THE ROLE OF THE CORPUS CALLOSUM IN THE REPRESENTATION OF LATERAL ORIENTATION

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Abstract—How do people recognize objects when they face in a novel lateral (left/right) orientation? The results of three experiments with a split-brain patient, who has a totally nonfunctional corpus callosum, demonstrate that the corpus callosum cannot play a critical role in allowing one to recognize mirror-reversed objects. First, both cerebral hemispheres could recognize mirror-reversed versions of pictures as accurately as the original renditions in an incidental memory task. Second, when asked to decide whether pictures faced the same way that they had originally, neither hemisphere performed better than chance in an incidental memory task—suggesting that the shape representations in the hemispheres do not specify lateral orientation. Third, neither hemisphere exhibited "priming" for lateral orientation, as assessed in an "object decision task", and only the left hemisphere exhibited priming for encoding the shape (independent of its lateral orientation).

DURING THE EARLY DAYS of computer vision, researchers tried to program computers to recognize objects by matching templates. An object was recognized by finding the stored pattern that had the greatest overlap with the encoded shape. The limitations of this technique became obvious very quickly. Among these limitations was the fact that objects often appear in novel orientations, and the shape of an asymmetric object facing left may overlap only minimally with its shape when it faces right. Nevertheless, humans have no problem recognizing objects even when they face in novel directions. Indeed, we have very poor memory for the lateral orientation of objects (e.g. Refs [3] and [20]). The puzzle remains, how are we able to recognize objects even when they appear in novel lateral orientations (that is, facing to the left or to the right)?

A number of neuropsychological types of answers to this question have been offered. For example, CORBALLIS and BEALE [2] suggested that the process of transferring information across the corpus callosum might engender "mirror-image generalizations" in the cerebral hemispheres. Corballis and Beale theorize that both orientations are encoded in each of the hemispheres: the veridical orientation is encoded during perception, and the reverse image is generated by the homotopic mapping across the corpus callosum. As a second hypothesis, it is possible that each hemisphere has only a single representation, but one of the cerebral hemispheres stores representations of shapes facing left, and the other stores representations facing right.

We investigated these hypotheses by testing a split-brain patient. This patient offers a

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unique opportunity to evaluate these hypotheses because he has no spared fibers in his corpus callosum [18]. Thus, if the corpus callosum is responsible for creating mirror-image representations, then he should have difficulty recognizing objects in reversed orientations if the object is seen by a single hemisphere, but should have excellent memory for orientation in both hemispheres; thus, if the corpus callosum cannot perform this role, each hemisphere should store only a single, viewed, orientation. In contrast, if one hemisphere is specialized to store objects facing left and the other is specialized to store objects facing right, then we should find that each hemisphere effectively processes objects oriented in one direction only.

EXPERIMENT 1

In this experiment we investigated directly J.W.'s ability to recognize pictures when they are in familiar or novel lateral orientations. We began by showing our patient half of the stimuli, and then showed him these stimuli intermixed with the other half of the stimuli. His task was to indicate which pictures were presented during the initial exposure phase. The pictures were lateralized at the time of test, and half of the familiar stimuli faced the way they had during the exposure phase and half faced the opposite way.

If the corpus callosum is necessary for generating the representations that are used to recognize mirror-reversed shapes, then our split-brain patient should perform this task poorly. This procedure not only allows us to examine whether the hemispheres have poor memory for lateral orientation, but also allows us to determine whether the hemispheres preferentially encode different lateral orientations. If one hemisphere more accurately represents a particular lateral orientation, then it should respond faster and more accurately to stimuli in that lateral orientation. Not only should this hemisphere encode that orientation of the test stimuli more effectively, but it also should have encoded that orientation of the study stimuli more effectively (even though they were presented in free view).

Method

Subject. J.W. was 38 years old at the time of testing, with a high school education and FSIQ of 97. Full details of his surgical history are reported elsewhere [18]. He is right-handed with left-hemisphere dominance, although some variable right hemisphere language has been observed. He underwent a two-stage operation with division of 3 cm of posterior callosum (including the splenium) in 1979, followed by complete callosal section after 10 weeks.

