

Does a causal relation exist between the functional hemispheric asymmetries of visual processing subsystems? ☆

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Abstract

Past research indicates that specific shape recognition and spatial-relations encoding rely on subsystems that exhibit right-hemisphere advantages, whereas abstract shape recognition and spatial-relations encoding rely on subsystems that exhibit left-hemisphere advantages. Given these apparent regularities, we tested whether asymmetries in shape processing are causally related to asymmetries in spatial-relations processing. We examined performance in four tasks using the same stimuli with divided-visual-field presentations. Importantly, the asymmetry observed in any one task did not correlate with the asymmetries observed in the other tasks in ways predicted by extant theories. Asymmetries in shape processing and spatial-relations encoding may not be due to a common causal force influencing multiple subsystems.

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1. Introduction

A well-established distinction in visual processing is that a ventral visual stream underlies shape recognition, whereas a dorsal visual stream underlies spatial-location or action-guidance processing (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Additional evidence indicates that dissociable subsystems in the ventral stream

underlie a left-hemisphere (LH) advantage for recognition of abstract categories of shapes (e.g., cups vs. pens, etc.) and a right-hemisphere (RH) advantage for recognition of specific exemplars of shapes (e.g., individual pens, etc.; see Marsolek, 1999; Marsolek & Burgund, 1997), and dissociable subsystems in the dorsal stream underlie a LH advantage for encoding categorical spatial relations (e.g., above vs. below) and a RH advantage for encoding coordinate spatial relations (e.g., metrically precise relations; see Chabris & Kosslyn, 1998; Kosslyn, 1987). Regularities are apparent in these functional asymmetries; the LH advantages have the commonality of abstract/categorical processing, and the RH advantages have the commonality of specific/precise processing. Do these regularities reflect a fundamental hemispheric difference or some other causal relation influencing multiple subsystems? Or, do they reflect independent sources such that the regularities are only probabilistic or statistical in nature, and thus become apparent only after sample-level averaging?

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2. Theories of relations among asymmetries

At least three different classes of theories have been put forward concerning the cause of the observed relations among functional asymmetries. These theories make different predictions regarding the patterns of asymmetries that should be observed across different subsystems within individuals, and are tested in the following experiment.

2.1. Causal complementarity

One class of theory (cf. Bradshaw & Nettleton, 1981) posits that although subsystems in the two hemispheres may be nearly symmetric at an initial time point, the growth of an asymmetry for one subsystem plays a causal role in the development of the opposite asymmetry for a complementary subsystem. For example, if a subsystem in one hemisphere (e.g., a spatial processor in the RH) becomes more efficient at one kind of processing (e.g., metrically specific spatial-relations encoding) than its counterpart in the other hemisphere (e.g., a spatial processor in the LH), this would cause that counterpart to become more efficient at a complementary type of processing (e.g., abstract/categorical spatial-relations encoding).

Potential mechanisms for such a causal effect vary, but one is the “snowball” mechanism (Hellige, 1993; Kosslyn, 1987). First, a small number of “seed” asymmetric subsystems must be in place (perhaps innately). Then, because interactions are more effective among subsystems in the same hemisphere than among subsystems in opposite hemispheres, any tuning of the function of a subsystem that occurs with practice and training should be more influenced by within-hemisphere subsystems than by across-hemisphere subsystems. Eventually, such tuning should have the effect that asymmetries similar in nature to the seed asymmetries will be found in the other subsystems as well (i.e., asymmetries “snowball” from seed subsystems to other subsystems). Another example comes from the notion of homotopic callosal inhibition (Cook, 1984), according to which the homotopic areas of the hemispheres mutually inhibit each other, and adjacent areas within one hemisphere also mutually inhibit one another. In this way, when an area in one hemisphere is inhibited, the surrounding area in that hemisphere is activated, which inhibits its homotopic area in the other hemisphere. As the cycle continues between hemispheres, the result is that different hemispheres become dominant for the different processes performed in closely contiguous neural areas (of one hemisphere) and hence for complementary functions (i.e., become dominant for two different ways of processing information in the same general brain region). Examples of similar mechanisms are cited in the next section.

