A deficit in perceptual matching in the left hemisphere of a callosotomy patient

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Abstract

Decades of research have demonstrated dramatic differences between the hemispheres of the brain. While the most obvious asymmetries are in the areas of language and motor control, the visuospatial abilities of the left hemisphere are also known to differ from those of the right hemisphere. This hemispheric difference has been demonstrated empirically but its basis is thus far unclear. In this paper, we investigate the hypothesis that the left hemisphere is capable of sophisticated visual processing, but represents spatial information relatively crudely compared to the right hemisphere. The implication of this hypothesis is that pattern recognition is a function of both hemispheres but the right hemisphere is further specialized for processing spatial information. In a series of seven experiments we examined perceptual matching of mirror-reversed stimuli by the divided cerebral hemispheres of a callosotomy patient. In each experiment the left hemisphere's performance was impaired relative to the right hemisphere. This finding was independent of stimulus type, response bias and stimulus duration. These results are consistent with the idea that visual processing in the left hemisphere is directed towards pattern recognition at the expense of spatial information. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Corpus callosum; Hemispheric asymmetries; Split brain; Visuospatial processing

1. Introduction

Although they are roughly symmetrical in appearance, the two hemispheres of the human brain are known to have many functional asymmetries. The most obvious of these asymmetries are in fine motor control and the production and comprehension of language, both of which are lateralized to the left hemisphere in most right-handed people. A variety of other perceptual and cognitive functions also appear to show systematic lateralization towards one hemisphere or the other in the majority of the population. For example, early studies with callosotomy ('split-brain') patients revealed that the right hemisphere performed most visuospatial tasks better than the left [13]. In addition, unilateral right hemisphere damage often results in deficits in visuospatial tasks [23,32,33]. These results, amongst others, have led to the popular characterization of the right hemisphere as 'specialized' for visuospatial processing, in much the same way as the left hemisphere is described as 'specialized' for linguistic processing. Although a great deal of effort has been expended to describe the nature of these asymmetries, to date no entirely satisfying account has been given for the basis of hemispheric asymmetries in perceptual and cognitive functions. In this paper we investigate asymmetries in visuospatial abilities. We hypothesize that these asymmetries result from a right hemisphere specialization for processing spatial information.

Although some visuospatial functions are asymmetric, many are bilaterally represented. It has been suggested that there is evolutionary pressure for basic perceptual processes to be bilaterally symmetric since it would be adaptive to be equally alert to both sides of space [4]. In addition, some degree of perceptual

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analysis is required in both hemispheres to support higher level processing of sensory information. There is ample evidence that the surgically isolated left hemispheres of callosotomy patients are capable of sufficiently detailed visual discriminations to enable them to read tachistoscopically-presented words, and recognize and name objects [13,15]. This evidence suggests that both hemispheres are capable of reasonably sophisticated visual analysis to support these higher level cognitive functions. Thus, on both theoretical and empirical grounds, any global visuospatial advantage of the right hemisphere is likely to reflect a quantitative, rather than qualitative, difference between the hemispheres.

A number of theories have been suggested to account for the hemispheric difference in visuospatial abilities. Rather than an overall right-hemisphere visuospatial specialization, several authors have suggested that hemispheric asymmetries in visuospatial processing reflect a tendency for each hemisphere to process particular aspects or components of a visual stimulus, with each contributing its expertise to the final percept. For example, Sergent [27] has proposed that the left hemisphere selectively processes high-spatial-frequency information, and the right hemisphere selectively processes low-spatial-frequency information. This would result in a right hemisphere superiority for processing stimuli degraded by reduced luminance, blurring, decreased presentation time, and low-pass filtering. Similarly, Delis, Robertson, and Efron [7] have suggested that the left hemisphere preferentially encodes the local details of a stimulus, whereas the right hemisphere encodes the global layout (see [20] for a discussion of the computational advantages of such a 'double filtering' of visual inputs). This theory is consistent with Sergent's view since information about global aspects of stimuli tend to be contained in the lower spatial frequencies and local aspects in the higher spatial frequencies [18]. A third theory has been advanced by Kosslyn and his colleagues [21], who proposed that the left hemisphere tends to represent spatial relations between stimuli 'categorically' (i.e., with symbolic descriptions such as 'above', 'below', 'left', 'right', and so forth) and that the right hemisphere represents visuospatial information in a finer-grained, 'coordinate' framework which preserves metric information about spatial relationships. This hypothesized right hemisphere function would presumably result in a right hemisphere superiority in representing spatial information. Although there is some empirical support for these processing dichotomies, it is relatively weak. Furthermore, to the extent that they hold up to empirical scrutiny, it is unclear whether they accurately depict the fundamental differences between the visuospatial processing styles of the two hemispheres, or whether they are manifestations of some more elementary hemispheric asymmetry [18].

In this paper, we explore the idea that the hemispheres are equally adept at pattern recognition, but differ in their abilities to represent the spatial relationships between elements in the visual array. Specifically, we are investigating the hypothesis that the left-hemisphere representation of spatial information is significantly impaired relative to that of the right hemisphere. This would account for the early findings suggesting that the right hemisphere is specialized for visuospatial processing. It has been established that both hemispheres are capable of sophisticated pattern recognition [1,2,8,11,14] despite the hypothesized right hemisphere specialization for processing spatial information [23]. Evidence for a dissociation between visual pattern recognition and the representation of spatial relationships can be found in the neuropsychological literature. In split-brain patients, it has been noted that the left hemisphere is impaired relative to the right on tasks that require detailed spatial discriminations [2,11]. This is in contrast to the relatively good performance of both hemispheres on tasks requiring pattern-recognition [1,14]. Warrington and Taylor [33] have shown that patients with lesions in the right parietal lobe often have trouble recognizing objects in unusual orientations. Patients with lesions in the homologous regions of the left hemisphere seldom exhibit this deficit. This suggests that the mechanisms for the spatial transformations required to recognize objects from unusual viewpoints are not supported by the left hemisphere. Evidence from these neurospsychological populations provides support for the dissociation of pattern recognition and spatial processing, with spatial abilities seemingly lateralized to the right hemisphere.

