Results

Allocentric WM. There was no difference between lesioned and control rats; i.e., there was an equal proportion of rats from the two groups in the target quadrant (saline, 100%; lesioned, 80%, n.s.).

Egocentric WM. Lesioned rats were less frequently found in the target quadrant compared to control rats (saline, 50%; lesioned, 9%, χ^2 (17.67, $df = 1$), $p < .00003$). Lesioned rats were neither found in the previous trial's target quadrant. Rather, 9/11 (88.1%) of the lesioned rats were found in the starting quadrant.

Discussion

We found no difference between control and lesioned rats in the allocentric WM while mPFC rats were impaired in the egocentric WM. In the egocentric WM test, behavioral analysis showed that lesioned rats were neither located in the previous trial's target quadrant, suggesting that they also did not use an allocentric navigation strategy as an alternative. The fact that they were located back in the starting quadrant could suggest that rats with a lesion of the mPFC are not capable of correcting a deficient navigational strategy as it is being elaborated and that they choose to home the starting position upon navigational strategy difficulties.

REFERENCES

de Bruin, J. P. C., Swinkels, W. A. M., & de Brabander, J. M. (1997). Response learning of rats in a Morris water maze: Involvement of the medial prefrontal cortex. *Behavioural Brain Research,* **85,** 47–55.

Hemispheric Processing Asymmetries: Implications for Memory

Margaret G. Funnell, Paul M. Corballis, and Michael S. Gazzaniga

Center for Cognitive Neuroscience, Dartmouth College

Recent research has demonstrated that memory for words elicits left hemisphere activation, faces right hemisphere activation, and nameable objects bilateral activation. This pattern of results was attributed to dual coding of information, with the left hemisphere employing a verbal code and the right a nonverbal code. Nameable objects can be encoded either verbally or nonverbally and this accounts for their bilateral activation. We investigated this hypothesis in a callosotomy patient. Consistent with dual coding, the left hemisphere was superior to the right in memory for words, whereas the right was superior for faces. Contrary to prediction, performance on nameable pictures was not equivalent in the two hemispheres, but rather resulted in a right hemisphere superiority. In addition, memory for pictures was significantly better than for either words or faces. These findings suggest that the dual code hypothesis is an oversimplification of the processing capabilities of the two hemispheres.

Observations of patients with unilateral brain lesions hint at a multitude of functional asymmetries between the two hemispheres of the brain. Paul Broca first noted the left hemisphere's dominance for language after an autopsy on his famous aphasic patient, Tan. Other syndromes resulting from unilateral brain damage also sparked interest in the specialized functions of the two cerebral hemispheres. Patients with right parietal damage would ignore the right half of visual space and, to the amazement of their families and doctors, might only dress one half of their bodies or put makeup on the right side of their faces. These types of startling patient profiles led many researchers to begin to think about functional differences between the two hemispheres.

Research with patients who have undergone surgical separation of the two cerebral hemispheres, so-called "split-brain" patients, has confirmed and extended many of the findings from lesion patients and revealed much about the specialized functions of the two hemispheres. Early investigations confirmed the left hemisphere's specialization for language and demonstrated the right hemisphere's superiority for visuospatial functions. These differences in the way that the two hemispheres process information have potential implications for the way information is encoded. The two hemispheres might "remember" different aspects of events and split-brain patients might demonstrate deficits in various memory tasks. Although early studies demonstrated that callosotomy does not result in any general decrement in memory, subsequent research revealed specific memory functions that are affected by hemispheric separation. Phelps, Hirst, and Gazzaniga (1991) demonstrated that although callosotomy patients are not impaired in recognition memory, they are impaired in free recall. They speculate that the two hemispheres process and store different aspects of events, and therefore disconnecting the two hemispheres results in a degradation of the resulting mnemonic representation.

