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Hemispheric asymmetries for simple visual judgments in the split brain

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Abstract

While it is commonly noted that the right cerebral hemisphere is specialized for visuospatial processing, the scope and nature of this specialization remain somewhat ill defined. Our previous research with callosotomy ('split-brain') patients has suggested that the asymmetry may be limited to conditions that have an explicit spatial component. To investigate this we compared the performance of the divided hemispheres of two callosotomy patients on four simple visual-matching tasks. These tasks were orientation discrimination, vernier offset discrimination, size discrimination, and luminance discrimination. In each task, two stimuli were presented briefly to one visual hemifield and the patient was asked to discriminate whether they were the same or different. The first three tasks (orientation, vernier, and size) were all spatial in nature and were performed better by the right hemisphere. The luminance discrimination task, which is non-spatial, was performed equivalently by the two hemispheres. These results support the view that the fundamental difference in visual function between the hemispheres is in the ability to perform spatial discriminations. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The callosotomy or 'split-brain' operation involves the surgical section of the corpus callosum (and sometimes other forebrain commissures) for the relief of pharmacologically intractable epilepsy. A consequence of this operation is that the cerebral hemispheres are disconnected at the cortical level, so that most information cannot pass from one to the other. Although subcortical connections do remain intact, they do not appear to support interhemispheric transfer of any but the crudest perceptual information [21]. Thus, the study of split-brain patients affords a unique opportunity to research the abilities of the two hemispheres in isolation.

The left hemisphere's specialization for language has been known for more than a century. In contrast, the specialized abilities of the right hemisphere had been largely unrecognized before the systematic study of split-brain patients began in earnest during the 1960s. One of the earliest observations with split-brain patients was that right-handed patients were typically much better at solving visuospatial tasks with their left hands than with their right hands. For example, one task required patients to reproduce an abstract pattern by manipulating colored blocks using one hand or the other. The patients were able to perform this task quickly and accurately with their left hands, but were impaired when they used their right hands [2]. Similarly, patients were able to copy line drawings of simple three-dimensional objects (such as a Necker cube) with their left hands, but were impaired when drawing with their right hands [14]. This left-hand superiority was interpreted as a manifestation of a profound difference between the hemispheres for solving complex visuospatial tasks, with the right hemisphere performing better than the left [2,14].

These early studies investigated tasks that involved manual interaction with a stimulus, so although the results were consistent with the idea that the right

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hemisphere was specialized for complex visuospatial processing, it was unclear whether this asymmetry is in visual processing or arose at some later level. In fact, Gazzaniga and Le Doux [16] speculated that the right hemisphere specialization could be better conceived as manipulospatial than visuospatial. In other words, the asymmetry became evident only when the patient had to produce correct spatial arrangements using the hands.

Although the right hemisphere advantage may be exacerbated when direct manipulation is required, other research with split-brain patients confirms that there is indeed a perceptual asymmetry between the hemispheres. For example, Nebes [27–29] reported right-hemisphere advantages for several tasks requiring the integration of visual information across space. More recent split-brain research has shown that the right hemisphere outperforms the left hemisphere in a variety of other visual tasks. These include face recognition (e.g. [18]) mental rotation [3], amodal boundary completion [4], apparent motion perception [10], spatial matching [5] and mirror-image discrimination [11]. By the same token, other visual tasks have failed to yield any hemispheric asymmetry. These include spatial frequency discrimination [8], identity matching [5], anorthoscopic figure perception [9], and illusory-contour perception [4].

A key to understanding the hemispheric organization of the human brain is to determine whether there are some principles that would allow us to predict which tasks would be right lateralized. To date there is no completely satisfactory theory that can account for the pattern that has been observed in split-brain patients. One principle that emerges is that low-level visual processes seem to be essentially equivalent in the two hemispheres (e.g. [8]). This is logically appealing, since both hemispheres are evidently capable of some quite sophisticated visual processing. For instance, in most people the left hemisphere excels at reading and object recognition — tasks that both require fine visual discriminations. It follows that hemispheric asymmetries should arise at a relatively high level of visual processing. Furthermore, right-hemisphere specializations seem to appear consistently when the task requires an explicitly spatial judgement about the stimuli, whereas tasks that require judgements of object identity seem to be more or less equivalent in the two hemispheres (face recognition being a notable exception to this rule).