The strong assertion from causal-complementarity theories is the empirical claim that the two complementary kinds of processing should be advantaged in opposite hemispheres. In other words, a *negative correlation* should be observed between the functional asymmetries of the two complementary subsystems (e.g., individual participants who yield a *LH* advantage for *abstract* spatial-relations encoding also should yield a *RH* advantage for *specific* spatial-relations encoding in the dorsal visual stream).

2.2. Input asymmetry

Another class of theory (e.g., Ivry & Robertson, 1998; Jacobs & Kosslyn, 1994; Sergent, 1983) is similar to causal complementarity, but with a focus on how the asymmetries in lower-level perceptual processing (i.e., asymmetries in the visual input to each hemisphere) may be the root causes of asymmetries in higher-level processing. According to *input asymmetry*, lower-level mechanisms in one hemisphere (e.g., typically the RH, but not necessarily) become more efficient than those in the other hemisphere at processing (or attending to) information from cells with relatively large receptive fields (Jacobs & Kosslyn, 1994) or to information from relatively low spatial-frequency modules (Ivry & Robertson, 1998; Sergent, 1983). In addition, lower-level mechanisms in one hemisphere (e.g., typically the LH, but not necessarily) become more efficient than those in the other hemisphere at processing (or attending to) information from cells with relatively small receptive fields (Jacobs & Kosslyn, 1994) or to information from relatively high spatial-frequency modules (Ivry & Robertson, 1998; Sergent, 1983). Such input asymmetries may cause higher-level subsystems to become asymmetric. Higher-level subsystems that are advantaged by the input preferentially projected to one hemisphere should learn to operate more effectively in that hemisphere than in the other (e.g., specific spatial-relations encoding and specific shape recognition both may be advantaged by input from large receptive fields and hence may become lateralized to the hemisphere that receives that kind of information most effectively; see Jacobs & Kosslyn, 1994).

Note, however, that logically the asymmetries for complementary subsystems need not be in opposite directions; if one hemisphere processes all kinds of visual input more effectively than the other, all higher-level visual subsystems may operate most effectively in that hemisphere. Thus, unlike causal-complementarity theories, the strong empirical claim from input-asymmetry theories is a *positive correlation* between the asymmetries of higher-level subsystems that are advantaged by the input projected to one hemisphere (e.g., individual participants who yield a *RH* advantage for *specific* spatial-relations encoding in the dorsal visual stream should

also yield a *RH* advantage for *specific* shape recognition in the ventral visual stream).

2.3. Statistical complementarity

Another theory posits that there may not be a *causal* relationship between various hemispheric asymmetries, instead typical patterns of asymmetries (i.e., LH advantages for abstract shape recognition, RH advantages for specific shape recognition, etc.) may reflect independent probabilistic biases (Bryden, 1982; Bryden, Hécaen, & DeAgostini, 1983). According to *statistical complementarity*, a particular subsystem (e.g., an abstract shape-recognition processor) has a certain probability of being lateralized to one hemisphere (e.g., typically the LH, but not always), and another particular subsystem (e.g., a specific shape-recognition processor), has a different, independent probability of being lateralized to one hemisphere (e.g., typically the RH, but not always), with no common causal force contributing to the two probabilities. Although typical patterns of asymmetries tend to be observed across samples of participants, these typical patterns may simply reflect influences on the probabilities that stem from different, *independent* sources. In other words, if the sources are independent of each other, the probabilities would be independent of each other, despite any regularities in lateralization that tend to be observed when data from samples of participants are accumulated. By this theory, no direct relationship between the asymmetries of subsystems *within individual participants* should be found. Thus, the strong empirical claim from statistical complementarity is that there should be *no correlations* (negative or positive) between the asymmetries of complementary subsystems.

We tested these predictions from the three classes of theories in the following experiment. We calculated asymmetry scores associated with two subsystems in the dorsal visual stream (an abstract spatial-relations encoding subsystem and a specific spatial-relations encoding subsystem) and two subsystems in the ventral visual stream (an abstract-category shape recognition subsystem and a specific-exemplar shape recognition subsystem), within the same participants. Correlations among asymmetry scores within participants were examined to test the above theories directly.

