 shows that the right-hemisphere memory superiority is not attributable to the old faces, but rather to all of the lures. Unlike the college undergraduates, J W showed very poor discrimination between the old singles and the old composite of

EXPERIMENT 4 MEMORY FOR WORDS, 1

Does the superior performance of the right hemisphere in the first three experiments merely reflect a general right-hemisphere superiority for pictorial materials? To address this question, we used words as the stimuli in Experiments 4 and 5. J W is one of a few split-brain patients with a right hemisphere that is capable of recognizing and comprehending a good vocabulary On a modified Peabody Picture Vocabulary Test, J W 's left hemisphere consistently scored higher than the right (left visual 133, auditory 131, right visual 105, auditory 109), but both hemispheres were above the standardized norms for 18-year-olds (Gazzaniga, Smylie, Baynes, Hirst, & McCleary, 1984)

Method

The materials consisted of words from 33 categories of the Toronto Categorized Word Pool (Murdock, 1968) Words were



gies ('oid Composid) 3 6% of the time, gies old 4 7% of the at the old composites 1820 fc of the composites 1820 fc of the composites 1820 fc of the composites constructed from pairs of old singles ("oid" composites constructed from pairs of old singles ("oid" com-SANTA BARBARA of THE OF TH

selected to be short, concrete, and likely to be comprehensible by JW's ngth themsphere On each of the II trusls, the computer presented six words from Category A and six words from Category B for 2 s each. Then test words (six old and six new words from each category, and six new words from a different category) were flashed randomly to the left or right visual field, at 22 to 5° of visual angle, for 150 ms each. The patient indicated whether the word was old or new, and whether it was a word from Category A, Category B, or nether category

Results

The interaction between hemisphere and test probe on recognition was significant, F(2,20)=23 099, $MS_e=0$ 014, p=000 (see Fig. 4) The 28 7% difference in rejection of the within-category lures, showing right-hemisphere superiority, was significant by a Tukey test

As in Experiment 1, when J W called an item new, he always said it belonged to neither category, so only items that were called old were analyzed for classification Classification was the same in the left hemisphere (877) and the right (874). There was a small advantage for the old over the new category exemplars, F(1, 10) = 5.724, $MS_c = 0.012$, p = 0.38, but this effect of probe type did not interact with hemisphere Thus, it appears that the observed differences in recognition were not attributable to a classification difference in this task with these materials.

Discussion

We thought that the slight (and nonsignificant) advantage that the left hemisphere showed on the recognition of the outof-category items (see Fig. 4) might have resulted because the right hemisphere was less able than the left to perceive the test

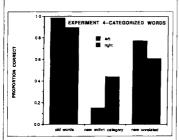


Fig 4 Results of the recognition memory test in Experiment 4 Words from two categories were presented in the study phase Proportion correct is plotted for old, words, new words that are members of the studied categories, and few in the studied categories, and few in the studied categories.

words (see Baynes & Gazzanga, 1988) If J W was sometimes unable to perceive the words in his right hemisphere, he would presumably have to guess, which would tend to produce a reduced hit rate on the old items and an increased false alarm rate on the lures—the pattern found in the data.

EXPERIMENT 5 MEMORY FOR WORDS, 2

Experiment 5 was conducted as a replication of Experiment 4, and in an attempt to equate the perceptibility of the test words in the left and right hemispheres

Method

The procedure was the same as in Experiment 4, except that the test probes were presented for 200 ms to the right hemisphere, and for 60 ms to the left hemisphere. The experiment was conducted 8 to 10 months after Experiment 4, and used different randomizations of word orders.

Results and Discussion

As is shown in Figure 5, there was a 34 9% (significant by a Tukey test) difference favoring the right hemisphere in rejecting the within-category lures. The interaction between hemisphere and probe type was significant, F(2, 20) = 19.762, $MS_c = 0.00$, p < 0.00. In the right hemisphere, correct classification of the old exemplars (924) and new exemplars (906) did not differ, nor did classification of the old exemplars (903) differ in the left hemisphere (all classification).

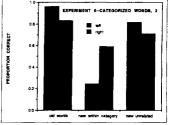


Fig. 5 Results of the recognition memory test in Experiment 5 Words from two categories were presented in the study phase. In the test phase, the amount of time test items appeared differed for the two visual fields in an attempt to equate the ability of JW 's two hemispheres to read the words 'Proportion correct is plotted for july angles, new words that are members of the studied visual points, and the firmclated words

cation $F_5 < 1$) As in the previous experiments, there was a right-hemisphere superiority on the closely related lures

GENERAL DISCUSSION

Although these five experiments all showed a righthemisphere memory advantage, the location of that advantage showed up on the within-category lures in Experiments 4 and 5. but primarily on the so-called unrelated lures in Experiments 1 through 3 The reason for this apparent discrepancy seems to be that I W could not distinguish the "related" lures from the presented stimuli in Experiments 1 through 3, as an analysis of hits minus false alarms illustrates (see Table 1) The new "unrelated" dot patterns and faces can be considered as belonging to the same preexisting classes as the presented stimuli dot patterns with the same number of vertices as the targets, faces of children in the same age group (which J W commented were all "cute little blond kids") From this perspective, there is no discrepancy among experiments. The critical stimuli for the right-hemisphere advantage in veridical memory appear to be items that are distinguishable from but in the same class as the targets