Visual information processing beyond the primary visual cortex is divided into two parallel pathways, dubbed the dorsal and ventral streams [33]. The dorsal visual stream includes areas in the superior occipital and parietal lobes, and is associated with spatial vision. The ventral stream, which includes areas in the inferior occipital and temporal lobes, has been associated with object recognition and related tasks. Functional neuroimaging studies in humans [6,19], as well as lesion studies [13] and electrophysiology [25] in primates all confirm this anatomical separation between spatial and object vision in higher visual processing.

An intriguing possibility that could account for the pattern of lateralization in visuospatial processing is that the functions of dorsal visual pathway are different in the two hemispheres, and tasks that rely heavily on processing in this pathway will be those that show hemispheric asymmetries. We have previously reported a dissociation between spatial and identity matching in two split-brain patients, with spatial matching performed better by the right hemisphere, and identity matching either bilateral or biased towards the left hemisphere [5]. Similarly, Koehler and colleagues [22] have reported a PET study that compared spatial and identity matching tasks. They found bilateral activation in ventral stream visual areas for identity matching, and right parietal activation for spatial matching. Taken together, these data support the idea that the functions of the dorsal visual pathway are lateralized so that spatial processing is better in the right hemisphere than in the left. The ventral pathway, in contrast, seems to be more or less bilateral.

In this series of experiments, we investigate this idea further. We hypothesize that split-brain patients will show robust hemispheric asymmetries in visual tasks requiring a spatial discrimination and little or no asymmetry when the discrimination is essentially non-spatial. We test the performance of two split-brain patients on four tasks that vary in their spatial demands. The tasks are orientation discrimination, vernier offset, size discrimination, and luminance discrimination. Of these, the first two are clearly spatial in nature, whereas luminance discrimination is essentially an intensity judgement. Size discrimination may fall somewhere in between. Although it is a spatial discrimination, it could also be considered as an intensity judgement, since large stimuli could be considered more intense than small stimuli. We therefore expect that the orientation discrimination and vernier offset detection tasks should yield a right hemisphere advantage and the luminance-discrimination task should be performed equivalently by the two hemispheres. We expect the size-discrimination task to yield a right-hemisphere advantage, but possibly smaller than that for the orientation and vernier tasks.

2. General methodology

2.1. Observers

Two right-handed split-brain patients, J.W. and V.P., served as observers in this series of experiments. J.W. is a 46-year-old man; V.P. is a 47-year-old woman. Both patients underwent two-stage callosotomy for the relief of intractable epilepsy in 1979. MRI scans acquired 5 years later confirmed the completeness of J.W.'s callosal section, but revealed some spared fibers in the rostrum of V.P.'s corpus callosum [15]. Despite this sparing, V.P.'s performance on perceptual tasks has revealed no evidence of interhemispheric transfer of visual information [12]. Further details of both patients' medical histories can be found in Gazzaniga et al. [17]. J.W. and V.P. are both experienced psychophysical observers and are familiar with the testing procedures employed.

2.2. Apparatus and procedures

The methodology employed in each experiment was identical save for the number and type of stimuli, which varied among experiments as described below. Examples of the stimuli used in each experiment are provided in Fig. 1. All stimuli were presented on an Apple multiple scan 720 monitor controlled by an Apple Macintosh G3 personal computer. The observer was seated in front of the monitor so that the distance from the center of the monitor to the observer's eyes was approximately 57 cm. Thus, 1 cm on the monitor subtended approximately 1° of visual angle. Throughout each experiment a small (0.5°) fixation cross was displayed in the center of the monitor, and the observer was instructed to fixate on the cross for the duration of each block of trials.

On each trial a pair of stimuli was presented for 150 ms, centered 4° to the left or right of the fixation point. The observer was required to indicate whether the two stimuli were the same or different by pressing the appropriate key on the computer keyboard. Responses were made with the first two fingers of one hand. The hand used to respond was counterbalanced between blocks. Each response initiated the next trial after a 500-ms delay. The number of trials in each block varied between experiments. At the conclusion of each block the observer was given a short break before continuing with the experiment.

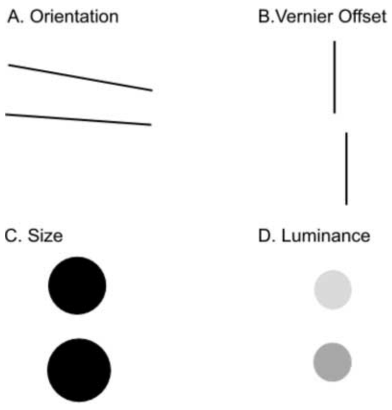

Fig. 1. Example of the stimuli used in the four experiments. (A) Experiment 1: orientation discrimination. (B) Experiment 2: vernier offset detection. (C) Experiment 3: size discrimination. (D) Experiment 4: luminance discrimination.