3. Method

3.1. Participants

Sixty-four male University of Minnesota students gave informed consent and were paid \$10 or given course credit to participate in the study. All had normal or corrected-to-normal vision, and all were right-handed as assessed through the Edinburgh Handedness Inven-

tory (mean laterality quotient = .83; Oldfield, 1971). Only right-handed male participants were tested because they tend to exhibit more consistent asymmetry of function compared with other groups (e.g., Bryden, 1982; Hellige, 1993), especially in spatial-relations encoding tasks (see Kosslyn et al., 1989).

3.2. Design

Three within-participants variables were manipulated: dorsal/ventral nature of the task (spatial-relations encoding or shape recognition), specificity of the task (abstract or specific), and hemisphere of direct stimulus presentation (LH or RH).

3.3. Materials

The same visual stimuli were used for all four of the tasks (see Fig. 1). The target patterns were four of the dot patterns used by Jacobs and Kosslyn (1994), in particular the first two exemplars in each of the two rows in their Fig. 1. Each pattern consisted of an arrangement of four squares that filled four of the potential 25 locations defined by a 5×5 grid (each square subtended $.57^\circ$ of visual angle, and each whole pattern subtended 2.85°). The first two exemplars (arbitrarily labeled “1” and “2”) were small distortions of the same prototype and hence belonged to one abstract category (arbitrarily labeled category “A”), and the other two exemplars (arbitrarily labeled “3” and “4”) were small distortions of another prototype and hence belonged to the other abstract category (arbitrarily labeled category “B”).

In each trial, one of these four target patterns was presented concurrently with a reference line, against which the spatial-relations judgments were made (or ignored if performing one of the shape tasks). As in Jacobs and Kosslyn (1994), this reference line was composed of two squares (each 0.57° of visual angle) positioned to represent the endpoints of an imaginary horizontal line subtending the same width as a target

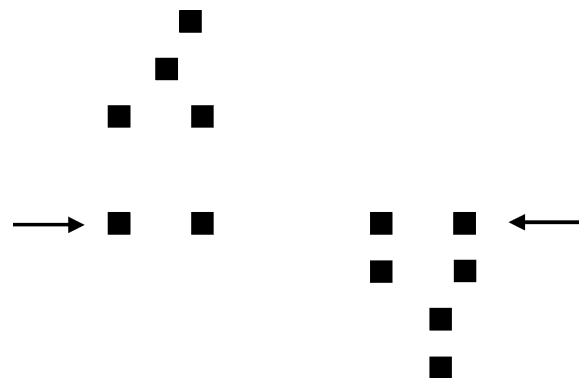


Fig. 1. Two examples of displays used in the experiment. The arrows (which were not presented in the displays) point to the reference midline.

stimulus (2.85°). The reference line appeared in one of three vertical positions in each trial: exactly halfway between the top and bottom of the display (and in line horizontally with the position of the central fixation point), 0.57° above or 0.57° below the horizontal midline of the screen. These conditions were labeled the middle, upper, and lower vertical positions, respectively. The position of the reference line was varied to encourage participants to process spatial relations per se between the pattern and the reference line during the spatial-relations encoding tasks. Static reference lines can lead participants to use extraneous or non-relational visual cues when making the putative spatial-relations judgments, such as the absolute position of the patterns on the computer monitor (see Banich & Federmeier, 1999).

In each trial, a target pattern and the reference line were presented simultaneously in one of 48 possible ways. The reference line could be in the upper, middle, or lower vertical position, the target pattern could be above or below the reference line (either 0,¹ 6, 12, or 18 mm between the closest edges of the target pattern and the reference line), and the entire configuration could be presented directly to the LH (in the right visual field, 2.10° between the inner edge of the stimulus configuration and the vertical midline of the display) or directly to the RH (in the left visual field, also 2.10° between the inner edge of the stimulus configuration and the vertical midline of the display).

