

Spatial Processing and Hemispheric Asymmetry: Contributions of the Transient/Magnocellular Visual System

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Abstract

■ Right-handed observers were presented with stimuli consisting of a line and two horizontally separated dots. A categorical spatial task required observers to indicate whether the dots were above or below the line, and a coordinate spatial task required observers to indicate whether the line could fit into the space between the two dots. For the coordinate task, reaction time was faster when the stimuli were presented to the left visual field (right hemisphere) than when the stimuli were presented to the right visual field (left hemisphere). The opposite hemispheric asymmetry was obtained for the categorical task. In addition, coordinate spatial processing took longer with stimuli presented on a red background than with

stimuli presented on a green background. The opposite trend characterized categorical spatial processing. Because the color red attenuates processing in the transient/magnocellular visual pathway, these results suggest that coordinate spatial processing is more dependent on the transient/magnocellular pathway than is categorical spatial processing. However, manipulations of color condition had no effect on visual field (hemispheric) asymmetries, suggesting that the two hemispheres rely on the same visual information and on the same computational mechanisms as each other—although they do not always use that information with equal efficiency. ■

INTRODUCTION

It has been hypothesized that the brain computes at least two kinds of spatial relation representations. One type of representation (categorical) is used to assign a spatial relation to a category such as “connected to” or “above,” whereas the other type of representation (coordinate) is used to represent precise distances and locations in a metric coordinate system. Recent experiments suggest that the right cerebral hemisphere makes more effective use of coordinate or metric distance information about spatial relationships, whereas there is either no hemispheric asymmetry or a left-hemisphere advantage for processing information about categorical spatial relationships (for reviews, see Hellige, 1993, 1995, 1996, 1997; Kosslyn, 1987, 1994; Kosslyn & Koenig, 1992; Kosslyn et al., 1989).

Several visual half-field experiments from a number of different laboratories have produced results consistent with the hypotheses just outlined. For example, in visual half-field experiments with normal, right-handed observers a left-visual-field/right-hemisphere (LVF/RH) advantage has been reported consistently for tasks that require observers to indicate whether or not two stimuli (e.g., a line and a dot) are within a certain distance of each other (e.g., nearer than 3 cm to each other or farther than 3 cm from each other). By way of contrast,

when observers are required to make a categorical spatial judgment about the same stimuli (e.g., is a dot above or below a line), there is typically a trend toward a right-visual-field/left-hemisphere (RVF/LH) advantage (with the RVF/LH advantage sometimes being statistically significant and sometimes not). In addition, in some studies, this Task by Visual Field interaction disappears with practice, possibly because observers learn to perform the distance judgment task in a more categorical way (for examples of this Task by Visual Field interaction see Cowin & Hellige, 1994; Crebolder & Bryden, 1996; Hellige et al., 1994; Hellige & Michimata, 1989; Kosslyn, 1987; Kosslyn et al., 1989; Koenig, Reiss, & Kosslyn, 1990; Laeng, 1994; Laeng & Peters, 1995; Michimata, 1997; Rybash & Hoyer, 1992).

Kosslyn, Chabris, Marsolek, and Koenig (1992; see also Kosslyn & Koenig, 1992) have provided a conceptualization of spatial processing that emphasizes the nature of the visual information that is most useful for computing categorical versus coordinate information. In a set of neural-network computer simulations, Kosslyn et al. (1992) found that networks that received input that had been filtered through units with relatively large, overlapping “receptive fields” computed coordinate spatial information better than networks that received input that had been filtered through units with relatively small, nonoverlapping receptive fields. Exactly the reverse was

found for the computation of categorical spatial information (for critique and additional discussion of these neural network simulations see Cook, Fruh, & Landis, 1995; Kosslyn et al., 1995).

It has been hypothesized that the processing of visual information in primates is accomplished by two parallel visual pathways with different spatial and temporal characteristics (for discussion, see Breitmeyer, May, & Heller, 1991; Breitmeyer & Williams, 1990; Livingstone & Hubel, 1984, 1987, 1988; Schiller & Malpeli, 1978; Shapley, 1994; Van Essen, 1985). In general, the *magnocellular* system is most sensitive to low spatial frequencies, has high temporal resolution, and responds quickly and transiently to moving targets. This system is thought to be involved in such things as brightness discrimination, the perception of motion and depth, and the localization of visual stimuli in coordinate space and in the global analysis of visual scenes. By way of contrast, the *parvocellular* system is most sensitive to high spatial frequencies, has a long response persistence, and responds in a sustained fashion to stationary targets. This system is thought to be involved in such things as the identification of visual patterns, especially small local details, and in color perception. Given the characteristics attributed to these two visual pathways, one possible interpretation of the neural network results described earlier is that categorical and coordinate spatial processing depend relatively more on information carried by the parvocellular and magnocellular pathways, respectively.

To account for the hemispheric differences in categorical versus coordinate processing, Kosslyn and colleagues (1992) hypothesized that the left hemisphere is predisposed toward efficient use of information from visual channels with small, nonoverlapping receptive fields, whereas the right hemisphere is predisposed toward efficient use of information from visual channels with large, overlapping receptive fields. In support of their hypothesis, Kosslyn et al. suggested that magnocellular ganglia (which tend to have relatively large receptive fields) may project preferentially to the right hemisphere (although, as discussed later, more recent results question such a low-level interpretation of hemispheric asymmetry). In addition, Kosslyn et al. noted that, at some level of processing beyond the sensory cortex, the left and right hemispheres seem to be dominant for processing visual information carried by channels tuned to relatively high and low spatial frequencies, respectively (e.g., Christman, 1989, 1990; Christman, Kitterle, & Hellige, 1991; Hellige, 1993, 1996, 1997; Ivry & Robertson, 1998; Kitterle, Christman, & Conesa, 1993; Kitterle, Christman, & Hellige, 1990; Kitterle & Selig, 1991; Sergent, 1983, 1987; Sergent & Hellige, 1986).

Although the neural network simulations reported by Kosslyn et al. (1992) have been criticized (Cook et al., 1995), and alternative interpretations of the simulations are possible, the hypotheses that were generated by the simulations can be subjected to empirical test. There are

two types of predictions about the effects of experimental manipulations that serve to accentuate or attenuate processing in visual streams that have characteristics similar to those attributed to the input filtering units of the neural network models. One type of prediction has to do with the effect of experimental manipulations on categorical versus coordinate processing tasks—and this type of prediction does not directly involve hemispheric asymmetry. For example, an experimental manipulation that attenuated processing along the magnocellular visual pathway would be expected to disrupt coordinate spatial processing more than categorical spatial processing. The other type of prediction has to do with the Task by Hemisphere interaction. For example, to the extent that the two hemispheres utilize different aspects of the visual information to perform efficiently, the attenuation of one type of information should have a greater detrimental effect on the hemisphere that is more dependent on that type of information (for examples of this logic in the domain of visual identification, see Hellige, 1993; Johnson & Hellige, 1986).