2.3. Data analysis

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 ensured that the stimulated hemisphere generated the response.

Because all these experiments involve analysis of single-subject data in which each hemisphere serves as a control for the other, statistical tests were carried out on the individual responses from each observer using hierarchical-χ^2 analyses [36]. The factors in each analysis were visual field (left vs. right), difference (degree to which the stimuli differed), condition (same vs. different), and response (same vs. different). In these analyses, response accuracy is indexed by the contingency between condition and response, and 'interactions' influencing accuracy are indexed by higher-order contingencies involving these two factors. Significant effects involving response but not condition indicate response biases orthogonal to accuracy.

In addition to the hierarchical χ^2 analyses, d' was computed for each discrimination as a measure of observers' ability to perform the relevant comparison.

3. Experiment 1: orientation discrimination

Benton et al. [1] have reported that patients with right hemisphere lesions frequently have difficulty judging the orientation of briefly presented lines. By comparison, patients with left hemisphere lesions generally performed about as well as controls. This suggests that the perceptual mechanism supporting judgments of orientation may be lateralized to the right hemisphere. Gazzaniga and Smylie [18] investigated this idea in three split-brain patients, J.W., V.P., and P.S. They found a robust right-hemisphere advantage in all three patients, which they attributed to an overall right hemisphere advantage for performing discriminations that are difficult to verbalize. Similarly, Corballis et al. [4] found a right hemisphere advantage in patients J.W. and V.P. for a task that required an orientation discrimination.

In the present experiment we employ a simultaneous-matching procedure in which two line segments are presented simultaneously and the patient is asked to judge whether the orientations are the same or different. Since this procedure makes the discrimination relatively easy to verbalize, any right hemisphere advantage can be attributed to an advantage for visuospatial processing rather than for nonverbal discriminations.

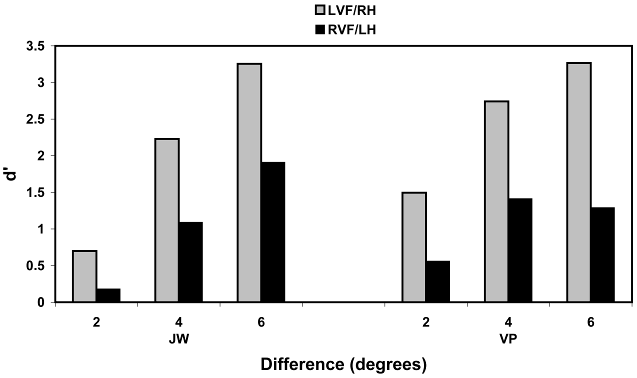

Fig. 2. Accuracy data for patients J.W. (left) and V.P. (right) in Experiment 1. Separate d'-values are shown for each visual field and orientation difference (2° increments). Data for stimuli presented to the left visual field (LVF/RH) are shown in gray, those for stimuli presented to the right visual field (RVF/LH) are shown in black.

3.1. Stimuli

Stimuli consisted of pairs of black line segments (luminance = 2.46 cd/m^2) presented side-by-side against a white background (luminance = 57.46 cd/m^2). The line segments each subtended approximately 3° of visual angle, and were separated by 1.5° at their midpoints. See Fig. 1 for an example. On half of the trials ('same' trials) the line segments were parallel. On the remaining trials ('different' trials) the line segments varied in orientation by 2, 4, or 6°. The orientations of the line segments were chosen so that no segment was ever exactly horizontal or vertical. The 'same' stimuli were created by generating a pair of horizontal parallel lines and rotating each about its midpoint by between 3 and 16°. The 'different' stimuli were created from the 'same' stimuli by rotating one of the lines by 2, 4, or 6° about its midpoint. The line chosen (top or bottom) and direction of rotation (clockwise or counterclockwise) were counterbalanced across trials within each block. On each trial the observer was required to judge whether or not the two line segments were parallel and respond by pressing the appropriate key on the computer keyboard. Each block of consisted of 96 trials. J.W. completed eight blocks and V.P. completed four blocks.