If the visual system of the left hemisphere is capable of sophisticated analysis of patterns, but poor at representing spatial relationships, we might expect it to be relatively insensitive to mirror reversal and to orientation differences between stimuli. Some degree of indifference to changes in orientation and to mirror reversal is a desirable feature for a pattern-recognition system [19], but not for a system that represents objects in a spatial context. Thus, we might expect the isolated left hemisphere of a split-brain patient to be relatively poor at judging whether two simultaneously-presented stimuli are identical, or are mirror images of one another. The series of experiments presented in this paper investigates this prediction.

2. Experiment 1: Rendered color pictures

In this experiment, we investigated perceptual matching in the two hemispheres of a split-brain patient to determine whether the hemispheres differed

in their ability to detect mirror reversals. Pairs of pictures that differed only in orientation were presented to each hemisphere and the patient was required to make a same/different judgment about each pair. The pictures were detailed rendered color images of everyday objects [30]. These objects were easily nameable (e.g., bicycle, glasses, etc.), but no semantic judgment was required in the task.

2.1. Methods

2.1.1. Subject

J.W. is a 45-year-old right-handed male who underwent a two-stage callosotomy at the age of 25 for control of intractable epilepsy which began at age 19. His post-operative IQ was in the normal range (VIQ 97, PIQ 95, FSIQ 96). Further details of his neurological profile can be found in Gazzaniga, Holzman, Deck and Lee [16]. He has been tested extensively and is familiar with all of the testing procedures used. J.W. was tested in all of the experiments that follow.

2.1.2. Apparatus and stimulus materials

Stimuli were presented on a Power Macintosh 7500 with an AppleVision monitor. The stimulus items were 50 rendered color pictures of common objects [30]. The pictures were scaled to fit within a 5 cm square on the computer monitor to ensure that they would each subtend approximately the same visual angle. Stimulus pairs consisted of two copies of the same picture vertically aligned such that the images were separated by at least two centimeters. Two stimulus pairs were constructed for each picture. In one pairing ('same'), the two copies of the picture appeared in the same orientation. In the second pairing ('different'), one copy of the picture was reflected about the vertical axis so that the two copies of the picture were mirror-images of each other. This resulted in a total of 100 stimulus pairs. Two sets of stimuli were constructed, with each including all 100 pairs. The first set was constructed by generating a random order of the stimulus pairs and assigning each to a visual field at random. In the second set, the visual field of each stimulus pair was reversed.

2.1.3. Procedure

Stimuli were presented tachistoscopically. J.W. was seated 57 cm in front of the computer screen and was instructed to fixate a central cross-hair. Fifty-seven centimeters was selected so that 1 cm on the screen subtends $1°$ of visual angle on the screen. Stimuli were then flashed to either the right or left visual field for 150 ms with their medial edges at least 2 cm to the right or left of fixation. Since the presentations times were too brief to permit the initiation of saccadic eye motions toward the lateralized stimuli and the medial edge of the stimuli fell outside any zone of naso-temporal overlap [9], these arrangements ensured that stimuli were only presented to the hemisphere contralateral to the visual field of the presentation.

Following each stimulus pair, the words 'yes' and 'no' were flashed for 150 ms to the same visual field. The words were vertically aligned and separated by five centimeters. In half of the trials, the word 'yes' appeared on top and in the other half, the word 'no' appeared on top. The order of these trial types was randomized.

J.W. was instructed to respond 'yes' if the two pictures were exactly the same (i.e. in the same orientation) and to respond 'no' if the two pictures were not exactly the same (i.e. mirror-images of each other). Instructions were provided verbally and were accompanied by examples. Prior to beginning the task, J.W. completed a practice set to ensure that both hemispheres understood the task. J.W. responded by pointing to the position where the word 'yes' or 'no' had appeared with the hand ipsilateral to the field of presentation. Responses were non-verbal because J.W.'s right hemisphere is only occasionally able to support speech [1].

J.W. was tested on two occasions, separated by a week. In each session, he completed both test sets with at least an hour between sets.

2.2. Results and discussion

Because this experiment involves analysis of single-subject data in which each hemisphere serves as a control for the other, the accuracy data were analyzed using multidimensional chi-squared analyses [34]. Discrimination accuracy in these analyses is indexed by the interaction between experimental condition and response. Response bias is indexed by response selection effects only. The factorial design of the experiment allows higher-order interaction effects to be evaluated in a manner directly analogous to analysis of variance.

The multidimensional chi-squared analysis was performed with visual field (right and left), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction (χ^2 (1) = 142.02, $P < 0.001$) which indicates that J.W. understood the instructions and was performing the task accurately overall. There were also significant visual field by response (χ^2 (1) = 9.18, $P < 0.01$) and visual field by condition by response (χ^2 (1) = 16.32, $P < 0.001$) interactions. The visual field by response interaction is due to a bias to respond 'no' ('different') in the right visual field/left hemisphere (129 'different' responses vs. 71 'same' responses). There was no such bias in the left visual

Table 1
Proportions of 'same' stimulus pairs in each set of 120 item pairs in Experiment 2