A number of researchers have further investigated the effect of hemispheric processing differences on memory. Kroll and colleagues tested callosotomy patients on memory for different types of stimuli (Jha, Kroll, Baynes, & Gazzaniga, 1997). They found that callosotomy patients are not impaired on verbal memory tasks, but do demonstrate significant deficits in memory for pictorial information. The authors conclude that the left hemisphere encodes the elements of verbal memories independently of the right hemisphere whereas memory for pictorial information requires integration between the two hemispheres. Consequently, callosotomy is detrimental to memory for pictorial information but not verbal information. This finding is consistent with previous research demonstrating differences in verbal and nonverbal memory in patients with unilateral brain lesions (Kroll, Knight, Metcalfe, et al., 1996).

Recent research by Kelley and colleagues is consistent with the idea of a dual coding of stimuli (verbal and nonverbal). They investigated the neural substrates of memory encoding using functional brain imaging (Kelley, Miezin, McDermott, et al., 1998). Subjects were presented with words, line drawings of common objects, and pictures of unfamiliar faces and asked to try to remember them for a subsequent memory test. Each category of stimuli elicited activation in dorsal frontal regions, but the lateralization of the activation differed depending on the type of stimuli being encoded. Encoding of words resulted in left frontal activation whereas encoding of faces resulted in right hemisphere activation. The line drawings of common objects, however, resulted in bilateral activation. The authors conclude that the left hemisphere is dominant for encoding of verbal information, whereas the right is superior for nonverbal encoding. Pictures of nameable objects can be encoded both visually and verbally, so both hemispheres have a mechanism available for encoding of this class of stimuli.

Based on these findings, it would be expected that the left hemisphere of split-brain patients would be superior to the right in memory for verbal information, whereas the right hemisphere would be dominant in memory for unfamiliar faces. There should be no significant difference between the two hemisphere in memory for line drawings of common objects since these can be encoded both visually and verbally. These predictions were tested in a series of experiments with a patient with a complete callosotomy.

Methods

Callosotomy patient J.W. participated in the reported experiments. J.W. is a 46-year-old right-handed man who underwent two-stage resection of the corpus callosum for the relief of intractable epilepsy in 1979. Further details of his medical history can be found in Gazzaniga, Nass, Reeves, and Roberts (1984).

The study sets consisted of 10 items presented center field for 3 s each. There was a 1.5-s interval between study items. Following each study set, there was a 4-min interval in which J.W. was asked to make simple visual discriminations as part of a separate experiment. J.W. was then presented with a test set which included the 10 items he had studied and 10 new items. Each item appeared once in the right visual field and once in the left, resulting in a total of 40 items in the test set. On each trial J.W. indicated whether he recognized the item as belonging to the study set by pressing a button on the computer keyboard.

J.W. was seated approximately 57 cm in front of a computer screen and told to fixate a central cross-hair. Stimuli were flashed to either the right (RVF) or left visual field (LVF) for 150 ms to ensure that stimuli are perceived only by the hemisphere contralateral to the visual field of the presentation.

There were a total of six study/test sets: two each of pictures, faces, and words. The pictures and words were taken from the set published by Snodgrass and Vanderwart (1980). The faces were provided courtesy of M. J. Tarr (Brown University, Providence, RI). J.W. was tested on each set four times, with at least 1 week between each testing session. The hand used to respond was counterbalanced between blocks.

Results and Discussion

Only responses made with the hand ipsilateral to the stimuli were analyzed. In other words, for left-hand blocks only responses to left-visual-field stimuli were included in the analysis and vice versa. This helped to ensure that the stimulated hemisphere generated the response. J.W.'s response accuracy for stimuli presented to each visual field in each task is shown in Fig. 1.

Because this experiment involves analysis of data collected from a single observer in which each hemisphere serves as a control for the other, statistical tests were carried out on J.W.'s responses using a hierarchical χ^2 analysis (Winer, Brown, & Michels, 1991). The factors in this analysis were Condition (old vs new), Response ("old" vs "new"), Visual Field (LVF vs RVF), and Task (pictures vs words vs faces). In this analysis, response accuracy is indexed by the contingency between Condition and Response, and "interactions" involving accuracy are indexed by higher-order contingencies between Condition, Response, and other factors.