3.2. Results

Accuracy data for both J.W. and V.P. (plotted as d') are shown in Fig. 2. Separate plots are shown for each visual field and orientation difference. Inspection of Fig. 2 reveals that both patients were able to perform the task relatively accurately. It is also evident that both patients were more accurate when the stimuli are presented to the left visual field/right hemisphere (LVF/RH) than when they were presented to the right visual field/left hemisphere (RVF/LH).

3.2.1. Patient J.W.

The multidimensional χ^2 analysis revealed significant contingencies between difference and response ($\chi^2(2) = 49.54$, $P < 0.001$), condition and response ($\chi^2(1) = 179.25$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 54.63$, $P < 0.05$). These contingencies reflect the fact that J.W. was performing the task accurately (overall $d' = 1.32$), and that his performance was more accurate when the angle between the line segments was greater. There was also a significant three-way contingency between visual field, condition, and response ($\chi^2(1) = 5.83$, $P < 0.05$). This indicates that J.W. performed the task significantly more accurately when the stimuli were presented to the LVF (overall d' for LVF stimuli = 1.62) than when they were presented to the RVF (overall d' for RVF stimuli = 1.05). No other contingencies approached significance.

3.2.2. Patient V.P.

On the whole, V.P.'s performance was similar to J.W.'s. There were significant contingencies between difference and response ($\chi^2(2) = 11.14$, $P < 0.01$), condition and response ($\chi^2(1) = 113.27$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 13.15$, $P < 0.05$), which indicate that V.P. was performing the task accurately (overall $d' = 1.49$), and that her performance was more accurate for greater angular disparities between the line segments. There was also a significant contingency between field and response ($\chi^2(1) = 9.43$, $P < 0.01$), which reflects a different response bias for stimuli presented in each visual field. When the stimuli were presented to her LVF, V.P. responded 'no' (i.e. that the orientations were different) on 39% of the trials. The bias disappeared (or was reversed) for RVF stimuli, on which she responded 'no' on 54% of the trials. This bias probably represents a response-compatibility effect in which V.P. tended to hit the leftmost response key ('yes' key) on LVF trials, and the rightmost response key ('no' key) on RVF trials. Finally, there was also a significant three-way contingency between visual field, condition, and response ($\chi^2(1) = 8.21$, $P < 0.01$), which indicates that V.P.'s response accuracy differed between the two visual fields. Like J.W., and despite her bias to respond 'yes', V.P. was more accurate for LVF (overall d' for LVF stimuli = 2.34) stimuli than for RVF stimuli (overall d' for RVF stimuli = 1.04). No other contingencies approached significance.

3.3. Discussion

Both patients performed the orientation discrimination much more accurately when the stimuli were presented to the left visual hemifield. This result confirms previous data from split-brain patients, as well as from patients with unilateral brain lesions, which suggested that the mechanism supporting orientation judgements is lateralized to the right hemisphere.

4. Experiment 2: vernier offset detection

In this experiment, we compared the abilities of the two hemispheres to judge whether two similar line segments were colinear. Previous research suggests that tasks requiring perceptual completion (i.e. the integration of visual information across space) may be better solved by the right hemisphere than the left hemisphere (e.g. [4,35]). We thus expected that this task, like the orientation-discrimination task used in Experiment 1, would be performed better when the stimuli were presented to the LVF.

4.1. Stimuli

The stimuli consisted of pairs of black vertical line segments (luminance = 2.46 cd/m^2) presented against a white background (luminance = 57.46 cd/m^2). Each line segment subtended 2.5° of visual angle vertically, and vertical gap between the two segments subtended 0.5°. See Fig. 1 for an example. On half of the trials ('same' trials) the line segments were collinear. On the remaining trials ('different' trials) the line segments were horizontally offset by 0.5, 1, 1.5, 2, or 2.5° of visual angle. Which segment was offset (top or bottom) was counterbalanced across trials within each block. On each trial the observer was required to judge whether or not the two line segments were collinear and respond by pressing the appropriate key on the computer keyboard. Each block of consisted of 80 trials. J.W. completed eight blocks and V.P. completed four blocks.

4.2. Results

Accuracy data for both J.W. and V.P. (plotted as d') are shown in Fig. 3. Inspection of this figure reveals that both patients were able to perform the task accurately. It is also evident that both patients were more accurate when the stimuli were presented to the LVF/RH than when they were presented to the RVF/LH.