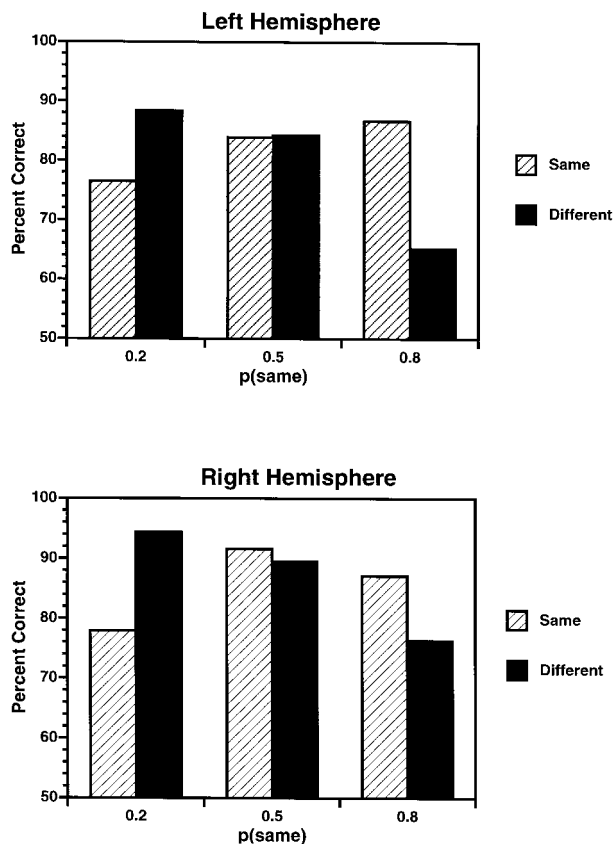|	RVF/left hemisphere	LVF/right hemisphere
Set 1	0.2	0.2
Set 2	0.2	0.5
Set 3	0.2	0.8
Set 4	0.5	0.2
Set 5	0.5	0.5
Set 6	0.5	0.8
Set 7	0.8	0.2
Set 8	0.8	0.5
Set 9	0.8	0.8

Fig. 1. Average percentages of correct responses for 'same' and 'different' stimulus pairs in each condition in Experiment 2. Top panel: Data for stimuli presented to the right visual field/left hemisphere. Bottom panel: Data for stimuli presented to the left visual field/right hemisphere.

field/right hemisphere (99 'different' responses vs 101 'same' responses). The significant visual field by condition by response interaction indicates that accuracy was different for stimuli presented to the two visual fields. Overall, J.W. was 69.5% accurate for right-visual-field/left-hemisphere stimuli (139/200 correct responses) and 89.5% accurate for left-visual-field/right-hemisphere stimuli (179/200 correct responses).

The difference in performance between the two hemispheres confirms that J.W.'s left hemisphere is significantly impaired relative to the right on the perceptual matching task. This is consistent with our hypothesis that the left hemisphere should be relatively indifferent to mirror reversals.

The stimuli used in this experiment were complex, color pictures of easily nameable objects. It is possible that some aspect of these pictures is processed poorly by the left hemisphere, and that the left-hemisphere deficit we observed here would not be found with visually simpler stimuli. In addition, the differences in response bias between the hemispheres may have exacerbated the left-hemisphere deficit. The following experiments were designed to investigate these possibilities.

3. Experiment 2: Response bias

In Experiment 1, the left hemisphere demonstrated a bias to respond "different" which was not present in the right hemisphere. Although this bias cannot account for the left-hemisphere deficit by itself, it may have magnified the performance difference between the hemispheres. This experiment was designed to manipulate the response biases of the two hemispheres independently by varying the proportions of each stimulus type presented to the two hemifields. The probability of 'same' stimuli in each hemifield was varied from 0.2 to 0.8 in separate blocks of trials. This manipulation should influence the response biases of each hemisphere to approximate the relative proportions of

'same' and 'different' stimuli in each block. We expect that the biases of both hemispheres will be affected by the proportion of 'same' items, and that the left hemisphere matching deficit will still be obtained.

3.1. Methods

3.1.1. Apparatus and Stimulus Materials

The apparatus and stimuli were the same as in Experiment 1. Nine different test sets were constructed with varying probabilities of 'same' and 'different' item pairs in each set. Each set consisted of 120 item pairs, 60 in each visual field. The sets were created by the factorial combination of three different probabilities of 'same' item pairs in each visual field. These probabilities were 0.2, 0.5, and 0.8 (see Table 1). For example, the probability of same item pairs in set 1 was 0.2 in the each visual field, so twelve item pairs were 'same' and 48 item pairs were "different" in each visual field. In set 2, the probabilities of 'same' pairs were 0.2 (12 'same' and 48 'different') in the right visual field, and 0.5 (32 'same' and 32 'different') in the left visual field, and so forth.

3.1.2. Procedure

The testing procedure was identical to that used in Experiment 1. J.W. was tested on each of these 9 sets twice over a period of six weeks.

3.2. Results and discussion

For each of the three probability levels in each visual field, the data were combined across the three relevant sets. For example, for the 0.2 probability level, the left-visual-field data from sets 1, 2, and 3 were combined, and the right-visual-field data from sets 1, 4, and 7 were combined. This yielded combined data sets of 360 trials for each probability level in each visual field. J.W.'s response accuracies for each probability level, visual field, and stimulus type are shown graphically in Fig. 1. Inspection of this figure reveals that the probability manipulations were effective in manipulating response bias in both hemispheres. When the probability of 'same' item pairs was 0.2, J.W. was more accurate for 'different' items than for 'same' items. When the 'same' and 'different' items were equiprobable J.W. was equally accurate for both item types. Finally, when the probability of 'same' items was 0.8, J.W. was more accurate for 'same' items than for 'different' items. This pattern was observed for stimuli presented to both the left and right visual fields. Overall performance was better in the left visual field/right hemisphere. This suggests that manipulating the response bias in each hemifield did not eliminate the left-hemisphere deficit we obtained in Experiment 1.