All stimuli were presented in black against a white background on an AppleVision 1710AV monitor, with a resolution of 832×624 pixels refreshed at 75 Hz. Stimulus presentation and response time measurements were controlled by a PowerMacintosh 7600 computer running PsyScope experimental software (Cohen, MacWhinney, Flatt, & Provost, 1993), and responses were typed into an AppleDesign keyboard (Model #M2980). A 0.19° dot served as a fixation point that was presented at the beginning of each trial. A chinrest was used to position the participants' eyes approximately 60 cm from the display.

3.4. Procedure

Each participant was tested on each of the four tasks (with task order counterbalanced across participants) in an individual session. For each task for each participant, the left hand was used to register responses in one block of trials and the right hand was used in another block of

trials (with the order of these blocks within task also counterbalanced across participants). Thus, each participant completed eight blocks of trials. Each block contained 48 trials, with each of the 48 stimulus conditions (defined above) being used for one trial per block. Presentation of the four target patterns was counterbalanced such that each was used an equal number of times per block and each was used to represent each experimental condition an equal number of times across participants. Trial orders were pseudorandomized within blocks, with the constraints that no more than three trials using the same position of reference line, hemisphere of direct stimulus presentation, or target pattern appeared consecutively, and no more than three trials requiring the same response appeared consecutively.

Across all four tasks, a trial began with the presentation of a fixation point in the center of the display for 500 ms, followed by an experimental stimulus (a target pattern and reference line presented simultaneously in one visual field) for 183 ms, followed by a blank display until the participant responded. The next trial began 500 ms after a response was made. An additional 16 trials were included at the beginning of each of the eight trial blocks to give the participants practice at performing that task with that response hand. Immediate auditory feedback (signaling a correct or an incorrect response) was given during the practice trials, but not during the experimental trials. In all other ways, the practice trials were conducted like the experimental trials, although responses in these practice trials were not included in the following analyses. The differences across the four tasks were as follows.

3.4.1. Abstract spatial-relations task

In this task, participants determined whether the target pattern was presented above or below the reference line, analogous to the "categorical" spatial-relations task first used by Hellige and Michimata (1989) and Kosslyn et al. (1989). Participants were asked to respond as quickly and accurately as possible. They rested their index and middle fingers of the appropriate hand on the 'f' and 'g' keys, which were used to register 'above' and 'below' responses, respectively.

3.4.2. Specific spatial-relations task

In this task, participants determined whether the closest edge of the target pattern was presented near to the reference line (i.e., within 9 mm) or far from the reference line (i.e., farther than 9 mm), regardless of whether the pattern was above or below the line, analogous to the "coordinate" spatial-relations task first used by Hellige and Michimata (1989) and Kosslyn et al. (1989). Visual examples were used to familiarize participants with the critical 9 mm distance for this task. Participants were asked to respond as quickly and accurately as possible. They rested their index and middle fingers of the

¹ We included this condition to replicate the distances used in the simulations of Jacobs and Kosslyn (1994). Although the closest edges of the pattern and reference line were contiguous in the '0' distance condition, participants indicated that they still could perform the tasks as instructed. Mean accuracy rates for the '0' distance condition were above chance (and response times were not disproportionately different for that condition), indicating that the contiguity did not selectively impair participants' performance in that condition.

appropriate hand on the ‘f’ and ‘g’ keys, which were used to register ‘near’ and ‘far’ responses, respectively.

3.4.3. Abstract-category shape recognition task

In this task, participants determined whether the target pattern belonged to abstract category A or to abstract category B, regardless of whether the pattern was presented near, far, above, or below the reference line. Participants were familiarized with the categories and verbally tested until they could correctly categorize all four target patterns twice in a row, before proceeding to the practice trials. Participants were asked to respond as quickly and accurately as possible. They rested their index and middle fingers of the appropriate hand on the ‘f’ and ‘g’ keys, which were used to register ‘A’ and ‘B’ responses, respectively.

3.4.4. Specific-exemplar shape recognition task

In this task, participants determined which (of the four possible) specific target patterns was presented, regardless of whether it appeared near, far, above, or below the reference line. Participants were familiarized with the specific target patterns and verbally tested until they could correctly identify all four exemplars twice in a row, before proceeding to the practice trials. Participants were asked to respond as quickly and accurately as possible. They rested four fingers of the appropriate hand (not including the thumb) on the ‘f,’ ‘g,’ ‘h,’ and ‘j’ keys, which were used to register ‘1,’ ‘2,’ ‘3,’ and ‘4’ responses, respectively.