EXPERIMENT 6 LATERALIZED WORD KNOWLEDGE

The words in Experiments 4 and 5 were selected to be those we thought J W 's right hemisphere could understand. Never- mance on the matches (927 correct) was better than on the

theless, comprehension may have been worse in the right than the left hemisphere, resulting in the slight left-hemisphere advantage observed on the extracategorical lures and old items We investigated this possibility in Experiment 6, which also examined hemispheric confusions within category. Tulving (personal communication, 1993) suggested that our results might not be attributable to memory. Perhaps the left hemisphere simply confuses within-category members whereas the right hemisphere does not

Method

J W was shown 3.552 pictures depicting the referents of 296 words (both the targets and the within-category lures) that had been used in Experiments 4 and 5. After viewing a picture, he was presented with either the correct word (match condition) or a within-category lure (mismatch condition) for 150 ms to either the left or right hemisphere. In the mismatch condition, for example, he might see the picture of a pear followed by the word apple. He then had to point to "ves" (same) or "no" (different) with the hand ipsilateral to probe presentation

Results and Discussion

The left hemisphere (910) was better than the right (827) at this task, $F(1, 295) = 68\ 202$, $MS_c = 0\ 030$, p = 000 Perfor-

Table 1 Proportion of hits minus proportion of fulse alarms for Experiments 1 through 5

	Hemisphere			
Comparison condition	Left	Right	Right - left	
Experiment I				
New dot patterns	322	552	230	
Unpresented within-category patterns	047	072	025	
Experiment 2				
New dot patterns	202	351	149	
Unpresented within-category patterns	- 053	026	079	
Experiment 3				
Old composite	- 012	083	095	
New single	310	488	179	
New composite	202	464	262	
Experiment 4				
Unrelated words	758	500	- 258*	
Within-category words	136	333	197	
Experiment 5				
Unrelated words	789	546	- 244*	
Within-category words	205	424	220	

Note In each experiment, the hits were calculated as the proportion of studied items that were recognized correctly. The false alarms were calculated separately for each condition as the proportion of nonstudied items that the subject incorrectly indicated he had seen previously

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[&]quot;These differences favoring the left hemisphere are apparently attributable to superior word knowledge in the left hemisphere, as is shown by Experiment 6

mismatches (810 correct), F(1, 295) = 63 399, MS_x = 0 064, p = 000 The interaction between condition (match vs mismatch) and hemisphere was significant, F(1, 295) = 4 339, MS_x = 0 028, p = 038, but in the direction opposite to that of the memory task, the left hemisphere was more likely than the memory task, the left hemisphere was more likely than the might to incorrectly state that plum had been presented, when the words in the list included apple and peach (but not plum) in the knowledge task, in contrast, the left hemisphere was less likely than the right to incorrectly say "yes" to the word plum when shown a picture of an apple or a peach (See Table 2) The high false alarm rate on the unpresented schematically consistent items seen in earlier experiments appears to be a genume memory effect. A priori knowledge differences are in the wrong direction to account for it.

We reanalyzed Experiments 4 and 5 using those words on which J W made no more than one (out of a possible 12) error in Experiment 6 The results are shown in Table 3. The effect of probe type was significant, F(2, 18) = 53 106, $MS_c = 0$ 028, p = 000, as was the interaction between probe type and hermsphere, F(2, 18) = 17 262, $MS_c = 0$ 013, p = 000 There was a trend toward an overall man effect favoring the right hermsphere, F(1, 9) = 2 719, $MS_c = 0$ 011, p = 06, one-tailed Tukey texts showed no hemispheric differences on the old terms or the new out-of-category lures—favoring the right hemisphere—was stendicant

CONCLUSION

These six experiments provide evidence that the right hemisphere stores more exact memory traces than does the left hemisphere Human cognition includes generalizations, conjectures, inferences, and fantasies, all, presumably, being enacted primarily in the left hemisphere. Such a complex cognitive organism would be vulnerable to mistaking constructed mental events for memones of external events were it not for a system that (a) tends not to enact these complex operations, (b) does not store the results, and hence (c) is not confused by them. We suggest that it may be that this more vendical right-hemisphere memory system may have a critical adaptive function—allowing the interpretations, interpolations, and inferences of the left hemisphere while still maintaining an accurate record of the past

Table 2 Proportions of correct responses in Experiment 6, by hemisphere and condition

Hemisphere		
Left	Right	
958	895	
862	758	
	Left 958	

Table 3 Reanalysis of Experiments 4 and 5 Proportions correct using data for only those words on which the patient made no more than one error in Experiment 6

Condition	Hemisphere	
	Left	Right
Old words	968	856
New within-category words	229	518
New unrelated words	760	717

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