With these predictions in mind, it is useful to consider the following experiment reported by Cowin and Hellige (1994), which examined the effects of dioptric blurring on categorical (above/below) and coordinate (near/far) spatial processing tasks using line and dot stimuli similar to those described earlier. Dioptric blurring selectively impairs processing of relatively high visual spatial frequencies and, according to the hypotheses outlined, such blurring should be particularly disruptive of categorical spatial processing. In fact, dioptric blurring consistently increased reaction time and error rate for a categorical task that required observers to indicate whether a dot was above or below a line. However, the amount of dioptric blurring that was used had no consistent effect on either reaction time or error rate for a coordinate task that required observers to indicate whether the dot was within 3 mm of the line. On an initial block of trials, there were significantly fewer errors on LVF/RH than on RVF/LH trials for the coordinate processing task, and this LVF/RH advantage was independent of whether the stimuli were clear or blurred. Although this experiment was not designed with parvocellular and magnocellular pathways in mind, a dioptric blurring manipulation might be expected to differentially attenuate processing along the *parvocellular* pathway. Thus, these results suggest that processing along this pathway is more critical for categorical than for coordinate spatial processing. The present experiment was designed to examine categorical and coordinate spatial processing for stimulus conditions that more directly attenuate processing along the *magnocellular* visual pathway.

Breitmeyer and his colleagues (e.g., Breitmeyer et al., 1991; Breitmeyer & Williams, 1990; Williams, Breitmeyer, Lovegrove, & Guitierrez, 1991) have reported that both metacontrast masking and the perception of strobo-

scopic motion are considerably weaker when stimuli are presented on a red background than on an isoluminant green background. Neurophysiologically based models of metacontrast and stroboscopic motion indicate that both phenomena result from the interaction of two visual subsystems: the sustained subsystem and the transient subsystem. As Breitmeyer and colleagues note, the parvocellular and magnocellular pathways in monkeys may be neural analogs of the more functionally defined sustained and transient channels, respectively. Within the context of a sustained-transient channel approach, metacontrast masking is produced when the faster responding transient channels activated by the subsequent mask inhibit the slower responding sustained channels activated by the target. The perception of stroboscopic motion is thought to be the result of response integration within the transient visual system. Thus, the fact that a red background reduces both metacontrast masking and the perception of stroboscopic motion indicates that the activity of transient visual channels is attenuated by red relative to green backgrounds. From this perspective, it is interesting that a subpopulation of magnocellular neurons have receptive fields that are characterized by a red-dominant surround mechanism (e.g., DeMonasterio, 1978; DeMonasterio & Schein, 1980; Livingstone & Hubel, 1984; Marrocco, McClurkin, & Young, 1988; Wiesel & Hubel, 1966). As noted by Breitmeyer and Williams (1990), this may be the reason why diffuse red light has been found to provide tonic suppression of activity in certain neurons contained in the magnocellular pathway (Dreher, Fukuda, & Rodieck, 1976; Livingstone & Hubel, 1984; Van Essen, 1985). In view of the results reported by Breitmeyer and colleagues, we reasoned that the use of green stimuli on an isoluminant red background would attenuate processing along the magnocellular pathway relative to the parvocellular pathway. To the extent that processing along the magnocellular pathway is more important for coordinate spatial processing than for categorical spatial processing, coordinate processing should be more disrupted by the use of green-on-red compared to red-on-green stimulus conditions.

EXPERIMENT 1

In the present experiments, the stimuli on each trial consisted of a horizontal line and two dots, with the dots being on the same horizontal level as each other (see Figure 1). The line varied in length from trial to trial as did the horizontal distance between the two dots. The categorical task required observers to indicate whether the dots were above or below the line, whereas the coordinate task required observers to indicate whether or not the line on that trial could fit between the two dots. These stimuli and tasks were patterned after those used by Rybash and Hoyer (1992) and were shown in previous experiments to produce a robust Task by Hemisphere interaction.

In Experiment 1, half of the observers performed the categorical (above/below) task and half performed the coordinate (fits/doesn't fit) task. Within each of these two groups, half of the observers received red stimuli on a green background and half received green stimuli on a red background. Each observer completed four 24-trial blocks, with each block consisting of each of the 12 possible stimuli shown in Figure 1 presented once to the LVF/RH and once to the RVF/LH. According to the hypothesis considered earlier, performance of the coordinate task should be worse (e.g., longer reaction times) for the green-on-red condition than for the red-on-green condition. By way of contrast, performance of the categorical task should show either no effect of color or an effect in the opposite direction. Furthermore, to the extent that right-hemisphere performance is more dependent than left-hemisphere performance on processing along the transient/magnocellular pathway, the use of green-on-red stimulus displays should be more disruptive on LVF/RH trials than on RVF/LH trials.

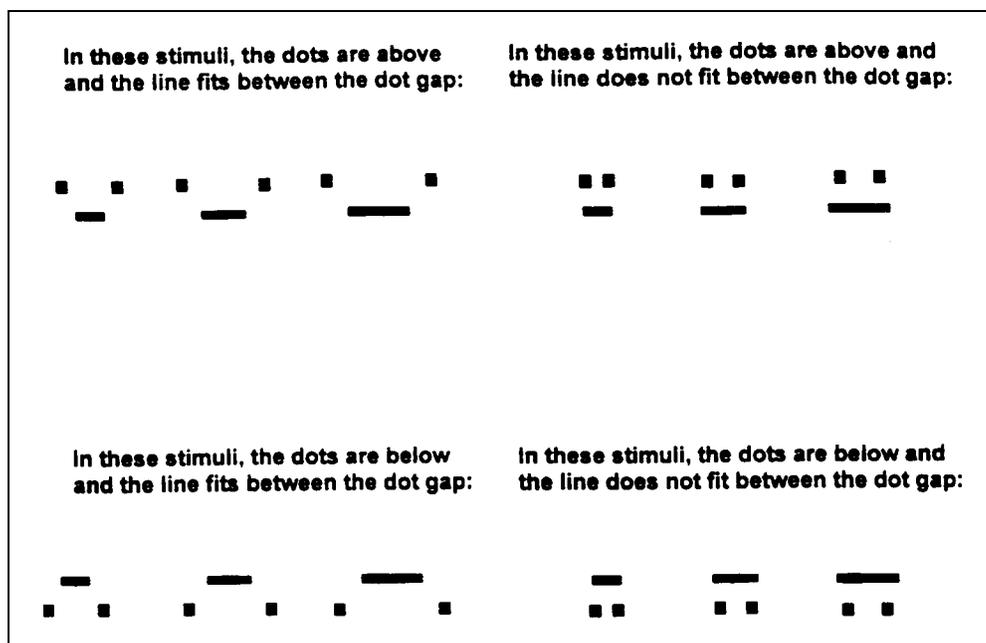
Results and Discussion

The median reaction time of correct responses and the percentage of errors were recorded for each subject for each of eight types of trials defined by the orthogonal combination of Trial Block (1, 2, 3, 4) and Visual Field (LVF, RVF). Recall that participants were placed into one of four groups, defined by the orthogonal combination of Task (Categorical, Coordinate) and Color Condition (green-on-red, red-on-green). The combination of all of these variables produces 32 experimental conditions and a mean reaction time score and mean percentage of error score for each. A positive correlation ($r = +0.68$) between these two scores indicates that the pattern of results was generally similar for both dependent measures. In view of this, and because the percentage of errors was so low (4.79%) as to produce ceiling effects, only the reaction time data are presented.

Reaction times were subjected to an analysis of variance (ANOVA) that included the between-subjects variables of Task, Background Color, Gender and Finger Order (a counterbalancing variable), and the within-subjects variables of Trial Block and Visual Field. There were no significant effects involving either Gender or Finger Order, so the results are presented collapsed across these variables.

The only effect involving visual field to approach statistical significance was the Task by Visual Field interaction, $F(1, 62) = 3.62$, $MSe = 2770.9$, $0.05 < p < 0.10$. Although not significant in the ANOVA, this interaction was statistically significant in a one-tailed planned comparison, $t(62) = 1.903$, $p < 0.05$. For the coordinate task, reaction time was faster on LVF/RH trials ($M = 746$ msec) than on RVF/LH trials ($M = 754$ msec), but for the categorical task, reaction time was faster on RVF/LH trials ($M = 593$ msec) than on LVF/RH trials ($M = 603$ msec).