4. Results

4.1. Analyses of variance

Mean response times for the correct responses² and mean accuracy (in terms of proportion accuracy above chance) were the dependent measures in separate repeated-measures analyses of variance. Accuracy was measured as proportions above chance because the specific-exemplar shape recognition had four response alternatives and hence a .25 correct level of chance performance, whereas the other three tasks had two response alternatives and hence a .50 correct level of chance performance. Analyzing accuracy as proportions above chance produced an index that could take a value between 0.0 and 1.0 (with 0.0 representing chance performance and 1.0 representing perfect performance), and allowed comparable accuracy measures across the four tasks. In both response time and accuracy analyses, the independent variables were dorsal/ventral nature of the

Table 1

Means (*M*) and standard errors (*SE*) of response times (in ms) and accuracy rates (above chance) for all conditions

Specificity	Task type			
	Shape		Spatial	
	LH	RH	LH	RH
<i>Response times</i>				
Abstract				
<i>M</i>	750	768	510	512
<i>SE</i>	26	28	23	24
Specific				
<i>M</i>	954	947	620	616
<i>SE</i>	37	37	21	20
<i>Accuracy</i>				
Abstract				
<i>M</i>	.32	.32	.75	.70
<i>SE</i>	.05	.05	.04	.04
Specific				
<i>M</i>	.35	.34	.35	.31
<i>SE</i>	.04	.04	.06	.06

task (spatial-relations encoding or shape recognition), specificity of the task (abstract or specific), and hemisphere of direct stimulus presentation (LH or RH). All mean response times and accuracy rates are in Table 1.

4.1.1. Response time

The most important result from the analysis of response times was that the interaction between specificity of task (abstract or specific) and hemisphere of direct stimulus presentation (LH or RH) was significant ($F(1, 63) = 5.54, p < .05, MSe = 1383.2$). In a pattern that replicates previous hemispheric asymmetries (for reviews, see Chabris & Kosslyn, 1998; Marsolek & Burgund, 1997), abstract processing was faster for stimuli presented directly to the LH (630 ms) than to the RH (640 ms), whereas specific processing was faster for stimuli presented directly to the RH (782 ms) than to the LH (787 ms). It is also important to note that this two-way interaction was not modulated by the dorsal/ventral nature of the task (spatial-relations encoding or shape recognition), as the three-way interaction between specificity of task, hemisphere of direct stimulus presentation, and dorsal/ventral nature of the task did not approach significance ($F(1, 63) = 1.12, p > .25, MSe = 2639.0$). This was expected, given that both spatial-relations encoding and shape recognition tasks tend to produce the same interaction of specificity of task by hemisphere of direct stimulus presentation.

The other significant results in the response time analysis were the following (all other $ps > .30$). Not surprisingly, participants responded faster in the relatively easier (dorsal) spatial-relations encoding tasks (564 ms) than in the (ventral) shape recognition tasks (854 ms; $F(1, 63) = 134.7, p < .001, MSe = 80157.8$, for the main

² Mean response times were calculated after eliminating outliers smaller than 100 ms, greater than 2000 ms, or $\pm 2.5 SD$ from the mean calculated separately for each condition.

effect of dorsal/ventral nature of the task). Also not surprisingly, participants responded faster in the abstract tasks (635 ms) than in the specific tasks (784 ms; $F(1,63)=88.1$, $p<.001$, $MSe=32396.3$, for the main effect of specificity of the task). These two variables interacted significantly ($F(1,63)=5.45$, $p<.05$, $MSe=41838.5$), with the abstract advantage in the (dorsal) spatial-relations encoding tasks (511 ms for abstract vs. 618 ms for specific) being smaller than in the (ventral) shape recognition tasks (759 ms for abstract vs. 951 ms for specific), possibly reflecting a greater influence from the statistical floor in the relatively easy spatial relations tasks than in the relatively difficult shape recognition tasks (see accuracy data below).