The χ^2 analysis revealed a significant contingency between Condition and Response (χ^2 (1) = 90.13, $p < .001$), which indicates that J.W. was performing the memory task accurately overall (overall accuracy = .717). The contingencies between Task, Condition, and Response (χ^2 (2) = 22.82, $p < .001$) and Task, Field, Condition, and Response (χ^2 (2) = 7.35, $p < .05$) were also significant. The first of these reflects different overall levels of response accuracy in the three tasks (pictures, .868; words, .663; faces, .619). The four-way contingency reflects the fact that the effect of visual field on response accuracy was not the same in each task. In the pictures and faces tasks responses were more accurate for LVF stimuli than for RVF stimuli (pictures, LVF = .938, RVF = .800; faces, LVF = .688, RVF = .550). By contrast, in the words task performance was more accurate for RVF stimuli (.725) than for LVF stimuli (.600). Post hoc tests were carried out in which the data from

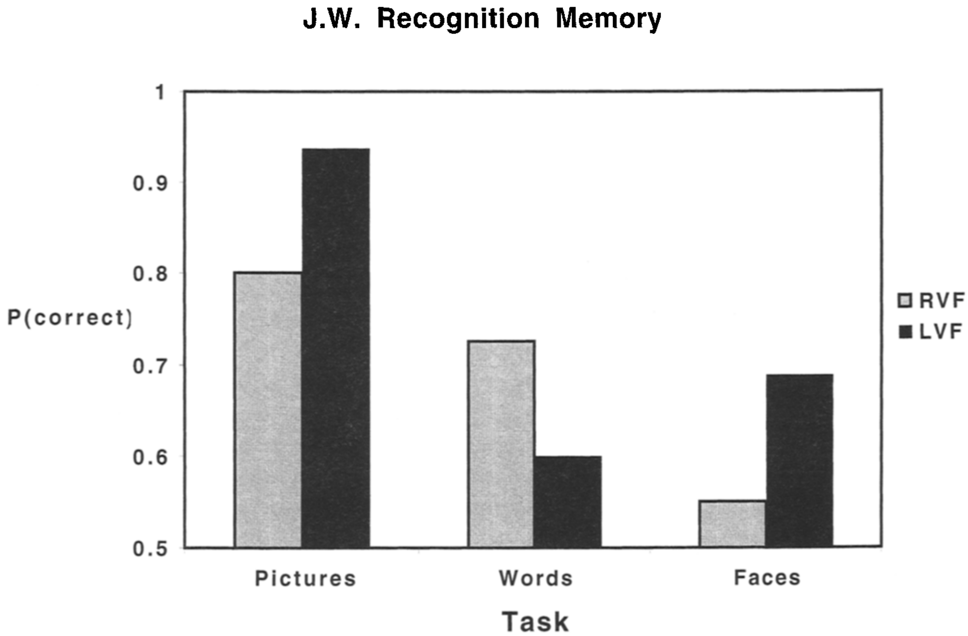

FIG. 1. J.W.'s recognition performance in the pictures, words, and faces tasks. The proportion of correct responses in each task is shown separately for each visual field.

each task were removed from the calculation in turn. This analysis revealed that the four-way contingency between Task, Field, Condition, and Response was statistically significant for the comparisons between the words and pictures (χ^2 (1) = 5.51, $p <$ .05) and words and faces (χ^2 (1) = 5.51, $p < .05$), but not between pictures and faces (χ^2 (1) = 0.00, n.s.). Thus it appears that the original four-way contingency was driven exclusively by the difference between the words task and the other two tasks—the effects of Visual Field on accuracy did not differ between the pictures and faces tasks.