Materials. The stimuli were based on the SNODGRASS and VANDERWART [19] pictures, which were reduced to fit within a 4.6 cm width. We selected eight pictures to be presented during the exposure phase of the experiment, each of which had a clear lateral orientation. These pictures were displayed in the center of the computer screen, half facing to the right, and half facing to the left. We created a second set of pictures for use in the test phase. Two versions of each of the eight pictures were then created, one facing left and one facing right. Each of these pictures was then placed 2.6 cm to the left of a centered fixation point, which corresponded to 2.6 of visual angle from the subject's point of view; another set of stimuli was then created, in which the pictures were placed the same distance to the right of a fixation point. During the test phase, all of the pictures were positioned twice (once facing left and once facing right) in the left visual field and twice in the right visual field. This set of 64 pictures was then divided in half such that each half was completely balanced across all conditions. The first half of this set was presented when J.W. responded with his right hand, and the second half when he responded with his left hand.

Procedure. J.W. was seated in front of a Macintosh SE computer, and his chin was placed on a chin rest to maintain a constant viewing distance 57.3 cm from the screen. He began the experiment by using his right hand to press the space bar, at which point instructions appeared on the screen. The experiment began with the exposure phase, which was designed to disguise the nature of the experiment and to ensure that J.W. studied the pictures. J.W. read instructions displayed on the screen, which explained that a picture would appear when he pressed the space bar. The instructions prior to the exposure phase requested him to observe the series of pictures about to be displayed. He was told that these pictures were being presented merely as an orienting exercise, and were not essential to the experiment. The eight pictures were then displayed in the center of the screen, each for 4 sec, with a

1500 msec inter-stimulus interval, and then were presented a second and third time in different orders. No three pictures facing in the same direction were presented in a row.*

After viewing all eight stimuli three times, the computer screen displayed instructions for the test phase. During the test phase, the eight novel pictures were intermixed with the pictures he had seen during the exposure phase, and J.W. was asked to decide whether each picture had been presented in the exposure phase. A trial began with an exclamation mark, which appeared for 500 msec in the center of the screen. An asterisk then appeared for 2 sec, and J.W. was to fixate on the asterisk; he was reminded that he should not shift his gaze from this fixation point at any time during a trial. A picture then appeared for 150 msec in either the right or left portion of the screen (while the asterisk remained). J.W. was to determine, as quickly and accurately as possible, whether the picture had been shown during the exposure phase.

J.W. received two practice trials to familiarize him with the procedure; these practice trials used pictures that were not presented in the exposure or test phases. Following practice, he was asked to fixate on the fixation point, and then received the first 32 test trials.+ He responded by pressing the "B" key to indicate "yes, a picture seen during the exposure phase" and the "N" key to indicate "no, not a picture seen during the exposure phase", using the middle and index fingers of his right hand to make all responses. After he completed these trials, a new set of instructions appeared on the screen. The instructions directed him to respond with his left hand, followed by two practice trials. The last 32 test trials were then presented, which completed the experiment. In each block of trials, the stimuli were presented in a pseudorandom order, such that pictures did not appear in the same visual field or facing in the same direction more than three trials in a row, and the same correct response could not occur more than two trials in a row. Different orders were used in the two blocks. The entire experiment required less than 20 min to complete.

Results

The data were analyzed using analyses of variance with trial as the random effect; the independent variables of interest were hand, visual field, and the lateral orientation ("direction") at exposure and at test. Because we were interested in the relation between the direction at exposure and at test, we only analyzed the response time data from familiar items. Moreover, we focused on trials in which the stimulus appeared on the side of the hand of response (i.e. left visual field and left hand, right visual field and right hand). These trials represent "pure" cases in which the hemisphere that received the stimulus also produced the response. In this and all following experiments, response times greater than 2.5 times the mean of the remaining scores in a cell were treated as outliers. Using this criterion, no outliers were detected in any of the experiments reported here.

The most striking finding is easy to summarize: J.W. made only two errors over the course of the experiment. Given this remarkable performance, we did not conduct inferential statistics on the accuracy data.