The responses were subjected to a four-way multidimensional chi-squared analyses with visual field (right and left), probability ($P(same) = 0.2$, $P(same) = 0.5$, and $P(same) = 0.8$), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction ($\chi^2 (1) = 1152.98$, $P < 0.001$) which indicates that J.W. was performing the task accurately. There was also a significant interaction of probability and response ($\chi^2 (2) = 405.85$, $P < 0.001$) which indicates that J.W.'s response selection was influenced by the relative probability of 'same' item pairs. When 'same' item pairs were likely, J.W. responded 'same' 75% of the time. When 'same' and 'different' item pairs were equiprobable, he responded 'same' on 50% of the trials. When 'different' item pairs were likely, he responded 'same' on 22% of the trials. This indicates that J.W.'s response selections were approximately matching the probabilities of 'same' and 'different' stimulus pairs.

Two three-way interactions also reached significance. These were probability by condition by response ($\chi^2 (2) = 521.01$, $P < 0.001$), and visual field by condition by response ($\chi^2 (1) = 4.82$, $P < 0.05$). The probability by condition by response interaction indicates that J.W.'s accuracy was different for each of the probability levels (89% for $P(same) = 0.2$, 87% for $P(same) = 0.5$, and 84% for $P(same) = 0.8$). This suggests that there was still a slight bias to respond 'different', despite the probability manipulations. The visual field by condition by response interaction indicates that J.W.'s accuracy was different in the two visual fields (84% in the right visual field/left hemisphere, and 89% in the left visual field/right hemisphere). The four-way interaction of visual field, probability, condition and response was not significant ($\chi^2 (2) = 0.24$, $P = 0.89$), which indicates that the three-way interactions were statistically independent, so we have no evidence that changes in stimulus probabilities were influencing the left-hemisphere deficit in perceptual matching.

The left hemisphere again was significantly impaired relative to the right in perceptual matching, although the magnitude of this impairment was smaller than that obtained in Experiment 1. The independent manipulation of the response biases of each hemisphere did not eliminate the hemispheric difference in accuracy. This implies that the left hemispheric deficit in perceptual matching is not solely the result of differing response biases between the hemispheres. The smaller magnitude of the left-hemisphere deficit in this experiment suggests that the left hemisphere's bias to respond "different" may have contributed to the deficit found in Experiment 1, but cannot account for all of it.

4. Experiment 3: Black-and-white line drawings

Experiment 2 demonstrated that response bias was not the cause of the left-hemisphere deficit in perceptual matching. Another possibility is that the complexity of the stimuli contributed to the hemispheric difference in accuracy. The stimuli used in the first two experiments were rendered color pictures of three-dimensional objects which contained a great deal of visual detail. It is conceivable that some aspect of these stimuli is not processed well by the left hemisphere, but that the two hemispheres would otherwise be equivalent for the matching task. In Experiment 3, we repeated the task with black and white stimuli that had significantly less visual detail but were still nameable common objects. If this manipulation eliminated the effect found in Experiments 1 and 2, then some idiosyncratic feature of the previous stimulus set could have produced the hemispheric difference.

4.1. Methods

4.1.1. Apparatus and stimulus materials
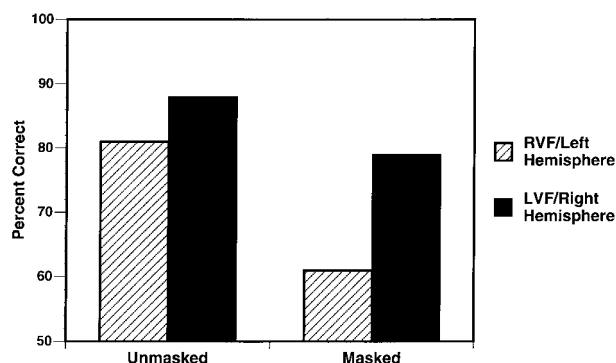
See Experiment 1 for a description of the apparatus.

Fig. 2. Average percentage of correct responses for stimulus pairs presented to each visual hemifield in Experiments 3 (Unmasked) and 4 (Masked). RVF = right visual field, LVF = left visual field.

Stimulus pairs were constructed in the same manner as Experiment 1. The only difference was that 50 black-and-white line drawings of common objects [28] were used instead of color pictures of rendered objects.

4.1.2. Procedure

The testing procedure was identical to that used in Experiment 1.

4.2. Results and discussion

Accuracy data were again analyzed using multidimensional chi-squared analyses with visual field (right and left), condition (same and different) and response (yes and no) as factors. Once again, there was a significant condition by response interaction (χ^2 (1) = 188.07, $P < 0.001$) which indicates that J.W. was performing the task accurately. The interaction between visual field and response was not significant (χ^2 (1) = 0.49, $P = 0.5$), indicating that there was no significant difference in response bias between the hemispheres. Although there was a difference in accuracy between the two hemispheres (81% for right visual field/left hemisphere, 88% for left visual field/right hemisphere), the three-way interaction of visual field by condition by response did not reach significance (χ^2 (1) = 2.26, $P = 0.13$). Discrimination accuracy for each hemifield is shown graphically in Fig. 2 ('unmasked').

The results of this experiment were somewhat equivocal. There was a hemispheric difference in the same direction as that found in Experiment 1, but the difference was not statistically significant. This finding has several possible explanations. This experiment could be considered a genuine replication despite the lack of statistical significance [31]. However, we cannot discount the possibility that the results of Experiment 1 were due to some idiosyncratic feature of the stimulus set or to type-1 error. Finally, it is possible that the difference between the two experiments may be the result of differences in the degree of difficulty of the tasks. The stimulus sets used differed significantly in visual complexity. It is possible that with relatively simple stimuli, each hemisphere has sufficient resources available to support rapid and accurate perceptual judgments.