4.1.2. Accuracy

Simple t tests revealed that mean performance in each condition was significantly above chance (all $ps<.001$). Most important, the interaction between specificity of task (abstract or specific) and hemisphere of direct stimulus presentation (LH or RH) was not significant ($F<1$). This result indicates that the significant interaction in the analysis of response times reported above was not compromised by a tradeoff between speed and accuracy of response.

The only significant effects (all other $ps>.10$) in this analysis were that participants were more accurate when performing the (dorsal) spatial-relations encoding tasks (.53 above chance) than the (ventral) shape recognition tasks (.34 above chance; $F(1,63)=21.0$, $p<.001$, $MSe=.22464$, for the main effect of dorsal/ventral nature of the task), and that participants were more accurate when performing the abstract tasks (.52 above chance) than the specific tasks (.34 above chance; $F(1,63)=17.5$, $p<.001$, $MSe=.24591$, for the main effect of specificity of the task). These two variables interacted significantly ($F(1,63)=31.6$, $p<.001$, $MSe=.17694$), with no abstract advantage in the (dorsal) spatial-relations encoding tasks (.32 above chance for abstract vs. .35 above chance for specific), but an abstract advantage in the (ventral) shape recognition tasks (.72 above chance for abstract vs. .33 above chance for specific). These effects parallel the analogous effects in the response-time analysis.

4.2. Correlations of asymmetry scores

Most important for the present study, we directly measured the correlations between individual-participant asymmetries in the four tasks to test the foregoing theories. In order to quantify both the magnitude and direction of asymmetry for a particular task in a particular participant, we calculated an asymmetry score (mean response time for correct responses when stimuli were presented directly to the LH minus when they were presented directly to the RH) for each task for each participant. Note that a positive asymmetry score

indicates a RH advantage for that task for that participant, a negative asymmetry score indicates a LH advantage for that task for that participant, and a 0 asymmetry score indicates no asymmetry. These asymmetry scores were then used to calculate Pearson correlations, and the scores are plotted as functions of different pairs of tasks in Figs. 2–5.

In addition to the raw asymmetry scores, we also calculated and analyzed normalized asymmetry scores. The four tasks differed in overall speed of performance and participants differed in their competencies with the four tasks, so we corrected for these factors by dividing the raw asymmetry score by the mean response time for each task for each participant. In the results that we report below, r_1 denotes correlations with the raw asymmetry scores and r_2 denotes correlations with normalized asymmetry scores.

As discussed above, the main prediction from causal-complementarity theories is that negative correlations should be observed between the asymmetries of complementary versions of dorsal or ventral visual subsystems. That is, negative correlations should be observed between the asymmetries of abstract and specific spatial-relations encoding subsystems as well as between the asymmetries of abstract and specific shape recognition subsystems. However, the correlation between abstract and specific versions of the shape recognition tasks did not approach significance ($r_1=-.10$, $p>.40$; $r_2=.06$, $p>.60$) as depicted in Fig. 2, and the correlation between abstract and specific versions of the spatial-relations encoding tasks was positive but not significant in the raw response times ($r_1=.13$, $p>.25$), and was positive and significant in the normalized response times ($r_2=.31$,

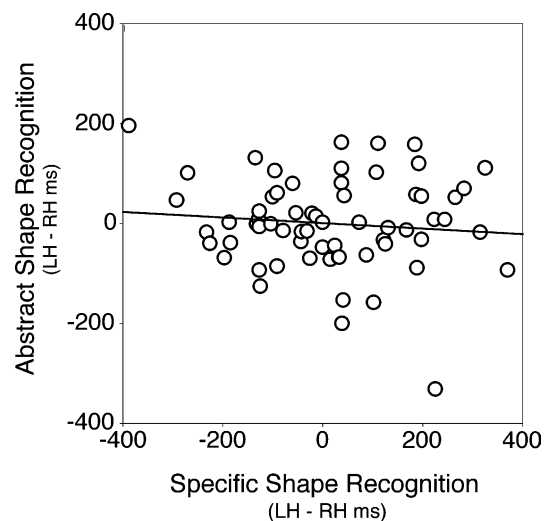


Fig. 2. Asymmetry scores from mean (raw) response times for the abstract shape recognition task plotted against the asymmetry scores from mean (raw) response times for the specific shape recognition task, in individual participants. A negative asymmetry score represents a LH advantage, whereas a positive asymmetry score represents a RH advantage. Also shown is the least-squares regression line.