We next considered J.W.'s response times. We found that he processed the stimuli more quickly in his right hemisphere (with means of 580 and 418 msec for the left and right hemispheres, respectively) $[F(1, 8) = 8.95, P < 0.02]$. We also found a compatibility effect: If the drawing faced in the same way in the exposure phase and at the time of test, J.W. evaluated it faster than if it faced the opposite way $[F(1, 8) = 7.83, P = 0.02]$. However, this

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*We presented the study stimuli in free view, rather than lateralizing them, for three reasons: First, to evaluate Corballis and Beale's hypothesis, we had to present the stimuli in free view; their theory makes predictions based on the optical and anatomical properties of viewing objects in the central field (as noted above). Second, the present technique seemed more "ecologically valid", allowing us to consider how the system works when it encodes objects in the usual way. Third, if we lateralized the initial exposure condition, we worried that the subject would not be able to encode enough information into memory. If we presented the stimuli for 4 sec, as we did, it is likely that the subject would move his eyes.

+Although we did not monitor J.W.'s eye movements, we had several reasons to be very confident that he did in fact maintain fixation. First, when POSNER et al. [6] did monitor eye position when subjects were asked to fixate on a point in a divided visual field experiment, they found that subjects made anticipatory eye movements very rarely (on only about 4% of the trials). Second, J.W. has participated in many such experiments, and is clearly able to maintain fixation on a fixation point as witnessed by clear laterality effects in many tasks (e.g. left-hemisphere superiority for generating multipart images; see Ref. [7]).

effect was the same in the two hemispheres, $F < 1$ for the interaction between compatibility and hemisphere.

We next analyzed the data by creating a single "same/different" variable, instead of considering direction at exposure and at test as separate variables. This analysis again revealed that J.W. evaluated objects faster when they faced the same way as they had during the exposure phase [$F (1, 12) = 6.76$, $P = 0.02$], and that he processed the stimuli faster in his right hemisphere [$F (1, 12) = 7.73$, $P < 0.02$]. Although we did not discover an interaction between hemisphere and direction compatibility [$F < 1$], we did find that the slowest responses were made by the left hemisphere to stimuli facing in different directions at test and exposure [$F (1, 12) = 12.19$, $P = 0.0044$], for a comparison of this response time with the mean of the others. As illustrated in Fig. 1, J.W.'s left hemisphere required more time to evaluate objects oriented differently at test and exposure than objects in their original orientations [$F (1, 12) = 5.34$, $P = 0.039$]; in contrast, his right hemisphere required comparable amounts of time in both cases [$F (1, 12) = 1.86$, $P > 0.1$].
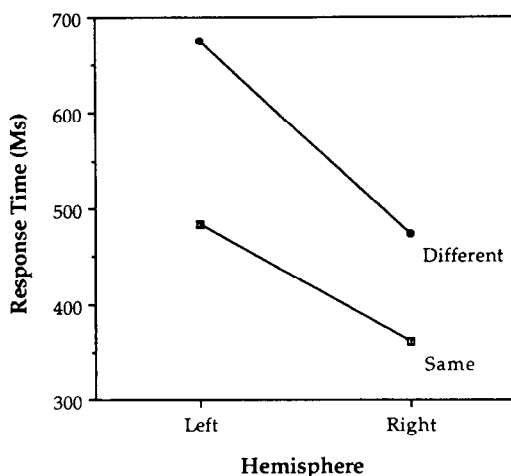

Fig. 1. Response times from Experiment 1 for each hemisphere, when stimuli faced the same or different ways at exposure and test.

Discussion

Perhaps the most interesting aspect of these results is J.W.'s remarkably accurate performance; it was clear that both hemispheres could recognize the familiar objects, regardless of which way they faced. This is good evidence that the hemispheres do not store only a single orientation. It also is good evidence that the corpus callosum does not play a critical role in the formation of the representation of lateral orientation. In this light, any differences in response times between the hemispheres reflect differences in relative efficiency of processing, not absolute specialization.