5. Experiment 4: Masked black-and-white line drawings

Experiment 4 is designed to assess the possibility that the differences between the results of Experiments 1 and 3 were due to differences in difficulty between the two tasks. This experiment is a replication of Experiment 3 with the addition of a pattern mask following the presentation of the item pairs. The mask should eliminate iconic storage of the stimuli, effectively reducing the exposure time and thereby increasing the difficulty of the task. We expect that increasing the task difficulty should tax the left hemisphere more than the right, and reinstantiate the significant hemispheric difference obtained in the earlier experiments.

5.1. Methods

5.1.1. Apparatus and Stimulus Materials

The apparatus and stimuli were the same as in Experiment 3.

5.1.2. Procedure

All aspects of the testing procedure were identical to those of Experiment 3 except that a pattern mask was presented for 500 ms immediately following the presentation of each stimulus pair.

5.2. Results and discussion

The data analysis was identical to that used in Experiment 3. There was a significant condition by response interaction (χ^2 (1) = 65.68, $P < 0.001$) which indicates that J.W. was still able to perform the task accurately. The interaction between visual field and response was not significant (χ^2 (1) = 0, $P = 1.0$), indicating that there was no observable difference in response bias between the hemispheres in this experiment. The three-way interaction of visual field by condition by response was significant (χ^2 (1) = 13.30, $P < 0.001$). This indicates that accuracy was different for stimuli presented to the two visual fields. Overall, J.W. was 61% accurate for right visual field/left hemisphere stimuli (122/200 correct responses) and 79% accurate for left visual field/right hemisphere stimuli (158/200 correct responses). This difference is shown graphically in Fig. 2 ('masked').

The addition of the pattern mask following the presentation of the stimulus pairs resulted in a lower over-

all accuracy in both hemispheres compared to the previous three experiments. This indicates that the mask was effective in increasing the difficulty of the task. The left hemisphere was once again significantly impaired relative to the right, as in Experiments 1 and 2. This suggests that the lack of a significant effect in Experiment 3 was due to the relative simplicity of the task or to type-2 error because of random variation from one experiment to another.

6. Experiment 5: Black-and-white pictures of rendered objects

The stimulus set used in Experiments 3 and 4 consisted of black-and-white line drawings of common objects. These drawings contain relatively little internal detail or depth information compared to the rendered color pictures of three-dimensional objects used in Experiments 1 and 2. The results of Experiments 3 suggest that the simpler line drawings used in those experiments produced a less drastic left hemisphere matching deficit when they were presented without the pattern mask. This experiment was designed to determine whether color and internal detail were factors in the differences between Experiments 1 and 3. To assess this, the rendered color pictures from Experiment 1 were converted to black and white and filtered to enhance edge contrast. This effectively made them more like black-and-white line drawings, but preserved their shape and major contours. We reasoned that by using stimuli that were as similar as possible to those used in Experiment 1 we would minimize any idiosyncratic differences between stimulus sets that may have contributed to the performance differences between Experiments 1 and 3.

6.1. Methods

6.1.1. Apparatus and stimulus materials
The apparatus and stimuli were the same as in Experiment 1 except that the color pictures of the rendered objects were filtered to produce black-and-white line-drawing versions.

6.1.2. Procedure
The testing procedure was identical to that used in Experiment 1.

6.2. Results and discussion

Accuracy data were again analyzed using multidimensional chi-squared analyses with visual field (right and left), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction (χ^2 (1) = 174.68,
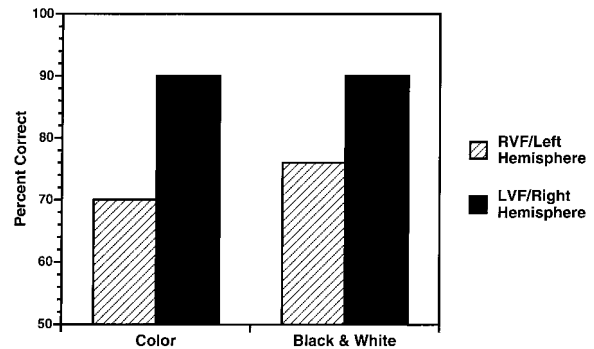

Fig. 3. Average percentage of correct responses for stimulus pairs presented to each visual hemifield in Experiment 5 (black & white). The data from Experiment 1 (color) are also shown for comparison. RVF = right visual field, LVF = left visual field.

$P < 0.001$) which indicates that J.W. was performing the task accurately. The interaction between visual field by response was not significant (χ^2 (1) = 0.04, $P = 0.84$), indicating that there was no significant difference in response bias between the hemispheres. The three-way interaction of visual field by condition by response was significant (χ^2 (1) = 7.86, $P < 0.01$). This indicates that accuracy was different for stimuli presented to the two visual fields. Overall, J.W. was 76% accurate for right visual field/left hemisphere stimuli (152/200 correct responses) and 90% accurate for left visual field/right hemisphere stimuli (180/200 correct responses). This difference is shown graphically in Fig. 3.

Response accuracy in each hemisphere was remarkably similar to that obtained in Experiment 1. This implies that color and internal detail were not critical factors in the differences between the experiments using rendered color pictures and those employing black-and-white line drawings.