4.2.1. Patient J.W.

The multidimensional χ^2 analysis revealed significant contingencies between difference and response ($\chi^2(4) = 12.53$, $P < 0.05$), condition and response($\chi^2(1) = 187.52$, $P < 0.001$), and condition, difference, and response ($\chi^2(4) = 12.53$, $P < 0.05$). As in Experiment 1, these contingencies indicate that J.W. performed the task accurately overall (overall $d' = 1.51$), and that his accuracy was higher for greater degrees of offset. There was also a significant three-way contingency between visual field, condition, and response ($\chi^2(1) = 8.78$, $P < 0.01$), which indicates that J.W. was more accurate for stimuli presented to the LVF (overall $d' = 1.94$ for LVF stimuli) than for stimuli presented to the RVF (overall $d' = 1.14$ for RVF stimuli).

4.2.2. Patient V.P.

In this experiment too, the pattern of V.P.'s performance was similar to J.W.'s, although she was more accurate overall. Significant contingencies between condition and response ($\chi^2(1) = 205.09$, $P < 0.001$), and condition, difference, and response ($\chi^2(4) = 12.53$, $P < 0.05$), indicate that V.P.'s overall performance was accurate (overall $d' = 2.58$), and that her accuracy was higher for larger offsets. There was also a significant contingency between visual field, condition, and response ($\chi^2(1) = 8.78$, $P < 0.01$). This reflects the fact that V.P. was more accurate for LVF/RH stimuli (overall $d' = 3.74$ for LVF stimuli) than she was for RVF/LH stimuli (overall $d' = 1.93$ for RVF stimuli).

4.3. Discussion

The results of this experiment were similar to those from Experiment 1. Both patients were significantly better at the vernier-offset task when the stimuli were presented to the right hemisphere than when they were presented to the left hemisphere. This pattern of results is consistent with previous data suggesting that the mechanism underlying perceptual completion may be lateralized to the right hemisphere.

5. Experiment 3: size discrimination

In this experiment we investigated the abilities of the divided hemispheres to discriminate whether two circles are the same size. Like the two previous experiments, this task requires a relatively fine-grained spatial dis-

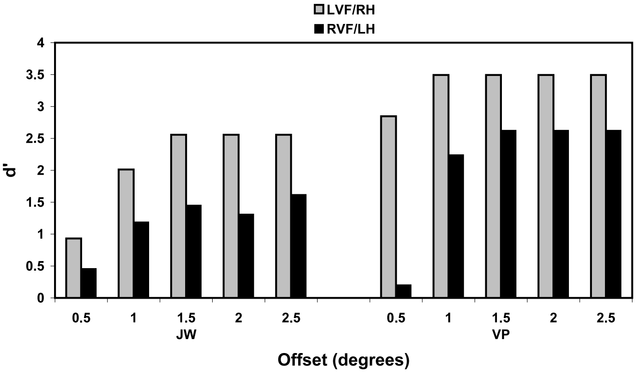

Fig. 3. Accuracy data for patients J.W. (left) and V.P. (right) in Experiment 2. Separate d'-values are shown for each visual field and offset (0.5° increments). Data for stimuli presented to the left visual field (LVF/RH) are shown in gray, those for stimuli presented to the right visual field (RVF/LH) are shown in black.

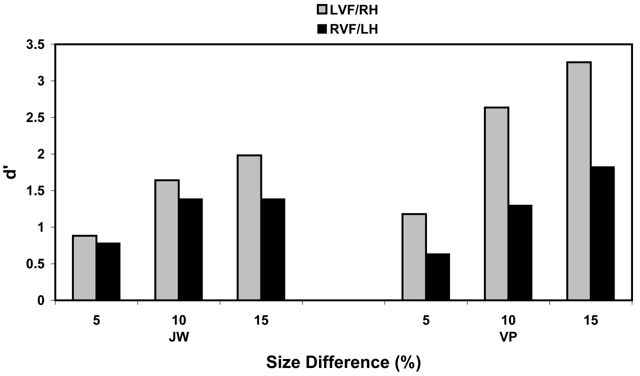

Fig. 4. Accuracy data for patients J.W. (left) and V.P. (right) in Experiment 3. Separate *d'*-values are shown for each visual field and size difference. Data for stimuli presented to the left visual field (LVF/RH) are shown in gray, those for stimuli presented to the right visual field (RVF/LH) are shown in black.

crimination. For this reason we expected the right hemisphere to perform the task more accurately than the left. Although this task was designed as a test of spatial discrimination, it could be approached as an intensity judgement, since large stimuli could be considered more intense than small stimuli. Thus, while we expect this task to yield a right-hemisphere advantage, the asymmetry may be less pronounced than for the two previous tasks.