The stimuli used were easily named, and one might argue that J.W. stored them in a symbolic form. We have two responses to this argument: First, this concern led us to use incidental learning paradigms; the subject was not asked to memorize the stimuli. The instructions in the exposure phase requested him to observe a series of pictures that were being presented merely as an orienting exercise, and were not essential to the experiment. We

know of no evidence that subjects encode only a label in such circumstances. Moreover, if J.W. had encoded a visual representation of the object in a single orientation, this presumably would have influenced the time to encode the stimuli prior to their being named and compared to stored names. Second, J.W. can read and understand language in both hemispheres, but does so more effectively in the left hemisphere [4]. Thus, if he had named the objects, we would have expected a left hemisphere superiority in the task. But we found no such result—indeed he processed the stimuli more quickly in his right hemisphere.

Although the results revealed that J.W.'s right hemisphere could perform the task faster than his left hemisphere, they failed to support the idea that the hemispheres are specialized for representing different lateral orientations. However, we did find evidence that his left hemisphere responded faster when the object faced in its original direction, whereas his right hemisphere did not. This result might hint that the process that matches input to stored representations is sensitive to the representation of the original lateral orientation in the left hemisphere. Alternatively, it might suggest that the left hemisphere includes a representation of the original orientation (perhaps in terms of specific features and their locations) as well as a representation that can be matched by either orientation, whereas the right hemisphere contains only the latter sort of representation.

EXPERIMENT 2

In the previous experiment, the subject only needed to compare the test stimuli to information about the shapes of previously seen stimuli. It is possible that shape and lateral orientation can be dissociated in memory; if so, then differences in how orientation is represented may have little or no effect on shape recognition. In this experiment we showed J.W. a set of pictures during the exposure phase, half of which faced left and half of which faced right. During the test phase, we showed J.W. only pictures that were presented during the exposure phase, but half of the time the pictures faced in the direction they had originally, and half of the time they faced in the opposite direction. We now asked him to decide whether each picture was facing in its original direction. Thus, we now studied explicit representations of lateral orientation per se.

Method

Materials. A new set of eight Snodgrass and Vanderwart pictures was selected, using the same criteria as in Experiment 1. The pictures were prepared for the exposure and test phases exactly as in Experiment 1, without including novel items. We again divided the total of 32 items (eight pictures oriented left and right in each visual field) into two sets, each set completely balanced for orientation and visual field, and presented one set when he was responding with his right hand and the other when he was responding with his left hand.

Procedure. The exposure and test phases were identical to those of Experiment 1, except that J.W. was now asked to determine whether each pictured object was facing the same way, left or right, that it had in the exposure phase of the experiment. This experiment required less than 15 min to complete and was conducted immediately after Experiment 1.

Results

The data were analyzed as in Experiment 1. There were 18 errors out of 32 trials overall, 10 of these for "pure" ipsilateral cases. Hence, we performed an analysis of variance on the error rates for the "pure" cases. J.W. performed equally poorly in both hemispheres [$F < 1$], but he made more errors when the stimuli faced right at test [$F(1, 8) = 18.0, P < 0.003$]. This difference was present within each hemisphere, $P < 0.02$ in each case, and $F < 1$ for the interaction of hemisphere and direction at test.

We also analyzed the response time data, and found an interaction between hemisphere and direction at test $[F(1, 8) = 5.15, P = 0.053]$: the left hemisphere tended to be faster for objects facing right at test $[F(1, 8) = 3.47, P < 0.10]$, but the right hemisphere showed no such trend, $[F = 1.8]$. A compatibility analysis found no evidence of a difference between the hemispheres $[F < 1]$, or of any interaction between hemisphere and direction, $[F < 1.5]$. Thus, the left hemisphere was marginally faster for right-facing than left-facing stimuli and made more errors for right-facing stimuli than left-facing stimuli, which might suggest a speed–accuracy trade-off.

Discussion

The results of this experiment were in sharp contrast to those from the previous one: Both hemispheres performed very poorly, and there was no longer a right hemisphere advantage for the task. In addition, we no longer found a left hemisphere compatibility effect, which belies the idea that the left hemisphere contains a representation of lateral orientation. It is important to note that J.W.'s average response times increased dramatically for this task (they more than doubled for the left hemisphere and more than tripled for the right hemisphere), and he was essentially responding at chance levels of accuracy in both hemispheres; in contrast, he made very few errors in Experiment 1—even though he learned the same number of stimuli in both experiments. These findings suggest that representations of lateral orientation per se were not stored in either hemisphere—even though only eight stimuli were learned.