7. Experiment 6: Abstract forms

In all of the previous experiments, the stimuli were pictures of nameable common objects. One possible explanation for the poor spatial abilities of the left hemisphere is that it is automatically engaged in picture naming because of its specialization for language. The process of naming could recruit cognitive resources that would otherwise be available for the perceptual task, resulting in a left-hemisphere perceptual deficit. This experiment is designed to test this by repeating the task using non-nameable abstract figures as stimuli. If the left hemisphere's tendency to name objects underlies the observed left-hemisphere deficit, then employing abstract figures as stimuli should mitigate this effect and result in hemispheric equivalence in this task.
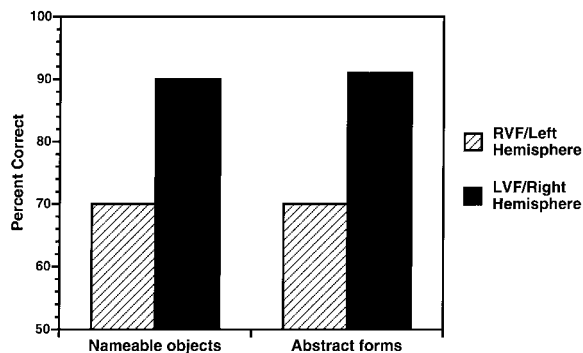
Fig. 4. Average percentage of correct responses for stimulus pairs presented to each visual hemifield in Experiment 6 (abstract forms). The data from Experiment 1 (nameable objects) are also shown for comparison. RVF = right visual field, LVF = left visual field.

7.1. Methods

7.1.1. Apparatus and Stimulus Materials

The apparatus was the same as in Experiment 1. Stimulus pairs were constructed in the same manner as Experiment 1. The only difference was that 50 computer-generated abstract forms [10] were used instead of color pictures of rendered objects. The abstract forms were generated using a computer program that placed six dots in random locations within a 5 cm square and connected the dots with lines.

7.1.2. Procedure

The testing procedure was identical to that used in Experiment 1.

7.2. Results and discussion

Accuracy data were analyzed using multidimensional chi-squared analyses with visual field (right and left), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction (χ^2 (1) = 148.37, $P < 0.001$) which indicates that J.W. was performing the task accurately. The interaction between visual field and response was not significant (χ^2 (1) = 0.50, $P = 0.51$), which suggests that there was no detectable difference in response bias between the two hemispheres. The three-way interaction of visual field by condition by response was significant (χ^2 (1) = 17.03, $P < 0.001$). This indicates that accuracy was different for stimuli presented to the two visual fields. Overall, J.W. was 70% accurate for right visual field/left hemisphere stimuli (140/200 correct responses) and 91% accurate for left visual field/right hemisphere stimuli (181/200 correct responses). The accuracy rates for each hemisphere are shown graphically in Fig. 4.

The accuracy rates in the two hemispheres were virtually identical to those obtained in Experiment 1.

This implies that the left-hemisphere deficit is not affected by the nameability of the stimuli.

8. Experiment 7: Processing speed

In all of the previous experiments, the stimuli were presented tachistoscopically for 150 ms. One possible explanation for the left-hemisphere deficit in perceptual matching is that the right hemisphere is able to process visual information faster than the left. The results of Experiments 3 and 4, in which masking affected the matching of black-and-white line drawings, suggest that this may in fact be the case [24]. It is possible that the left hemisphere, given sufficient processing time, would be as accurate as the right. This experiment is designed to test this by repeating Experiment 1 with increased stimulus presentation time. If the left hemisphere's performance is limited by processing speed, then increasing presentation time should mitigate this effect and result in hemispheric equivalence in this task.

8.1. Methods

8.1.1. Apparatus and Stimulus Materials

Stimuli were presented on an AppleVision monitor controlled by a Macintosh Powerbook 520C. A dual-Purkinje-image eyetracker with an attached image deflection system was used to stabilize images on the retina. The dual-Purkinje-image eyetracker is a stable high resolution system which allows the monitoring of both horizontal and vertical eye movements ranging from 1 arc minute to about 15°. The attached image deflection system permits retinal positions to be held constant within a few arc minutes [5,6]. This arrangement allows us to move stimuli on any presentation screen in tandem with a subject's eye motions so that lateralized stimuli remain lateralized even if a subject attempts to look at them. This allows for lateralization of stimuli when presentation times longer than 150 ms are needed. When this equipment is employed, all presentations must be right eye monocular.

Stimuli were the same as those used in Experiment 1, but the test sets were constructed so that all items in each set appeared in the same visual field. For each visual field, the order of the 100 stimulus pairs was randomized and divided into 4 sets of 25 pairs.

8.1.2. Procedure

J.W. was positioned in the eyetracker with the front of the stabilizer optics 38 cm from the computer screen. This distance was selected so that 1 cm on the screen would subtend 1° of visual angle on the screen. J.W.'s position was maintained with a bite bar and forehead rest. J.W. was instructed to fixate a central
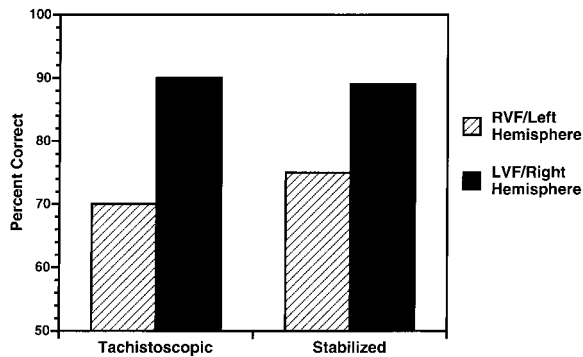
Fig. 5. Average percentage of correct responses for stimulus pairs presented to each visual hemifield in Experiment 7 (stabilized). The data from Experiment 1 (tachistoscopic) are also shown for comparison. RVF = right visual field, LVF = left visual field.

cross-hair and stimuli were presented for up to 3 s with their medial edges at least 2 cm to the right or left of fixation.