5.1. Stimuli

Stimuli consisted of vertically aligned pairs of black circles (luminance = 2.46 cd/m^2) that varied in size, presented against a white background (luminance = 57.46 cd/m^2). See Fig. 1 for an example. On half of the trials ('same' trials) the two circles were the same size (diameter subtending 2.2° of visual angle). On the remaining half of the trials ('different' trials), one circle subtended 2.2° of visual angle, and the diameter of the other was multiplied by a scaling factor. The scaling factors were 0.85, 0.90, 0.95, 1.05, 1.10, and 1.15. Which circle was scaled (top or bottom) was counterbalanced across trials within each block. On each trial the observer was required to judge whether or not the two circles were the same size and respond by pressing the appropriate key on the computer keyboard. Each block of trials consisted of 96 trials. J.W. completed 20 blocks over four sessions and V.P. completed eight blocks over two sessions.

5.2. Results

Accuracy data for both J.W. and V.P. (plotted as d') are shown in Fig. 4. Inspection of this figure reveals that both patients were able to perform the task reasonably accurately, although V.P.'s performance was better than J.W.'s. It also suggests that both patients were more accurate when the stimuli were presented to the left visual field/right hemisphere (LVF/RH) than when they were presented to the right visual field/left hemisphere (RVF/LH). This difference is much more pronounced for patient V.P. than for patient J.W., however.

5.2.1. Patient J.W.

The multidimensional χ^2 analysis revealed that there were significant contingencies between difference and response ($\chi^2(2) = 6.46$, $P < 0.05$), condition and response($\chi^2(1) = 132.41$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 6.46$, $P < 0.05$). These indicate that J.W. performed the task reasonably accurately overall (overall $d' = 1.10$), and that his performance was better when the size difference between the stimuli was greater. No other contingencies reached significance, although the three-way contingency between visual field, condition, and response was suggestive ($\chi^2(1) = 2.63$, $P \approx 0.10$). Thus, although J.W. was slightly more accurate for LVF stimuli (overall $d' = 1.21$ for LVF stimuli) than for RVF stimuli (overall $d' = 1.00$ for RVF stimuli), there was no statistically reliable hemispheric difference in the performance of this task.

5.2.2. Patient V.P.

The multidimensional χ^2 analysis revealed significant contingencies between difference and response ($\chi^2(2) = 26.90$, $P < 0.001$), condition and response($\chi^2(1) = 248.07$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 24.88$, $P < 0.001$). These indicate that V.P. performed the task accurately overall (overall $d' = 1.58$), and that she tended to be more accurate when the size difference between the stimuli was greater. Unlike J.W., V.P. also showed a significant contingency between visual field, condition, and response ($\chi^2(1) = 11.05$, $P < 0.001$), which indicates that she was more accurate when the stimuli were presented in the LVF (overall $d' = 2.03$ for LVF stimuli) than when they were presented in the RVF (overall $d' = 1.19$ for RVF stimuli).

5.3. Discussion

Patient V.P. showed the expected pattern of asymmetries, with the right hemisphere outperforming the left for the size discrimination task. Despite performing 20 blocks of trials, patient J.W. showed no significant hemispheric difference, although there was a trend in the direction of a right hemisphere advantage. The reduced asymmetry found in J.W. may be due to the nature of the size-discrimination task. Although it is clearly a spatial task (and thus, according to our hypothesis, should be right lateralized), it is possible that one or both of J.W.'s hemispheres treated this task as an intensity discrimination, which is non-spatial. This could mitigate the right hemisphere advantage for spatial tasks. The methodology may also have weakened any hemispheric difference. Because all the 'same' circles were the same size, all that was required to perform the task was to determine whether one of the circles differed from the standard. Although it is unclear why, it is possible that such a strategy would reduce the right-hemisphere advantage. These issues notwithstanding, however, the results of this experiment suggest that size discrimination, like the orientation-discrimination and vernier-offset tasks, is most likely performed better by the right hemisphere than the left.

6. Experiment 4: luminance discrimination

The results of Experiments 1–3 are consistent with the notion that the right hemisphere outperforms the left when a spatial judgement is required. However, they are also consistent with the hypothesis that the right hemisphere will be superior for any perceptual task that requires discrimination between two simultaneously presented stimuli. To distinguish between these alternatives we employed a luminance discrimination task that was of similar difficulty to the tasks employed in the previous experiments, but that lacked the spatial component. We expected to find that both hemispheres were equally capable of performing this task.