Figure 1. Illustrations of the line and dot stimuli used in the present experiments.



msec). This pattern is in the direction found in earlier experiments and is consistent with the hypothesis advanced by Kosslyn (1987). However, there were no indications that the nature of this interaction was influenced by practice or by the color condition of the stimuli. (Using red backgrounds, Categorical LVF/RH $M = 574$ msec, Categorical RVF/LH $M = 565$ msec, Coordinate LVF/RH $M = 791$ msec, and Coordinate RVF/LH $M = 800$ msec. Using green backgrounds, Categorical LVF/RH $M = 632$ msec, Categorical RVF/LH $M = 621$ msec, Coordinate LVF/RH $M = 700$ msec, and Coordinate RVF/LH $M = 707$ msec.) Because none of the other effects involving visual field even approached statistical significance, the remaining results are presented collapsed across visual field.

Figure 2 shows reaction time for categorical and coordinate processing tasks as a function of background color, with the results collapsed across the four trial blocks. As shown in Figure 2, reaction time was significantly faster for the categorical task than for the coordinate task, producing a significant main effect of task, $F(1, 48) = 54.35$, $MSe = 53774.3$, $p < 0.001$. Of particular theoretical importance was a significant Task by Background Color interaction, $F(1, 48) = 13.23$, $MSe = 53774.3$, $p < 0.001$. As shown in Figure 2, for the coordinate task, reaction time was significantly slower with a red background than with a green background, $F(1, 30) = 8.98$, $MSe = 60723.7$, $p < 0.01$. For the categorical task, there was a trend in the opposite direction. That is, reaction time was slower with a green background than with a red background, $F(1, 30) = 3.92$, $MSe = 52668.8$, $0.05 < p < 0.10$.

The Task by Background Color interaction was present as early as the first trial block, and its magnitude did not

change with practice. This can be seen clearly in Figure 3, which shows reaction time during each of the four trial blocks for each of the four experimental groups defined by the combination of task and color condition: categorical-red background (CAT-R), categorical-green background (CAT-G), coordinate-red background (COO-R), and coordinate-green background (COO-G). As Figure 3 also shows, reaction time generally decreased across trial blocks, producing a significant main effect of block, $F(3, 144) = 40.62$, $MSe = 5512.3$, $p < 0.001$. The decrease in reaction time across blocks was larger for

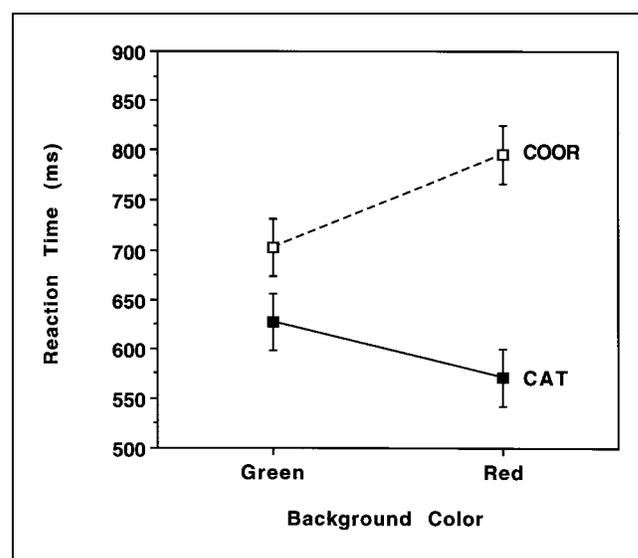


Figure 2. Reaction time for categorical (CAT) and coordinate (COOR) processing tasks in Experiment 1 as a function of background color. Error bars show standard errors computed from the between-subject error term (Loftus & Masson, 1994).

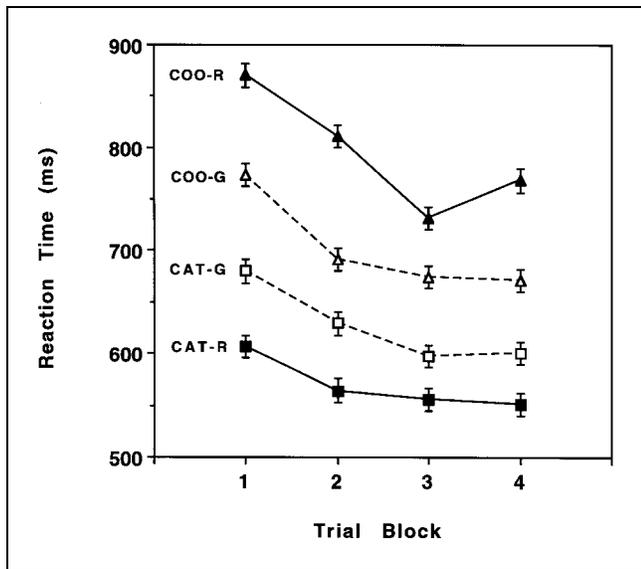


Figure 3. Reaction time during each of four trial blocks of Experiment 1 for each of the four experimental groups defined by the combination of task and color condition: categorical-red background (CAT-R), categorical-green background (CAT-G), coordinate-red background (COO-R), and coordinate-green background (COO-G). Error bars show standard errors computed from the within-subject error term (Loftus & Masson, 1994).

the coordinate task than for the categorical task, producing a significant Task by Block interaction, $F(3, 144) = 2.72$, $MSe = 5512.3$, $p < 0.05$.

We reasoned that the use of green stimuli on a red background would attenuate processing along the transient/magnocellular pathway relative to the opposite stimulus condition. With this in mind, it is interesting that there was a very robust Task by Color Condition interaction. As shown in Figures 2 and 3, for the coordinate task, reaction time was significantly longer in the red background condition than in the green background condition. For the categorical task, exactly the opposite was found. Note that this interaction is consistent with the hypothesis that the coordinate task is more dependent on magnocellular processing than is the categorical task. There was no indication that the Task by Visual Field interaction depended on the color condition of the display (even in analyses restricted to the first trial block), suggesting that the visual field differences that contribute to this interaction are independent of the efficiency with which information can be processed along the magnocellular visual pathway.

EXPERIMENT 2

It is not clear from the results of Experiment 1 how much of the color-condition effect is attributable to the background color and how much is attributable to the color of the stimuli. Because metacontrast masking using black stimuli is reduced with the use of red compared

to green backgrounds (e.g., Breitmeyer & Williams, 1990), much of the color-condition effect from Experiment 1 is probably attributable to background color. In order to examine this, Experiment 2 was identical to Experiment 1 with the exception that black stimuli were presented on red or green backgrounds on one set of trials and red or green stimuli were presented on a black background for another set of trials. Specifically, half of the observers were assigned randomly to the categorical task and the remainder were assigned to the coordinate task. For each task, half of the observers were assigned to receive the color green and half were assigned to receive the color red. Each participant performed a 96-trial task twice, once with black stimuli on the appropriately colored background and once with appropriately colored stimuli on a black background. The order of the colored stimuli and colored background conditions was counterbalanced across participants, creating groups that differed in the order of color components (background color first or stimulus color first).