These results suggest that the memory trace for words is lateralized differently from those for faces and pictures. As predicted, memory performance for words is better when the test stimuli are presented to the RVF (left hemisphere) than when they are presented to the LVF (right hemisphere). The opposite pattern was obtained for the faces task and, somewhat surprisingly, for the pictures task. For both these tasks test stimuli presented to the LVF (right hemisphere) resulted in better recognition than stimuli presented to the RVF (left hemisphere). Although pictures were recognized better than faces, the lack of a significant four-way contingency between Task, Field, Condition, and Response for the comparison between pictures and faces suggests that the memory traces are similarly lateralized.

General Discussion

At the outset of the experiment we anticipated that the left-hemisphere specialization for language would result in an advantage for recognizing words. Similarly, we expected that the right hemisphere would exhibit stronger memory for faces. Both these expectations were confirmed. However, we also anticipated that the hemispheres would be equivalent for the pictures task since both verbal and nonverbal codes would be available. Instead, we found that the lateralization pattern of recognition memory for nameable pictures was similar to that for faces, with the right-hemisphere recognition performance superior to the left. Levels of accuracy in both hemispheres, however, were significantly higher for pictures than for either words or faces.

The results of this experiment suggest that a dual-code model may be an oversimplification of the processing capabilities of the two hemispheres. Instead, each hemisphere brings to bear a variety of processing resources, with each contributing to the memory trace. If the left hemisphere had only the verbal code available, then there should be no difference in level of accuracy on words and pictures. The pictures should simply be stored as verbal labels. This, however, was not the case in this experiment. Similarly, if the right hemisphere had only a single nonverbal code available, then there should be no difference in recognition for faces and nameable objects. Because both hemispheres were better able to remember nameable objects than either words or faces, this suggests that each hemisphere has a variety of processing capabilities, and these are reflected in the memory trace for different categories of stimuli.

ACKNOWLEDGMENT

This research was supported by Grants 1 F32 NS10642-01 from NIH to M.G.F., RG 0161/1999-B from the Human Frontiers Science Program to P.M.C., and 1 R01 MH59825-01 from NIH to M.S.G.

REFERENCES

Gazzaniga, M. S., Nass, R., Reeves, A., & Roberts, D. (1984). Neurologic perspectives on right hemisphere language following surgical section of the corpus callosum. *Seminars in Neurology,* **4,** 126–135.

Jha, A. P., Kroll, N. E. A., Baynes, K., & Gazzaniga, M. S. (1997). Memory encoding following complete callosotomy. *Journal of Cognitive Neuroscience,* **9**(1), 143–159.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, M. J., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., & Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron,* **20,** 927–936.

Kroll, N. E. A., Knight, R. T., Metcalfe, J., Wolf, E. S., & Tulving, E. (1996). Cohesion failure as a source of memory illusions. *Journal of Memory and Language,* **135,** 176–196.

Phelps, E. A., Hirst, W., & Gazzaniga, M. S. (1991). Deficits in recall following partial and complete commissurotomy. *Cerebral Cortex,* **1,** 492–498.

Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning & Memory,* **6**(2), 174–215

Winer, B. J., Brown, D. R., & Michels, K. M. (1991). *Statistical principles in experimental design* (3rd ed.). New York: McGraw–Hill.

Imagined and Actual Limb Selection: A Test of Preference

Carl Gabbard and Casi Rabb

Department of Health & Kinesiology, Texas A&M University

Imagined and actual motor performance were compared to determine what factor(s) drive limb selection for programming movements in contralateral hemispace. Forty right-handed blindfolded subjects were asked to 'reach' via auditory stimulus for a small object placed at multiple locations in hemispace. Two conditions were included: arms uncrossed and arms crossed. With the uncrossed condition, responses were similar. With arms crossed, subjects had the choice of keeping the limbs crossed, reacting to proximity, or uncrossing the arms to reach ipsilaterally. In this condition subjects 'imagined' that they would maintain the crossed