EXPERIMENT 3

The previous experiments both tapped "explicit" memory. It is possible that the hemispheres differ in their "implicit" memory representations of lateral orientation. Whereas explicit memories can be evoked at will and used in a variety of contexts, implicit memories cannot be voluntarily called up and are embedded in a particular kind of processing (e.g. Refs [8] and [16]). This experiment was designed to investigate hemispheric differences in implicit memory for lateral orientation. We asked our subject to visualize a set of pictures during the exposure phase, and later asked him to decide whether pictures displayed objects or nonobjects. This task does not require memory at all; the subject is never told to recall or otherwise think about the stimuli presented during the exposure phase; indeed, the task is similar to the "object decision task" devised by Schacter and his colleagues to test implicit memory (e.g. Ref. [17]). Some of the test stimuli had been shown previously and some had not. We examined "priming" for stimuli when they were in their previous orientations, which is one measure of implicit memory; priming is inferred when a subject responds more quickly and/or more accurately to the previously exposed stimuli than to novel stimuli. As usual, we lateralized the test stimuli, so that they were presented to a single isolated hemisphere.

Method

Materials. We selected eight additional Snodgrass and Vanderwart pictures to be presented during the exposure phase of the experiment, using the same criteria as before. An additional set of eight novel pictures was added to this set for use in the test phase. Half the pictures to be presented in the exposure phase and half the new pictures were then "distorted" to form nonobjects. We distorted pictures by moving parts to inappropriate locations, as illustrated in Fig. 2. Two versions of each of the eight objects and eight nonobjects were then created, one facing left and one facing right. Each of these pictures was then lateralized as described in Experiment 1, for a total of 64 items. These items were then divided into two sets of 32, and each set was completely balanced for all conditions as described.
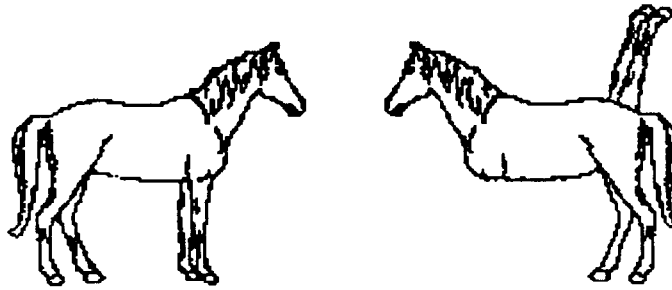
Fig. 2. Examples of the objects and distorted objects used in Experiment 3.

Procedure. The procedure was the same as in the previous experiments, with the following exceptions. First, the exposure phase was altered to further disguise the nature of the experiment and led J.W. to study the pictures. J.W. read instructions displayed on the screen, which explained that a picture would appear when he pressed the space bar. These instructions told him that we were interested in visual mental imagery, and the effects of various kinds of tasks on the vividness of imagery. Thus, we asked him to look at a picture until he felt confident that he could visualize it. When he felt ready, he was to press the space bar again, and the picture would disappear. At this point he was to close his eyes and try to visualize the drawing as vividly as he could. When he felt he had as vivid an image as possible in his "mind's eye", he was to open his eyes and rate the vividness of his image. The ratings were made with a 7-point scale, with "1" indicating that the image was "not vivid at all" and "7" indicating that it was "extremely vivid". After entering his vividness rating by pressing one of the keys at the top of the keyboard, he was to press the space bar for the drawing to reappear. At this point, he was to compare his image to the drawing, correcting his image so that it matched the picture. He then rated the accuracy of his image, again using the top row of the keyboard, with "1" indicating not accurate at all and "7" indicating "extremely accurate". There were two practice trials to familiarize J.W. with these ratings tasks. Half of the pictures faced left and half faced right during the exposure phase.