The task was similar to the previous experiments. J.W. was instructed to respond 'yes' if the two pictures were exactly the same (i.e. in the same orientation) and to respond 'no' if the two pictures were not exactly the same (i.e. mirror-images of each other). Responses were made via keypress with the hand ipsilateral to the field of presentation. Instructions were provided verbally and were accompanied by examples. Prior to beginning the task, J.W. completed a practice set with feedback to ensure that both hemispheres understood the task.

J.W. was tested on two occasions, separated by two weeks. In each session, he completed all four test sets in each visual field with at least an hour between visual fields.

8.2. Results and discussion

Accuracy data were analyzed using multidimensional chi-squared analyses with visual field (right and left), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction (χ^2 (1) = 160.71, $P < 0.001$) which indicates that J.W. was performing the task accurately. The interaction between visual field and response was not significant (χ^2 (1) = 1.46, $P = 0.22$). This demonstrates that there was no significant difference in the response biases of the two hemispheres. The three-way interaction of visual field by condition by response was significant (χ^2 (1) = 7.94, $P < 0.01$). This indicates that accuracy was different for stimuli presented to the two visual fields. Overall, J.W. was 75% accurate for right visual field/left hemisphere stimuli (149/200 correct responses) and 89% accurate for left visual field/right hemisphere stimuli (177/200 correct responses).

Performance in the two hemispheres is shown graphically in Fig. 5.

Increasing the presentation time of the stimuli had essentially no effect on the accuracy of either hemisphere. This implies that the brief presentation times used in the previous experiments were not limiting the amount of information available to either hemisphere, and that the left-hemisphere deficit is not the result of a difference in processing speed between the hemispheres. This suggests that the lack of a significant effect in Experiment 3 was most likely the result of type-2 error or some idiosyncratic feature of the stimulus set.

9. Experiment 8: Identity matching of pictures of rendered objects

In all of the previous experiments, the left hemisphere was impaired relative to the right in making judgments about whether pictured objects appeared in the same orientation or were mirror reversed. It is possible that the left hemisphere would be impaired on any type of visual judgment and that the deficit is not specific to orientation. To assess this possibility, this experiment was designed to determine whether the left hemisphere is able to distinguish between pictures of different objects rather than between pictures of the same object in different orientations. Because we wanted to investigate the capacity of both hemispheres for pattern recognition, we used black-and-white pictures so that judgments could not be made simply on the basis of differences in color. The black-and-white pictures of the rendered objects (Experiment 5) resulted in a larger left hemisphere impairment than did the black-and-white line drawings (Experiment 3), so the former were selected as stimuli for this experiment.

9.1. Methods

9.1.1. Apparatus and stimulus materials

The apparatus was the same as in Experiment 1. The black-and-white pictures of rendered objects from Experiment 5 were used to make the stimulus pairs for this experiment. The stimulus pairs consisted of two vertically aligned pictures of two different objects. The objects were oriented in the same direction.

9.1.2. Procedure

The testing procedure was identical to that used in Experiment 1.

9.2. Results and discussion

Accuracy data were again analyzed using multidi-

mensional chi-squared analyses with visual field (right and left), condition (same and different) and response (yes and no) as factors. There was a significant condition by response interaction (χ^2 (1) = 173.0, $P < 0.001$) which indicates that J.W. was performing the task accurately. The interaction between visual field by response was not significant (χ^2 (1) = 0.5, $P = 0.51$), indicating that there was no significant difference in response bias between the hemispheres. The three-way interaction of visual field by condition by response was not significant (χ^2 (1) = 0.02, $P = 0.88$). This indicates that accuracy was not different for stimuli presented to the two visual fields. Overall, J.W. was 97% accurate for right visual field/left hemisphere stimuli (97/100 correct responses) and 96% accurate for left visual field/right hemisphere stimuli (96/100 correct responses).

Response accuracy in both hemispheres was high. When asked to make orientation judgments about these same pictures in Experiment 5, the left hemisphere was significantly impaired relative to the right. The performance of the left hemisphere in this identity matching task provides evidence that it does not have a global deficit in making judgments about visually presented objects. The left and right hemispheres appear to be equally capable of encoding the stimuli. Further evidence that J.W.'s left hemisphere is able to encode visually presented stimuli comes from experiments in which he is able to name color pictures and line drawings and to read text presented tachistoscopically to his right visual field [1]. He performs these tasks with a very high degree of accuracy. In order to do this, the left hemisphere must be capable of relatively sophisticated pattern recognition.

10. General discussion

The results of this series of experiments indicate that J.W.'s left hemisphere demonstrates a striking deficit in a simple visual matching task. This deficit is independent of response bias, and is found regardless of whether the stimuli are color pictures of nameable objects, black-and-white line drawings, or abstract geometrical forms. Providing the left hemisphere with more time to process the stimuli does not improve its performance. This deficit was specific to spatial judgments since the left hemisphere was equivalent to the right in identity matching. Overall, these results demonstrate that the left hemisphere is relatively insensitive to mirror reversal compared to the right hemisphere, but both are capable of encoding visual stimuli. This is consistent with our hypothesis that the right hemisphere is specialized for processing spatial relationships. The left hemisphere is able to encode visual stimuli as well as the right, but visual processing

in the left appears to be directed towards pattern recognition at the expense of spatial information.

Although the left-hemisphere deficit in perceptual matching demonstrated by this series of experiments could not be accounted for by response bias, differences in response bias may have influenced accuracy levels in Experiment 1. In that experiment, the left hemisphere exhibited a marked bias to respond 'different', which was not observed for the right hemisphere. The results of Experiment 2, in which response bias was artificially manipulated by varying the probabilities of 'same' and 'different' item pairs in each hemisphere, suggested that the left hemisphere's bias to respond 'different' may have contributed to its poor overall performance. The left-hemisphere deficit was significant but smaller in Experiment 2 than it had been in Experiment 1. No significant response bias in either hemisphere was observed in any of Experiments 3–7. Nevertheless, there was a significant left-hemisphere deficit in Experiments 4–7. The results of these experiments provide further evidence that response bias in fact played a relatively minor role in producing the left-hemisphere matching deficit.