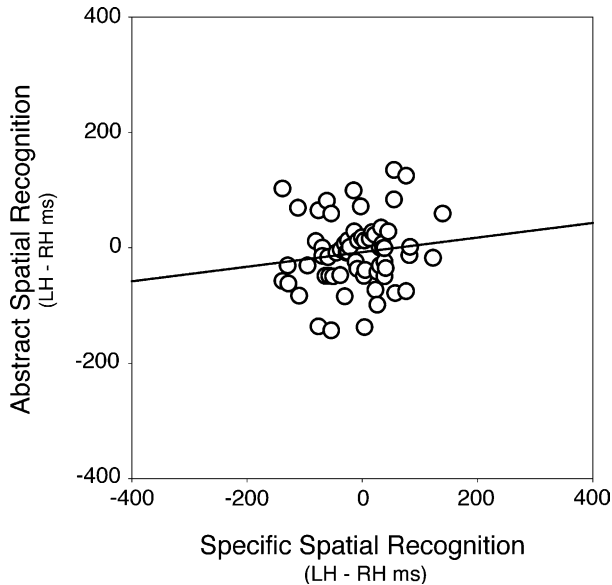


Fig. 3. Asymmetry scores from mean (raw) response times for the abstract spatial-relations encoding task plotted against the asymmetry scores from mean (raw) response times for the specific spatial-relations encoding task, in individual participants. A negative asymmetry score represents a LH advantage, whereas a positive asymmetry score represents a RH advantage. Also shown is the least-squares regression line.

$p < .05$) as depicted in Fig. 3.³ Note that this significant correlation is in the opposite direction predicted by causal complementarity.

Also as discussed above, the main prediction from input-asymmetry theories is that positive correlations should be observed between the asymmetries of visual subsystems advantaged by the same kind of low-level input. That is, positive correlations should be observed between the asymmetries of abstract spatial-relations encoding and abstract shape recognition subsystems as well as between the asymmetries of specific spatial-relations encoding and specific shape recognition subsystems. However, the correlation between the abstract

³ Although the correlation between the raw response-time asymmetry scores for abstract and specific spatial-relations encoding tasks was not significant, this correlation was significant in the normalized response-time asymmetry scores, so we suggest the following potential explanation. It may reflect what Kosslyn et al. (1989) observed when they found that asymmetries between abstract and specific spatial-relations encoding were more likely to be observed in early blocks of trials than in later blocks, possibly because participants can learn over trials the relevant “categories” of near versus far, which then can be used to perform the putatively non-categorical coordinate/specific task. If so, performance in the specific and abstract spatial-relations encoding tasks may initially rely upon processing in different subsystems, but as the “categories” of near versus far are learned across trials, a common neural substrate may be able to subserve performance in both tasks such that a positive correlation would be observed. To examine this possibility, we correlated the normalized response time asymmetry scores between the abstract and specific spatial tasks separately for the first and second halves of the trials. In line with the above suggestion, the correlation between asymmetries grew from the first half of the trials ($r = .07$) to the second half ($r = .12$).