6.1. Stimuli

Stimuli consisted of vertically aligned pairs of circles that varied in luminance, presented against a white background (luminance = 57.47 cd/m^2). See Fig. 1 for an example. The circles each subtended 1.2° of visual angle. The luminance values for each circle were chosen from a list of seven possible values: 12.96, 19.67, 25.07, 33.07, 38.30, 47.54, 52.67 cd/m^2. On half of the trials ('same' trials) the two circles were the same luminance. On the remaining half of the trials ('different' trials), the circles differed in luminance by one, two, or three 'steps.' On each trial the observer was required to judge whether or not the two circles had the same luminance and respond by pressing the appropriate key on the computer keyboard. Each block consisted of 72 trials. J.W. completed 16 blocks and V.P. completed eight blocks. The hand used to respond was counterbalanced across trial blocks.

6.2. Results

Accuracy data for both J.W. and V.P. (plotted as *d′*) are shown in Fig. 5. Inspection of this figure reveals that both patients were able to perform the task relatively accurately. There are no obvious systematic differences in *d′* between LVF/RH and RVF/LH stimuli, although there is some suggestion that V.P. performed better when the stimuli were presented in the RVF/LH than when they were presented in the LVF/RH, especially for greater luminance differences.

6.2.1. Patient J.W.

The multidimensional χ^2 analysis revealed significant contingencies between difference and response ($\chi^2(2) = 31.81$, $P < 0.001$), condition and response($\chi^2(1) = 250.08$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 37.30$, $P < 0.001$), which indicate that J.W. was performing the task accurately (overall $d' = 1.98$), and that his performance was better when the luminance difference between the stimuli was greater. No other contingencies approached significance. The overall *d′* for LVF stimuli was 1.99, and the overall *d′* for RVF stimuli was 1.97. Thus, there was no evidence for any difference between the hemispheres for the performance of this task.

6.2.2. Patient V.P.

There were again significant contingencies between field and response ($\chi^2(1) = 31.22$, $P < 0.001$), difference and response ($\chi^2(2) = 11.74$, $P < 0.01$), condition and response($\chi^2(1) = 146.22$, $P < 0.001$), and condition, difference, and response ($\chi^2(2) = 14.24$, $P < 0.001$). These contingencies reflect the fact that V.P. performed the task accurately (overall $d' = 1.36$), and that her performance was better when the luminance difference between the stimuli was greater. No other contingencies approached significance. The overall *d′* for LVF stimuli was 1.31, and the overall *d′* for RVF stimuli was 1.62. Thus, if anything there was a slight RVF advantage for performance of this task, although it did not reach statistical significance.

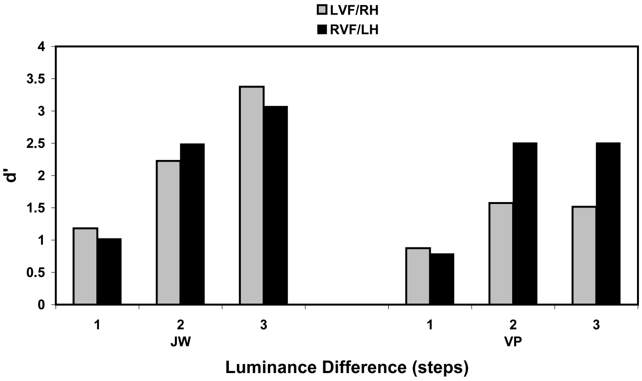

Fig. 5. Accuracy data for patients J.W. (left) and V.P. (right) in Experiment 4. Separate *d′*-values are shown for each visual field and luminance step. Data for stimuli presented to the left visual field (LVF/RH) are shown in gray, those for stimuli presented to the right visual field (RVF/LH) are shown in black.

6.3. Discussion

No evidence for hemispheric asymmetry was found for this task. In fact, the only hint of asymmetry in this task is in the opposite direction to the right-hemisphere dominance for the spatial tasks used in the previous experiments. Although the lack of a statistically-significant difference is not conclusive evidence against the existence of a hemispheric asymmetry, comparison with Experiments 1–3 suggests that any asymmetry for luminance discrimination is likely to be quite small and qualitatively different from the asymmetry underlying the performance of spatial discriminations. Taken together with the previous results, these data support our hypothesis that hemispheric asymmetries would only manifest when a spatial judgement was required.