We consistently found the left-hemisphere deficit across a variety of stimulus and task conditions. The deficit observed in Experiment 3 (black-and-white pictures) did not reach statistical significance, but was in the same direction as in Experiment 1 (rendered color pictures). Subsequent experiments indicated that the deficit could be found if the stimuli were followed by a pattern mask (Experiment 4), and that the difference in the size of the left-hemisphere deficit between Experiments 1 and 3 was most likely not due to differences in either color information or complexity of the stimuli (Experiment 5). To assess whether nameability was a critical factor in the left-hemisphere deficit, the stimuli used in Experiment 6 were abstract forms rather than pictures of common objects. We postulated that the left hemisphere's tendency to name objects may have recruited cognitive resources that would otherwise have been available for the perceptual judgment. The left-hemisphere deficit was the similar to that found with pictures of common objects, indicating that nameability of the stimuli did not influence the magnitude of the effect. In summary, the left-hemisphere deficit in perceptual matching was not due to the nature of the stimuli.

In Experiments 1–6, stimuli were presented for 150 ms. In Experiment 4, however, the exposure time was effectively limited by presenting a pattern mask immediately following stimulus presentation. Without the pattern mask, the left hemisphere was impaired relative to the right although this difference was not significant. Addition of the pattern mask resulted in decreased performance in both hemispheres but the difference between hemispheres returned to significance. The fact

that masking the stimuli appeared to affect the relative performance of the two hemispheres gave rise to the possibility that the left-hemisphere deficit in perceptual matching was the result of insufficient processing time. In Experiment 7, presentation times were increased to 3 sec to explore this possibility. Accuracy levels were virtually identical to those found with brief tachistoscopic presentations (Experiment 1). This implies that the hemispheric difference in perceptual matching was not the result of the left hemisphere having insufficient time to process the stimulus pairs. The nonsignificant effect found with the unmasked black-and-white line drawings (Experiment 3) therefore could be a genuine replication despite the lack of significance [31] or could be the result of type-2 error. Nicholls and Atkinson [24] have suggested that the left hemisphere is specialized for rapid processing of information so perhaps it is not surprising that increasing presentation time did not improve the left hemisphere's performance. This finding is contrary, however, to predictions derived from the spatial-frequency hypothesis [27]. In a review of the literature, Christman [3] noted that decreasing exposure time reduces access to higher spatial frequencies as compared to low frequencies. According to the spatial frequency hypothesis, this should impair left hemisphere performance more than right hemisphere performance. The fact that exposure time did not affect the magnitude of the left-hemisphere deficit suggests that the spatial-frequency hypothesis may not accurately characterize the underlying nature of the hemispheric difference in visuospatial functions, although this conclusion remains tentative.

While the data are not necessarily consistent with the spatial-frequency hypothesis, they are consistent with the suggestion that the left hemisphere preferentially encodes the local features of a stimulus, while the right hemisphere encodes the global configuration [7,20,26]. In our experiments the stimuli contain the same local details, and differ only in their global configuration. Thus, the left-hemisphere deficit in the perceptual matching task is consistent with the global/local hypothesis.

Our data are also consistent with Kosslyn's hypothesis that the left hemisphere encodes information about the position and orientation of objects crudely while the right hemisphere encodes spatial relations metrically [21]. According to this hypothesis, the right hemisphere should have no difficulty with the matching task, since its fine-grained spatial representation would make the differences between the mirror-image stimuli fairly salient. In contrast, if the left hemisphere's representation of the stimuli contains only descriptive spatial information, which may not always include orientation information, it may perform the matching task poorly. The results of this series of experiments, therefore, are consistent with this theory.

These experiments do not constitute a critical test of either the global/local or categorical/coordinate hypotheses, and it is not clear which of them, if either, best accounts for the results. Both hypotheses imply that the left hemisphere has a relatively poor representation of the spatial relationships between elements in the visual array, but that it is reasonably adept at pattern analysis and so is able to read and recognize objects.

The left hemisphere's relatively crude representation of spatial relationships may be the result of the operation of the 'left-hemisphere interpreter', which attempts to make sense of stimuli and events, and tends to represent information in a symbolic, or categorical manner [12]. The operation of this interpreter may interfere with the left hemisphere's ability to maintain accurate representations of stimuli and events. Experiments with visual-search paradigms have suggested that the visual system uses the highest level representations available for decision-making rather than relying on low-level features—even when this is detrimental to performance [17,29]. If this is the case, then the isolated left hemisphere's tendency to represent stimuli symbolically may result in quite drastic impairments when relatively fine spatial discriminations are required. Consistent with this suggestion, previous research with split-brain patients has shown that the left hemisphere tends to make 'elaborative' or 'schematic' errors in visual memory tasks, while the right hemisphere appears to represent stimuli more veridically [22,25].

In summary, the results of this series of experiments indicate that the left hemisphere is relatively insensitive to mirror reversal compared to the right hemisphere which is consistent with our hypothesis that the right hemisphere is specialized for processing spatial relationships. This finding may be the result of the right hemisphere's tendency to process the global configuration of visual scenes or to represent spatial information in a coordinate system that preserves metric information about spatial relations. Alternatively, the left hemisphere's deficit in perceptual matching may be due to the left hemisphere's propensity to elaboratively and symbolically encode stimuli and events. Further research is necessary to distinguish between possible underlying mechanisms.

Acknowledgements

reviewers for their helpful comments on an earlier draft of this paper.

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