To the extent that the color condition effects from Experiment 1 were produced by background color, similar effects should be found in Experiment 2 when color is restricted to the background. For example, for the coordinate spatial processing task, reaction time should be longer with a red background than with a green background—despite the fact that the stimuli are black. To the extent that the color condition effects from Experiment 1 were produced by stimulus color, similar effects should be found in Experiment 2 when color is restricted to the stimulus. For example, for the coordinate spatial processing task, reaction time should be longer with a green stimulus than with a red stimulus—despite the fact that the background is black.

Results and Discussion

The median reaction time of correct responses and the percentage of errors were recorded for each subject for each of 16 types of trials defined by the orthogonal combination of Trial Block (1, 2, 3, 4), Visual Field (LVF, RVF), and Color Component (Background Color, Stimulus Color). Recall that participants were placed into one of eight groups, defined by the orthogonal combination of Task (Categorical, Coordinate), Color (green, red), and Order of Color Components (Background Color First, Stimulus Color First). The combination of all of these variables produces 128 experimental conditions and a mean reaction time score and a mean percentage of error score for each. A positive correlation ($r = 0.46$) between these two scores indicates that the pattern of results was generally similar for both dependent measures. In view of this, and because the percentage of errors was very low (4.0%), only the reaction time data are presented.

Reaction times were subjected to an ANOVA that included the between-subjects variables of Task, Color, Or-

der of Color Components, Gender and Finger Order (a counterbalancing variable), and the within-subjects variables of Trial Block, Visual Field, and Color Component. There were no effects involving either Gender or Finger Order, so the results are presented collapsed across these variables.

As in Experiment 1, the only significant effect involving visual field was the Task by Visual Field interaction, $F(1, 96) = 8.46$, $MSe = 2518.9$, $p < 0.005$. For the coordinate task, reaction time was significantly faster for LVF/RH trials (660 msec) than for RVF/LH trials (666 msec) and for the categorical task, reaction time was significantly faster for RVF/LH trials (573 msec) than for LVF/RH trials (582 msec), both $ps < 0.05$. Note that this interaction pattern is similar to that found in Experiment 1 and in previous investigations of hemispheric asymmetry for categorical versus coordinate spatial processing. As in Experiment 1, there were no indications that the nature of this interaction was influenced by either practice or by the color present in the display. (Using red backgrounds or stimuli, Categorical LVF/RH $M = 571$ msec, Categorical RVF/LH $M = 569$ msec, Coordinate LVF/RH $M = 699$ msec, and Coordinate RVF/LH $M = 706$ msec. Using green backgrounds or stimuli, Categorical LVF/RH $M = 593$ msec, Categorical RVF/LH $M = 578$ msec, Coordinate LVF/RH $M = 620$ msec, and Coordinate RVF/LH $M = 626$ msec.) Because none of the other effects involving visual field approached statistical significance, the remaining results are presented collapsed across visual field.

Figure 4 shows reaction time for categorical and coordinate processing tasks as a function of the color contained in the display, with the results collapsed across all trial blocks. The upper panel shows the results when black stimuli were presented on a colored background, and the lower panel shows the results when colored stimuli were presented on a black background. As shown in Figure 4, reaction time was significantly faster for the categorical task than for the coordinate task, producing a significant main effect of task, $F(1, 96) = 22.98$, $MSe = 134676.1$, $p < 0.001$. Of particular theoretical importance was a significant Task by Color interaction, $F(1, 96) = 7.16$, $MSe = 134676.1$, $p < 0.01$. As suggested by Figure 4, for the coordinate task, reaction time was significantly slower when the display contained red than when the display contained green, $F(1, 48) = 10.04$, $MSe = 138247.4$, $p < 0.005$. For the categorical task, there was a small, nonsignificant trend in the opposite direction. As a comparison of the upper and lower panels of Figure 4 suggests, the Task by Color interaction was independent of whether the color was contained in the background or in the stimulus. That is, there was no hint of a Task by Color by Color Component interaction or of any higher-order interaction that involved these three variables.

As in Experiment 1, the Task by Color interaction was present as early as the first trial block and its magnitude

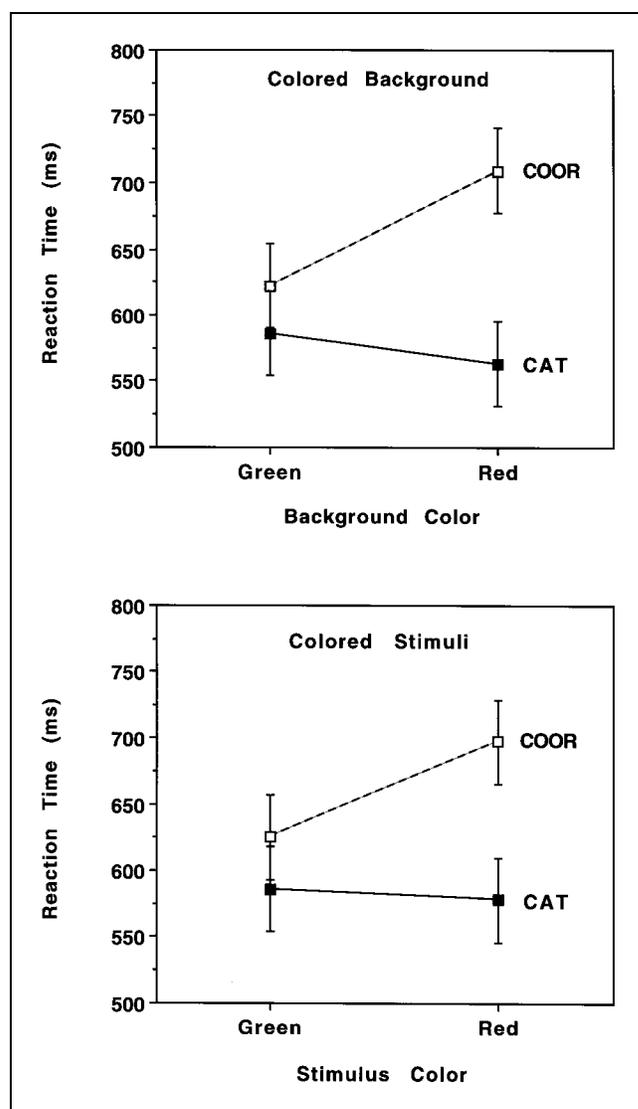


Figure 4. Reaction time for categorical (CAT) and coordinate (COOR) processing tasks in Experiment 2 as a function of the color contained in the display. The upper panel shows the results when black stimuli were presented on a colored background and the lower panel shows the results when colored stimuli were presented on a black background. Error bars show standard errors computed from the between-subject error term (Loftus & Masson, 1994).

did not change with practice. This can be seen clearly in Figure 5, which shows reaction time during each of the eight trial blocks for each of the eight experimental groups. The results in the upper panel are from participants who received the background color condition first and then switched to the stimulus color condition. That is, on trial blocks 1 through 4 black stimuli were presented on a colored *background* and on trial blocks 5 through 8 colored *stimuli* were presented on a black background. The results in the lower panel are from participants who received the stimulus color condition first and then switched to the background color condition. Within each panel, the results are shown for each of the four groups defined by the combination of task

and color: categorical-red (CAT-R), categorical-green (CAT-G), coordinate-red (COO-R), and coordinate-green (COO-G).