Second, after viewing all eight stimuli, the computer screen displayed instructions for the test phase. J.W. was to determine whether the picture displayed a real object or a distorted one. Examples of real and distorted objects were shown along with the instructions. J.W. received two practice trials to familiarize him with the procedure; these practice trials used pictures that were not presented in the exposure or test phases. Following this, he received the first 32 test trials and responded by pressing the "B" key for "yes, an object" and the "N" key for "no, not an object", using the index and middle fingers, respectively, of his right hand to make all responses. He was told to respond as quickly and accurately as possible. After he completed these trials, a new set of instructions appeared on the screen. These instructions directed him to respond with his left hand. The second 32 test trials were then presented, which completed the experiment. In each block of trials, the stimuli were presented in a pseudorandom order, using the same constraints as in Experiment 1.

Following the test phase, the exposure phase was repeated with the explanation that we were interested in discovering the effects of the test on the subject's imagery ratings. The entire experiment required approx. 20 min to complete. This experiment was conducted approx. 1 month after Experiment 2, and J.W. later reported that he had no idea that we were interested in the effects of lateral orientation, and indeed had no recollection of the previous experiments.

Results

The data were analyzed as in Experiment 1. J.W. made only three errors out of the total 32 "pure", ipsilateral trials. Thus, we did not analyze his accuracy data in more detail. In our first analysis of his response times, we examined possible effects of hemisphere, direction (at the time of test), stimulus type (object/nonobject), and familiarity (familiar/unfamiliar). This analysis revealed that J.W. was faster when his right hemisphere received the input and produced the response (with means of 792 and 619 msec, for left and right hemisphere trials, respectively) [$F (1, 16) = 14.29$, $P = 0.0016$]. In addition, he evaluated objects faster than nonobjects [$F (1, 16) = 5.29$, $P = 0.035$] and tended to evaluate familiar objects faster than unfamiliar objects, familiar nonobjects, or unfamiliar nonobjects, as reflected in a marginal interaction between stimulus type and familiarity [$F (1, 16) = 3.27$, $P < 0.09$]; a comparison revealed that J.W. did indeed evaluate familiar objects faster than the other types

$[F(1, 16) = 7.85, P = 0.013]$. This finding documents that the exposure phase did in fact prime J.W. However, although we did not find an interaction between familiarity and hemisphere $[F < 1]$, planned comparisons revealed that J.W.'s left hemisphere exhibited priming (with means of 635 and 825 msec for the familiar and unfamiliar objects, respectively) $[F(1, 16) = 4.36, P = 0.05]$, whereas his right hemisphere did not (with means of 554 and 597 msec for familiar and unfamiliar objects) $[F < 1]$.

We also found an interaction between direction, stimulus type, and familiarity, $[F(1, 16) = 4.25, P = 0.056]$: When the test objects faced left, J.W. was fastest for familiar objects, and then for unfamiliar objects, familiar nonobjects, and unfamiliar nonobjects; in contrast, there was no systematic pattern for the conditions in which the stimuli faced to the right. However, as illustrated in Fig. 3, when we subtract the response times for familiar stimuli from those for unfamiliar stimuli, we see that priming varied for the different directions. For left-facing items, objects and nonobjects were primed approximately equally poorly. For right-facing items, objects showed the expected priming effect, whereas J.W. actually evaluated unfamiliar nonobjects more quickly than familiar nonobjects. We found no hint of an interaction between hemisphere, direction, stimulus type, and familiarity $[F < 1]$.
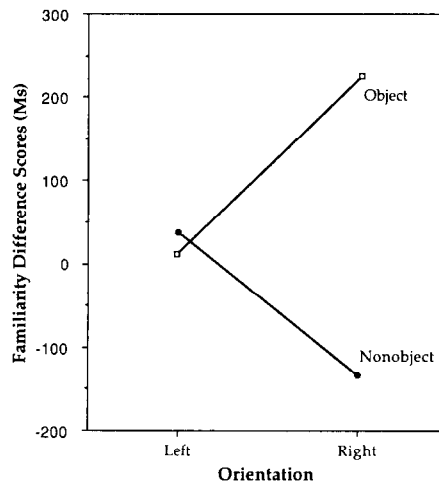

Fig. 3. Response times from Experiment 3, illustrating priming (the difference between familiar and novel objects) in the hemispheres when objects and nonobjects faced left or right at test.