7. General discussion

The results of the four experiments reported here confirm our hypothesis that hemispheric asymmetries in visual matching tasks would be restricted to conditions that require a spatial discrimination. Right-hemisphere advantages were found for the three spatial tasks (orientation discrimination, vernier offset detection, and size discrimination), but not for the non-spatial task (luminance discrimination). Our data must be considered in the context of the experimental situation. That is, the stimuli were all briefly presented, unmasked, and presented outside of foveal vision. The stimulus parameters were chosen to ensure that the stimuli would be processed by the appropriate hemisphere, and without regard for the optimal parameters for performing visual discriminations. It is possible, albeit unlikely, that variations in the stimulus presentation time could reduce, eliminate, or even reverse the hemispheric asymmetry we report here. In a previous study [11] we found that allowing effectively unlimited presentation time had no effect on hemispheric differences in a mirror-image discrimination task. Because of the similarities between that paradigm and the one used in this study, we think it unlikely that longer presentations would have any effect on the asymmetry here either.

Several theories have been proposed to account for the differences in visual function between the hemispheres in humans. These theories all posit that different aspects of visual processing are lateralized to each hemisphere, and that each hemisphere contributes its expertise to the final percept. For example, Sergeant [31] has suggested that the left hemisphere is biased towards processing the high spatial frequency components of a visual stimulus, whereas the right hemisphere is biased towards the low spatial frequencies. Similarly, Robertson and colleagues [7,30] have proposed that the left hemisphere preferentially processes the local details of a visual stimulus, whereas the right hemisphere processes its global configuration. A third theory suggests that the fundamental hemispheric difference between the two hemispheres lies in the way in which they represent spatial information. According to this theory, the left hemisphere tends to represent spatial information using categorical labels such as ‘above’ or ‘to the right of.’ In contrast, the right hemisphere represents spatial relationships in a metric, coordinate framework [23,24]. This proposal is not unlike that of Gazzaniga and Smylie [18], who proposed that the right hemisphere had an advantage for representing spatial relationships that could not be easily verbalized.

Our results are more-or-less consistent with the ‘global/local’ and ‘categorical/coordinate’ hypotheses insofar as both of them suggest that the left hemisphere will tend to represent spatial relationships less accurately than the right hemisphere. However, the spatial judgements required in our experiments are fairly easily represented categorically or verbally so it is not obvious that these theories would necessarily predict our results a priori. Instead, we suggest that both the global/local and categorical/coordinate distinctions between the hemispheres are secondary to a hemispheric difference in the functions of the dorsal visual stream. This idea accounts for the observation that perceptual asymmetries do not occur across the board, but are generally limited to spatial tasks.

The tasks we have chosen could, in principle, all be solved early in visual processing, so these results could be taken as evidence for asymmetries as early as the primary visual cortex. We suspect, however, that basic visual processes are probably more-or-less bilateral, and that the asymmetry arises later in the visual system [8]. Our previous research [5] has shown that hemispheric asymmetries are more dependent on the task than on the stimulus, which suggests that they arise after basic visual analysis has been completed. Furthermore, evidence from visual-search studies indicates that the visual system relies on the highest level representations available for decision making rather than using low-level analyses — even when this is detrimental to performance [20,32]. Thus, if asymmetries exist at stages of processing between low-level analysis and response selection they may be reflected in task performance, even if the output of low-level areas ought to be sufficient to perform the task.

The appearance of asymmetries relatively late in visual processing makes computational sense. Since both hemispheres require accurate visual representations of the visual field at a variety of spatial scales, it seems unlikely that the fundamental visual asymmetry arises in visual areas with unilateral receptive fields. Instead, visuospatial asymmetries might be expected to evolve in cortical areas with bilateral receptive fields (such as most of the dorsal visual stream; e.g. [26]), leaving the homologous visual areas in the other hemisphere unaffected. This would allow asymmetric mechanisms to develop with little or no overall processing cost. Modifications to the processing of one hemisphere would not affect existing functions since the other hemisphere could still perform them. Asymmetries in visual areas with small, unilateral receptive fields seem unlikely, since they could result in quite dramatic differences in processing of different regions of the visual field, which may have serious evolutionary consequences[1].

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[1] Visual asymmetries have, in fact, been documented in several vertebrate species. For example asymmetries can be observed in the lateral, monocular visual fields of species with laterally placed eyes such as fish, reptiles, and birds. As might be expected, these asymmetries do have observable behavioral implications for members of these species (see Ref. [34] for a review). Whether these asymmetries have the same evolutionary origins as the asymmetries we observe in humans is unknown.

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