In addition to the effects already discussed, Figure 5 shows that observers were generally faster during the second half of the experiment (blocks 5 through 8) than during the first half of the experiment (blocks 1 through 4). Because the order of the color component was varied across participants, in the present ANOVA this is

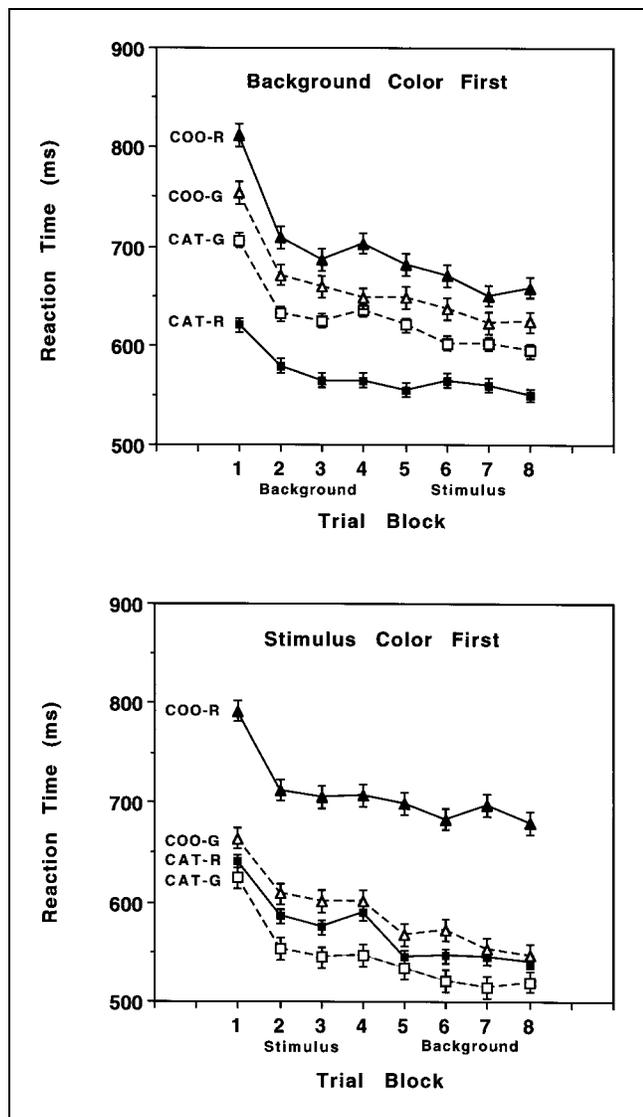


Figure 5. Each panel shows reaction time during each of the eight trial blocks of Experiment 2 for each of the four experimental groups defined by the combination of task and color condition: categorical-red (CAT-R), categorical-green (CAT-G), coordinate-red (COO-R), and coordinate-green (COO-G). The results in the upper panel are from participants who received the background color condition first and then switched (on trial block 5) to the stimulus color condition. The results in the lower panel are from participants who received the stimulus color condition first and then switched (on trial block 5) to the background color condition. Error bars show standard errors computed from the within-subject error term (Loftus & Masson, 1994).

reflected in a significant Order of Color Component by Color Component interaction, $F(1, 96) = 94.63$, $MSe = 10320.7$, $p < 0.001$. Within each half of the experiment, reaction time generally decreased across the four-trial blocks, with the decrease being far more pronounced during the first half of the experiment than during the second half of the experiment. In the present ANOVA, these effects are reflected in a significant main effect of block, $F(3, 288) = 37.19$, $MSe = 5951.9$, $p < 0.001$, and in a significant Order of Color Component by Color Component by Block interaction, $F(3, 288) = 38.99$, $MSe = 2943.6$, $p < 0.001$.

With respect to the primary purpose of Experiment 2, the results are quite clear in showing that the Task by Color Condition interaction from Experiment 1 was produced primarily or exclusively by the color of the background. For example, Experiment 2 demonstrates that, for coordinate spatial processing, reaction time is longer with a red background than with a green background even when the stimuli are black. In order for the stimulus color to have produced the effects found in Experiment 1, reaction time for coordinate spatial processing should be longer with green stimuli on a black background than with red stimuli on a black background. This is clearly not the case. In fact, the results of Experiment 2 indicate just the opposite. That is, when color is restricted to the stimuli, reaction time for coordinate spatial processing is longer with red stimuli than with green stimuli.

GENERAL DISCUSSION

The results of the present experiments are clear in demonstrating that color conditions have differential effects on two types of spatial processing performed on the same set of stimuli. In both experiments, there is a robust Task by Color interaction. For coordinate spatial processing, reaction time is longer when stimuli are presented on a red background than when stimuli are presented on a green background, regardless of whether the stimuli are also colored. Furthermore, when colored stimuli are presented on a black background, reaction time for coordinate spatial processing is longer with red stimuli than with green stimuli. By way of contrast, for categorical spatial processing, there are generally nonsignificant color effects in the opposite direction. These results suggest that some of the same visual mechanisms that are responsible for metacontrast masking and for the perception of stroboscopic motion are also responsible for coordinate (but not categorical) spatial processing. Although other interpretations may be possible, a variety of converging evidence implicates the transient/magnocellular visual system.

Experiment 2 indicates that, when only the stimuli are colored, coordinate spatial processing is more difficult with red than with green stimuli. In Experiment 1, however, coordinate spatial processing was more difficult

when the stimuli were green than when the stimuli were red. At first glance, this appears contradictory. However, it is important to keep in mind that, in Experiment 1, stimuli were presented on a background of the complementary color and that stimuli were chosen to be isoluminant. Thus, when the stimuli were green, the overwhelming color in the display was actually red and vice versa. To the extent that processing along the transient/magnocellular visual pathway is disrupted by red as opposed to green, the present pattern of results can be understood. Even when color is present in both the stimuli and the background, the continuously presented background color is far more important for determining the relative efficiency of processing along the magnocellular and parvocellular pathways. If the color of the stimuli were completely irrelevant, there should have been no color effects in Experiment 2 when colored stimuli were presented on a black background. In fact, this is what we expected to find. However, to the extent that processing along the magnocellular pathway is attenuated by exposure to the color red, it may not be surprising to find some attenuation to red stimuli—at least relative to green stimuli and as long as there is no other color in the display.

With respect to hemispheric asymmetry for processing different types of spatial information, both of the present experiments produced a Task by Visual Field interaction similar to that reported in other experiments. The interaction was more robust in terms of statistical significance in Experiment 2 than in Experiment 1. This is probably attributable to the increased sample size of Experiment 2 because the numerical magnitude of the interaction was very similar in the two experiments. In neither experiment did the Task by Visual Field interaction change across trial blocks. As noted earlier, in some (but not all) previous experiments, the LVF/RH advantage for making distance judgments has been restricted to the first trial block, perhaps because observers learn to perform the task in a more categorical way. The present results suggest that it may be more difficult to perform the fits/doesn't fit task without attending to the coordinate spatial relations contained in the stimuli. It was also the case in both experiments that the Task by Visual Field interaction was independent of the color of the stimuli or background. To the extent that the various color conditions were successful in manipulating the efficiency of processing along the transient/magnocellular pathway, this result suggests that the visual field differences that contribute to the Task by Visual Field interaction are independent of the efficiency of processing along that pathway.