When we considered only the undistorted familiar objects as truly "familiar" stimuli, we again found that J.W. evaluated the stimuli faster when they were presented to his right hemisphere $[F(1, 8) = 27.60, P = 0.0008]$, and evaluated the familiar stimuli faster than the unfamiliar ones $[F(1, 8) = 15.70, P = 0.0042]$. We also found that J.W. required more time to evaluate novel objects than familiar objects in his left hemisphere, $[F(1, 8) = 20.93, P = 0.0018]$, but required comparable amounts of time for the two types of stimuli in his right hemisphere $[F(1, 8) = 1.044]$; this pattern of results was also witnessed by an interaction of familiarity and hemisphere $[F(1, 8) = 6.33, P = 0.036]$. These findings are illustrated in Fig. 4.
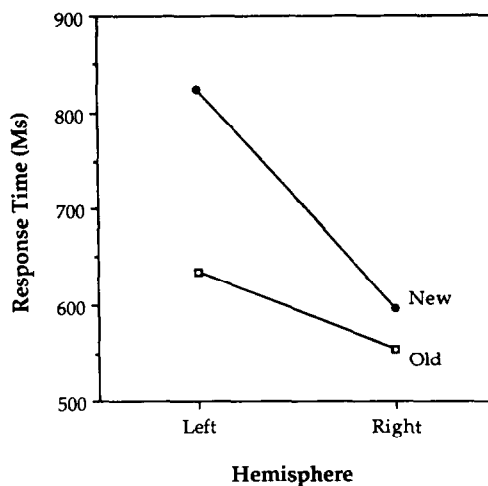
Fig. 4. Response times from Experiment 3, illustrating priming in the left hemisphere to undistorted objects.

Our analysis of the undistorted objects also revealed that J.W. evaluated right-facing familiar objects fastest, and right-facing unfamiliar objects slowest, and required intermediate amounts of time for the left-facing objects, familiar or not; this pattern was documented by an interaction of familiarity and direction at test [F (1, 8) = 12.33, P = 0.0079]. Finally, there was a marginal tendency for the left hemisphere to respond faster to left-facing objects, with no such difference in the right hemisphere, as reflected in a trend towards an interaction of hemisphere and orientation [F (1, 8) = 4.06, P = 0.079]. Given that this trend was the same for familiar and novel stimuli, it cannot reflect properties of memory for lateral orientation, but instead may suggest that stimuli can be encoded more easily when their front portions are nearest the fixation point. Alternatively, it is possible that the left hemisphere directs attentional scanning from left to right, perhaps as a consequence of its facility with reading.

We next analyzed only the data from the familiar objects to consider the compatibility between the direction at the time of exposure and the time of test, along with hemisphere and stimulus type. The right hemisphere advantage was again in evidence (with means of 768 and 608 msec for the right and left hemispheres, respectively), [F (1, 8) = 9.91, P = 0.014]. In addition, J.W.'s right hemisphere had a tendency to respond faster when stimuli faced the original way than when they were reversed (i.e. it was faster on compatible trials than on incompatible trials), but vice versa for his left hemisphere (i.e. it tended to be faster on the incompatible trials) [F (1, 8) = 3.68, P = 0.09], for the interaction between hemisphere and compatibility. (Note that this trend is, if anything, opposite to the left-hemisphere compatibility effect we found in Experiment 1.)

Discussion

At first glance, the results may appear paradoxical: We found that J.W. was faster when stimuli were processed by his right hemisphere, but his left hemisphere showed priming and the right did not. These results suggest that two separate processes may be at work: The right hemisphere may generally be better at encoding pictures, but the left hemisphere has more

effective implicit memory representations of shape. The first part of this interpretation is consistent with the long-standing idea that the right hemisphere has better representations of pictorial material (e.g. Ref. [6]), but the second is not. We did not find that the left hemisphere has better representations of orientation *per se*; rather, equivalent amounts of priming occurred for both the original and novel orientations. Thus, the left-hemisphere priming suggests that there is something different about its underlying representation. MARSOLEK et al. [13] suggest that the left hemisphere may rely on abstract representations of shape, which presumably would represent—and prime—each lateral orientation equally well (see also Ref. [7]). However, they also found that the right hemisphere represents specific shapes more effectively than the left, and we found no evidence of such processing here—at least insofar as lateral orientation can be considered a specific aspect shape.