With respect to the hypotheses derived from Kosslyn's computational model (Kosslyn et al., 1992), the results are somewhat mixed. The robust Task by Color Condition interactions are consistent with the hypothesis that the transient/magnocellular pathway is more important for coordinate than for categorical spatial processing. In

view of what is known about receptive field sizes, this is consistent with the simulation models indicating that coordinate spatial information is computed more efficiently when input is filtered through units with relatively large receptive fields than through units with relatively small receptive fields, whereas the opposite may be the case for computing categorical spatial information (e.g., the dioptric blurring results reported by Cowin & Hellige, 1994). At the same time, these perceptual manipulations do not change the hemispheric asymmetries. Or, to put it in a slightly different way, the perceptual manipulations seem to have the same effect on both hemispheres. This suggests that, for both categorical and coordinate tasks, the two hemispheres rely on the same visual information and on the same computational mechanisms as each other—although they do not always use that information with equal efficiency. For example, a red background interferes with coordinate spatial relations encoding equally in both visual fields. This suggests that coordinate processing depends on the transient/magnocellular visual pathway to the same extent in both hemispheres. Nevertheless, there is a clear LVF/RH advantage for the coordinate processing tasks. The fact that this right-hemisphere advantage does not change with the perceptual manipulations that we have used suggests that it arises at a level of processing beyond the early sensory level, a general conclusion that is consistent with what is known about a variety of other types of hemispheric asymmetry (for discussion, see Bradshaw, 1989; Hellige, 1993; Moscovitch, 1986). To be sure, we must be cautious in speculating about the anatomical locus of these hemispheric asymmetries for components of spatial processing. It is worth noting, however, that diffuse red light has been found to suppress activity of certain neurons (so-called Type IV neurons) not only in the retinal ganglia and in cells within the lateral geniculate nucleus but also in the magnocellular layers of Area 17 (V1) in the primate visual cortex (Livingstone & Hubel, 1984). In view of the fact that the color manipulations had similar effects on LVF/RH and RVF/LH trials, this suggests that the hemispheric asymmetries of the sort we have studied arise at some level subsequent to Area 17.

The pattern of results just described is also generally consistent with other recent findings that question low-level, wired-in interpretations of visual laterality. For example, based on visual half-field experiments in which observers indicated whether two successive line segments had the same orientation, Kosslyn, Anderson, Hillger and Hamilton (1994; see also Kosslyn, 1994) reject the idea that there are hemispheric differences in such things as the number of projections of magnocellular ganglion cells or that hemispheric differences in the sizes of receptive fields are wired-in. Instead, they argue for a right-hemisphere bias to *attend* to larger patterns and a left-hemisphere bias to *attend* to smaller patterns, biases that can be overcome by specific task demands.

Ivry and Robertson (1998) have also emphasized an attentional account of hemispheric asymmetry for processing visual information, including information about categorical and coordinate spatial relationships. According to their Double Filtering by Frequency (DFF) model, initial sensory processing is identical in the two cerebral hemispheres. An early attentional mechanism is proposed to select task-relevant information by choosing the region of the sensory spectrum to be enhanced for further processing. In vision, this selection is proposed to be in terms of spatial frequency. This first frequency-filtering stage is hypothesized to be identical for the two hemispheres, so any manipulation that influences only this stage of processing should have identical effects on both hemispheres. From this perspective, it is interesting that a manipulation (e.g., a red background) that should interfere more with the processing of low spatial frequency selectively disrupted a coordinate spatial processing task whereas a manipulation (e.g., dioptric blurring; Cowin & Hellige, 1994) that should interfere more with the processing of high spatial frequency information selectively disrupted a categorical spatial processing task, with the effects of both manipulations being the same for both hemispheres.

According to the DFF model, hemispheric asymmetries arise as the result of a subsequent, second frequency-filtering stage. During this second filtering stage, low spatial frequencies are enhanced in the right hemisphere and high spatial frequencies are enhanced in the left hemisphere. Because this second filtering stage operates only on the information that is still available as a result of the first filtering stage, the DFF model predicts hemispheric asymmetry in terms of *relative* rather than *absolute* spatial frequencies: Specifically, left hemisphere superiority for processing spatial frequencies that are high *relative* to others that have made it through the first filtering stage and right hemisphere superiority for processing spatial frequencies that are low *relative* to others that have made it through the first filtering stage. Although it is clear that the type of perceptual manipulations we have discussed here would influence the range of spatial frequencies made available to this second filtering stage, these manipulations do not necessarily change whether the spatial frequencies demanded by the categorical and coordinate tasks are high or low *relative* to each other. With this in mind, it is interesting that the Task by Hemisphere interaction was not influenced by the perceptual manipulations that we have used. In this manner, the present results can be accommodated by the DFF account. However, it must be noted that the present experiments were not designed to be a test of the DFF model or to discriminate between the DFF model and other possibilities. Nevertheless, in view of the promise shown by the DFF model, we believe that it would prove worthwhile to design future experiments with it in mind.

It is also important to consider possible contributions

of the transient/magnocellular visual system to visual shape processing. For example, Jacobs and Kosslyn (1994) have extended the neural network models of Kosslyn et al. (1992) to examine the possible importance of receptive field sizes in the encoding of shape information. They found that networks that received input from units with large, overlapping receptive fields coded the identity of specific shapes better than networks that received input from units with small, nonoverlapping receptive fields. Exactly the opposite was found for the assignment of shapes to categories (see also Brown & Kosslyn, 1995). Thus, there would seem to be a connection between categorical spatial processing and the assignment of shapes to categories without regard for distinctions among the exemplars within a category and a connection between coordinate spatial processing and the ability to distinguish among the specific exemplars (for more discussion of this, see Kosslyn, 1994). Furthermore, Marsolek (1995) provides evidence that the left hemisphere is superior for extracting and identifying a category-defining prototype, whereas the right hemisphere is superior for processing specific shape information of the sort that would be needed to distinguish among exemplars within a single category. In addition, Marsolek, Kosslyn, and Squire (1992) have reported that, at least for words, a highly form-specific type of visual priming is restricted to the right hemisphere (see also Marsolek, Schacter, & Nicholas, 1996). Jacobs and Kosslyn relate this effect to their neural network models by suggesting that form-specific priming depends on information filtered through units with large, overlapping receptive fields. To the extent that this is the case, we might expect to find that various experimental manipulations have consistent effects across a range of computationally related experimental tasks that appear unrelated at first glance. The techniques employed in the present experiments may prove especially useful in examining the contributions of the transient/magnocellular visual system.

METHODS

Experiment 1

Subjects

Sixty-four undergraduate volunteers (32 women, 32 men) participated in Experiment 1. All participants were right-handed, native speakers of English who had normal or corrected-to-normal visual acuity and normal color vision as assessed with Ishihara's (1984) Design Charts for Color-Blindness.

Apparatus and Stimulus Material

During the experiment, each participant was seated at a table approximately 70 cm from the screen of an Apple-Color high resolution RGB monitor (M1297) connected

to a Macintosh IIsi computer, which controlled stimulus presentation and recorded response accuracy and reaction time using the MacProbe software package from Aristometrics. Prior to the beginning of the experiment, the participant's chin was placed in a chin rest with the forehead pressed flush against a stabilization bar to steady the gaze and help ensure a relatively constant viewing distance. Participants registered their response on each trial by pressing a labeled key on the keyboard positioned in front of them.

A small black fixation cross, consisting of a 1-cm horizontal line bisected by a 1-cm vertical line, appeared on the screen at appropriate times to serve as a fixation stimulus. Twelve stimulus patterns, each consisting of a horizontal line and two square dots, were created to be similar to those used by Rybash and Hoyer (1992). Examples are shown in Figure 1. These stimuli were used because they have been found to produce somewhat more reliable visual field differences than the line-and-dot stimuli used by Cowin and Hellige (1994). When presented on the viewing screen, the horizontal line in each stimulus pattern was 5 mm high and either 18, 28, or 38 mm in length. The horizontal line was always presented at the level of the fixation cross and presented to the left or right side of the viewing screen so that the distance between the end of the line closest to the center and the center of the fixation cross measured 26 mm (approximately 3° of visual angle). Each of the two square dots measured approximately 7 mm on each side. The two dots were positioned along the same horizontal plane as each other so that both were located either 13 mm above or 13 mm below the horizontal line. The distance between the two dots varied according to the line length with which they were paired: With the 18-mm line, the distance between the dots was either 7 or 27 mm; with the 28-mm line, the distance between the dots was either 12 or 44 mm; with the 38-mm line, the distance between the dots was either 17 or 53 mm. Thus, there were an equal number of line and dot pairings where the specific line could fit between the dot gaps and where the specific line could not fit between the dot gaps. Each of the six different "line length-dot distance" pairings appeared once with dots above and once with the dots below the horizontal line, for a total of 12 different stimulus arrangements. A total of 24 stimuli were constructed from the original 12 stimuli because each stimulus could appear in either the LVF or RVF on a trial. These 24 LVF and RVF stimuli were ordered randomly to produce a single 24-trial block. During the experiment, each subject received four such 24-trial blocks, for a total of 96 experimental trials.

During the experiment, different groups of participants saw either green lines and dots presented on a continuous red background or red lines and dots presented on a continuous green background. The stimuli were created using CANVAS 3.5 (Deneba Software). Fol-

lowing the procedure outlined by Williams et al. (1991), red stimuli were created by activating only the red CRT gun (with the green and blue values set to zero), and green stimuli were created by activating only the green CRT gun (with red and blue values set to zero). All participants were presented with the same red color, but the specific intensity of green was chosen for each subject to be approximately equivalent to the red color in subjective luminance. The red standard stimulus was presented at a luminance of 14.0 cd/m^2 and produced x and y chromaticity values of 0.599 and 0.342, respectively, as measured from the computer screen using a Photo Research PR-650 SpectraColorimeter. The mean luminance of the green stimulus was 15.3 cd/m^2 , with a range from 12.7 to 18.1 cd/m^2 . The green stimuli produced mean x and y chromaticity values of 0.278 and 0.554, respectively.

Procedure

Each participant first completed a brief questionnaire to verify handedness (based on Oldfield, 1971) and native language. Following this, a specific intensity of green was chosen for each participant using the method of heterochromatic flicker photometry (after Breitmeyer et al., 1991; Breitmeyer & Williams, 1990). The participant viewed a small 1-by-1 cm square in the center of the computer screen, in which red and green alternated at a rate of 50 Hz. The area of the screen surrounding the square was gray. The red standard stimulus alternated with each of 14 different green stimuli, differing in intensity from a value that was clearly less intense than the red standard to a value that was clearly greater in intensity than the red standard. The participant was asked to choose the value of green that minimized the perception of blinking. Each participant made this choice twice, once in a series in which the intensity of green increased gradually and once in a series in which the intensity of green decreased gradually. The intensity of the green used during the experiment was obtained by averaging the participant's responses from the ascending and descending series.

Half of the participants (16 women, 16 men) were randomly assigned to perform the categorical Above/Below task and the remainder (16 women, 16 men) performed the coordinate Fits/Doesn't Fit task. In addition, half of the participants (8 women, 8 men) within each of these two groups received red stimuli on a green background and the remainder (8 women, 8 men) received green stimuli on a red background. Participants assigned to the categorical task were instructed to indicate as quickly and as accurately as possible whether the dots were above or below the line on each trial. Participants assigned to the coordinate task were instructed to indicate as quickly and as accurately as possible whether the line segment could or could not fit into the gap between the two dots.

Finger press responses were required for both tasks. The participant placed the index finger of the left hand on the V key and the index finger of the right hand on the M key. For participants in the categorical Above/Below task, each response key was labeled with either an "A" (for Above) or a "B" (for Below). For participants in the coordinate Fits/Doesn't Fit task, each response key was labeled with either a "Y" (for Yes, it fits) or "N" (for No, it doesn't fit). For each of the two tasks, participants were instructed to press the appropriately labeled key on each trial. For each task, the assignment of the two labels to the two keys was counterbalanced across participants. For purposes of analysis, the grouping that results from this counterbalancing procedure is referred to as Finger Order.

Because some of the visual field differences found in previous studies of categorical and coordinate spatial processing were attenuated or disappeared completely with practice, participants were not given any practice trials. Instead, during the instruction period, they were allowed as much time as they wanted to study the computer screen displaying examples of the stimuli they would receive. Prior to the beginning of the experiment, the computer screen became uniformly red or green (depending on the background color that would be used) and remained that background color throughout the experiment. Participants were instructed to fixate their gaze on the black cross when it appeared and keep their eyes in that position until after they had responded on that trial. At the beginning of each trial, the fixation cross was presented for 1050 msec, followed by a 150-msec presentation of the colored stimulus pattern. There was a 1995-msec interval between the participant's response on a trial and the onset of the fixation cross for the next trial. No feedback was given regarding accuracy or reaction time.

Experiment 2

Subjects

One hundred and twenty-eight individuals (42 men, 87 women) from the same population used in Experiment 1 participated in Experiment 2.

Apparatus and Stimulus Materials

Apparatus and stimulus materials were identical to those used in Experiment 1, with the following exceptions. In Experiment 2, either colored stimuli (red or green) were presented on a black background or black stimuli were presented on a colored background (red or green). When the background was black, the fixation cross was the same color as the stimuli, and when the background was colored, the fixation cross was black. During Experiment 2, the red stimulus was always presented at a luminance of 15.1 cd/m². The mean luminance of the green stimu-

lus was 14.9 cd/m², with a range from 11.7 to 16.4 cd/m².

Procedure

With the following exceptions, the procedures were identical to those of Experiment 1. In Experiment 2, approximately half of the men and half of the women were assigned randomly to the categorical Above/Below task and the remainder were assigned to the coordinate Fits/Doesn't Fit task. For each task, approximately half of the men and half of the women were assigned to receive one of the two colors (green or red). Each participant performed the 96-trial task twice, once with black stimuli on the appropriately colored background and once with appropriately colored stimuli on a black background. The order of the colored stimuli and colored background conditions was counterbalanced across participants, creating groups that differed in the order of color components (background color first or stimulus color first). Participants who received only red stimuli and the red background all received the red standard color used in Experiment 1. For participants who received only green stimuli and the green background, the specific intensity of green was chosen using the method of heterochromatic flicker photometry as in Experiment 1.

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REFERENCES

- Bradshaw, J. L. (1989). *Hemispheric specialization and psychological function*. Chichester, England: Wiley.
- Breitmeyer, B. G., May, J. G., & Heller, S. S. (1991). Metacontrast reveals asymmetries at red-green isoluminance. *Journal of the Optical Society of America*, 8, 1324-1329.
- Breitmeyer, B. G., & Williams, M. C. (1990). Effects of isoluminant-background color on metacontrast and stroboscopic motion: Interactions between sustained (P) and transient (M) channels. *Vision Research*, 30, 1069-1075.
- Brown, H. D., & Kosslyn, S. M. (1995). Hemispheric differences in visual object processing: Structural versus allocation theories. In R. J. Davidson & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 77-122). Cambridge, MA: MIT Press.
- Christman, S. (1989). Perceptual characteristics in visual laterality research. *Brain and Cognition*, 11, 238-257.
- Christman, S. (1990). Effects of luminance and blur on hemispheric asymmetries in temporal integration. *Neuropsychologia*, 28, 361-374.
- Christman, S., Kitterle, F. L., & Hellige, J. B. (1991). Hemispheric asymmetry in the processing of absolute versus relative spatial frequency. *Brain and Cognition*, 16, 62-73.