Neither hemisphere was better at processing items that faced in the same direction at test and acquisition. Nor did we find evidence that the hemispheres differ in their efficacy of encoding objects facing in different directions. But these results do not speak to priming, and do not clearly speak to the issue of what is stored in the hemispheres. In addition, although J.W. was very accurate in this task, these findings do not bear on the issue of what is stored; he was asked simply to decide whether the picture was an object. Indeed, the high level of accuracy precluded our using these data to assess implicit memory.

GENERAL DISCUSSION

We began with the question, how do people recognize objects when they face in novel lateral orientations? We considered two hypotheses, and are now in a position to evaluate them. First, CORBALLIS and BEALE [2] suggested that the process of transferring information across the corpus callosum might engender "mirror-image generalization" in the cerebral hemispheres. This theory can be ruled out by our results: J.W. performed at "ceiling" levels of accuracy in Experiment 1, even when pictures were presented in the opposite direction to that used in the exposure phase. Given that J.W. does not have a functional corpus callosum, he cannot be relying on this structure to produce the requisite representations. This finding is a good example of the power of single-case studies; if Corballis and Beale were correct, such a result should never have occurred, even in a single case.

Second, the very high levels of accuracy in Experiment 1 allow us to eliminate the idea that each hemisphere has only a single representation, with each hemisphere storing a mirror-reversed image. Moreover, the very poor levels of accuracy in Experiment 2 are inconsistent with this hypothesis, as are the patterns of response times in each of the experiments.

Although the results appear to rule out the two theories considered at the outset—that the corpus callosum produces mirror-reversed representations in the hemispheres or that each hemisphere stores a representation in only one direction—many alternative theories are viable. For example, LOWE [10, 11] built a computer vision system that recognizes objects when they appear at novel lateral orientations. His system relies on only a single stored representation of a shape, and matches input to it via the "viewpoint consistency constraint": The critical variable is whether the relative positions of the components of a stimulus are consistent with seeing an object from a single point of view, regardless of what that point of view happens to be. Indeed, any theory that posits "object centered" representations (see Ref. [12]) can account for the present findings. Similarly, because the subject was familiar with the objects that were used as stimuli, it is possible that he encoded the stimuli by tagging representations of prototypes in memory—and these representations would not specify

left/right orientation. It would be interesting to repeat the experiment with nonsense shapes and with a larger number of stimuli.

In addition, ACHIM and CORBALLIS [1] suggested that the anterior commissure, not the corpus callosum, plays the critical role in producing mirror image representations in the cerebral hemispheres. They reviewed data originally reported by NOBLE [14], and noted that monkeys that have had their anterior commissures sectioned have good memory for lateral orientation. Because normal monkeys do not have good memory for lateral orientation, Achim and Corballis suggest that the anterior commissure might mirror-reflect memory traces about the midsagittal plane. Although this hypothesis may be reasonable for monkeys, one version of it can be ruled out for humans: When stimuli are presented to a single hemisphere of a split-brain patient who has an intact anterior commissure, the other hemisphere cannot recognize the shape even when it is in the same lateral orientation (e.g. Ref. [5]). Thus, the anterior commissure does not transmit high-resolution information about shape. However, it is possible that the anterior commissure transmits information about lateral orientation, and coordinates separate representations of the same shape in the two hemispheres—producing mirror-reflections of these representations in each hemisphere. It is unclear, however, whether it makes sense that information about lateral orientation per se could be transmitted independently of shape; the proper test of this theory would require administering our tasks to a split-brain patient who had both the corpus callosum and anterior commissure transected.

The present results also point to an intriguing difference between the hemispheres: Only the left hemisphere exhibited priming. This result is strikingly different from that reported by MARSOLEK et al. [13], who found that both hemispheres exhibited priming—albeit in different ways. We only tested one patient, of course, and it will be of interest to discover whether this aspect of the results proves general for a wider range of subjects.

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