- Cook, N. D., Fruh, H., & Landis, T. (1995). The cerebral hemispheres and neural network simulations: Design considerations. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 410–422.
- Cowin, E. L., & Hellige, J. B. (1994). Categorical versus coordinate spatial processing: Effects of blurring and hemispheric asymmetry. *Journal of Cognitive Neuroscience*, *6*, 156–164.
- Crebolder, J. M., & Bryden, M. P. (1996). Assessing verbal and spatial hemispheric performance with identical material. *Brain and Cognition*, *30*, 383–385.
- DeMonasterio, F. M. (1978). Center and surround mechanisms of opponent-color X and Y ganglion cells of retina of macaques. *Journal of Neurophysiology*, *41*, 1418–1434.
- DeMonasterio, F. M., & Schein, S. J. (1980). Protan-like spectral sensitivity of foveal Y ganglion cells of the retina of macaque monkeys. *Journal of Physiology, London*, *299*, 385–396.
- Dreher, B., Fukuda, Y., & Rodieck, R. W. (1976). Identification, classification, and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of old-world primates. *Journal of Physiology, London*, *258*, 433–452.
- Hellige, J. B. (1993). *Hemispheric asymmetry: What's right and what's left*. Cambridge, MA: Harvard University Press.
- Hellige, J. B. (1995). Hemispheric asymmetry for components of visual information processing. In R. J. Davidson & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 99–121). Cambridge, MA: MIT Press.
- Hellige, J. B. (1996). Hemispheric asymmetry for visual information processing. *Acta Neurobiologiae Experimentalis*, *56*, 485–497.
- Hellige, J. B. (1997). Hemispheric asymmetry for components of spatial processing. In S. Christman (Ed.), *Cerebral asymmetries in sensory and perceptual processing* (pp. 83–124). Amsterdam: Elsevier.
- Hellige, J. B., Bloch, M. I., Cowin, E. L., Eng, T. L., Eviatar, Z., & Sergent, V. (1994). Individual variation in hemispheric asymmetry: Multitask study of effects related to handedness and sex. *Journal of Experimental Psychology: General*, *123*, 235–256.
- Hellige, J. B., & Michimata, C. (1989). Categorization versus distance: Hemispheric differences for processing spatial information. *Memory & Cognition*, *17*, 770–776.
- Ishihara, S. (1984). *Ishihara's tests for color-blindness*. Tokyo: Kanehara.
- Ivry, R. & Robertson, L. C. (1998). *The two sides of perception*. Cambridge, MA: MIT Press.
- Jacobs, R. A., & Kosslyn, S. M. (1994). Encoding shape and spatial relations: The role of receptive field size in coordinating complementary representations. *Cognitive Science*, *18*, 361–386.
- Johnson, J. E., & Hellige, J. B. (1986). Lateralized effects of blurring: A test of the visual spatial frequency model of cerebral hemisphere asymmetry. *Neuropsychologia*, *24*, 351–362.
- Kitterle, F. L., Christman, S., & Conesa, J. (1993). Hemispheric differences in the interference among components of compound gratings. *Perception & Psychophysics*, *54*, 785–793.
- Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric differences are found in the identification but not the detection of low vs. high spatial frequencies. *Perception & Psychophysics*, *48*, 297–306.
- Kitterle, F. L., & Selig, L. M. (1991). Visual field effects in the discrimination of sine wave gratings. *Perception & Psychophysics*, *50*, 15–18.
- Koenig, O., Reiss, L. P., & Kosslyn, S. M. (1990). The development of spatial relation representations: Evidence from studies of cerebral lateralization. *Journal of Experimental Child Psychology*, *50*, 119–130.
- Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemispheres: A computational approach. *Psychological Review*, *94*, 148–175.
- Kosslyn, S. M. (1988). Aspects of a cognitive neuroscience of mental imagery. *Science*, *240*, 1621–1626.
- Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge, MA: MIT Press.
- Kosslyn, S. M., Anderson, A. K., Hillger, L. A., & Hamilton, S. E. (1994). Hemispheric differences in sizes of receptive fields or attentional biases? *Neuropsychologia*, *8*, 139–147.
- Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., & Koenig, O. (1992). Categorical versus coordinate spatial relations: Computational analyses and computer simulation. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 562–577.
- Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., Jacobs, R. A., & Koenig, O. (1995). On computational evidence for different types of spatial relations encoding: Reply to Cook et al. (1995). *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 423–431.
- Kosslyn, S. M., & Koenig, O. (1992). *Wet mind: The new cognitive neuroscience*. New York: Free Press.
- Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 723–735.
- Laeng, B. (1994). Lateralization of categorical and coordinate spatial functions: A study of unilateral stroke patients. *Journal of Cognitive Neuroscience*, *6*, 189–203.
- Laeng, B., & Peters, M. (1995). Cerebral lateralization for the processing of spatial coordinates and categories in left- and right-handers. *Neuropsychologia*, *33*, 421–439.
- Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience*, *4*, 309–356.
- Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, motion, and depth. *Journal of Neuroscience*, *7*, 3416–3468.
- Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*, 476–490.
- Marrocco, R. T., McClurkin, J. W., & Young, R. A. (1988). Spatial summation and conduction latency classification of cells in the lateral geniculate nucleus of macaques. *Journal of Neuroscience*, *2*, 1275–1291.
- Marsolek, C. J. (1995). Abstract-visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 375–386.
- Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*, 492–508.
- Marsolek, C. J., Schacter, D. L., & Nicholas, C. D. (1996). Form-specific visual priming for new associations in the right cerebral hemisphere. *Memory & Cognition*, *24*, 539–556.
- Michimata, C. (1997). Hemispheric processing of categorical and coordinate spatial relations in vision and visual imagery. *Brain and Cognition*, *33*, 370–387.
- Moscovitch, M. (1986). Afferent and efferent models of visual

- perceptual asymmetries: Theoretical and empirical implications. *Neuropsychologia*, *24*, 91-114.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97-113.
- Rybash, J. M., & Hoyer, W. J. (1992). Hemispheric specialization for categorical and coordinate spatial representations: A reappraisal. *Memory & Cognition*, *20*, 271-276.
- Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, *41*, 788-797.
- Sergent J. (1983). The role of the input in visual hemispheric asymmetries. *Psychological Bulletin*, *93*, 481-514.
- Sergent J. (1987). Failures to confirm the spatial-frequency hypothesis: Fatal blow or healthy complication? *Canadian Journal of Psychology*, *41*, 412-428.
- Sergent, J., & Hellige, J. B. (1986). Role of input factors in visual-field asymmetries. *Brain and Cognition*, *5*, 174-199.
- Shapley, R. (1994). Parallel neural pathways and visual function. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 315-324). Cambridge, MA: MIT Press.
- Van Essen, D. C. (1985). Functional organization of primate visual cortex. In E. G. Jones & A. A. Peters (Eds.), *Cerebral cortex* (vol. 3, pp. 259-329). New York: Plenum.
- Wiesel, T. N., & Hubel, D. H. (1966). Laminar and columnar distribution of geniculocortical fibers in the macaque monkey. *Journal of Neurophysiology*, *29*, 1115-1156.
- Williams, M. C., Breitmeyer, B. G., Lovegrove, W. J., & Guitierrez, C. (1991). Metacontrast with masks varying in spatial frequency and wavelength. *Vision Research*, *31*, 2017-2023.