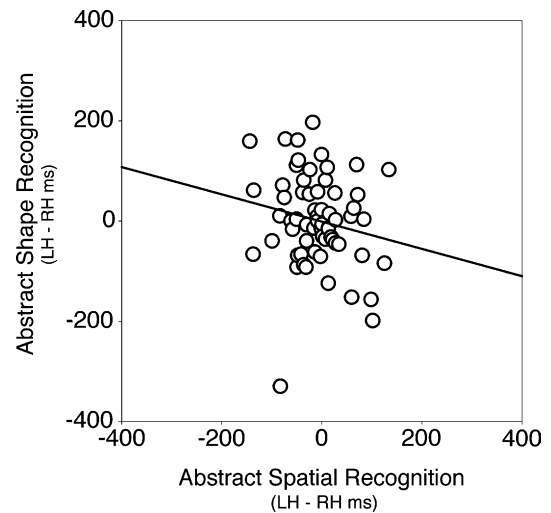


Fig. 4. Asymmetry scores from mean (raw) response times for the abstract shape recognition task plotted against the asymmetry scores from mean (raw) response times for the abstract spatial-relations encoding task, in individual participants. A negative asymmetry score represents a LH advantage, whereas a positive asymmetry score represents a RH advantage. Also shown is the least-squares regression line.

shape recognition task and the abstract spatial-relations encoding task was *negative* but not significant ($r_1 = -.18$, $p > .15$; $r_2 = -.14$, $p > .25$) as depicted in Fig. 4, likewise the correlation between the specific shape recognition task and the specific spatial-relations encoding task was *negative* but not significant ($r_1 = -.18$, $p > .15$; $r_2 = .04$, $p > .70$) as depicted in Fig. 5.

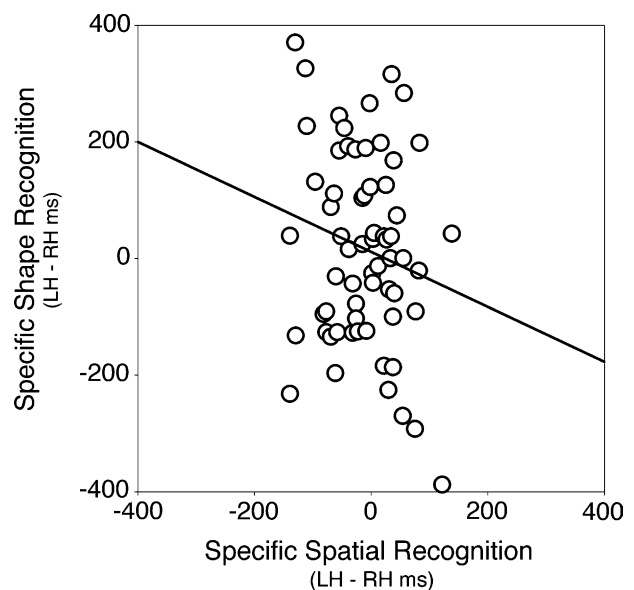


Fig. 5. Asymmetry scores from mean (raw) response times for the specific shape recognition task plotted against the asymmetry scores from mean (raw) response times for the specific spatial-relations encoding task, in individual participants. A negative asymmetry score represents a LH advantage, whereas a positive asymmetry score represents a RH advantage. Also shown is the least-squares regression line.

We also analyzed correlations of asymmetry scores based on accuracy (in a manner analogous to the asymmetry scores based on response times). Only the correlation between the abstract and specific spatial-relations task approached significance, $r = .21$, $p = .09$ (all other $ps > .20$). Note, however, that this positive correlation was in the opposite direction predicted by causal complementarity.

4.3. Reliability of asymmetry scores

A potential concern, especially given that no predicted significant correlations were observed between different task asymmetry scores, is whether the asymmetry scores were reliable. If these measures were very noisy within a participant, this could be responsible for the lack of significant correlations between asymmetry scores. To address these concerns and establish reliability, we calculated split-half reliability estimates (Spearman–Brown corrected) as recommended by Crocker and Algina (1986) for the raw (r_1) and normalized (r_2) response-time asymmetry measures for each of the four tasks. The measures were highly reliable (specific shape task, $r_1 = .60$, $p < .001$ and $r_2 = .61$, $p < .001$; specific spatial-relation task, $r_1 = .34$, $p < .01$ and $r_2 = .51$, $p < .001$; abstract shape task, $r_1 = .44$, $p < .001$ and $r_2 = .37$, $p < .01$; abstract spatial-relation task, $r_1 = .69$, $p < .001$ and $r_2 = .64$, $p < .001$). These results indicate that performance in each of our four tasks correlates significantly with additional performance in that task.

4.4. Power to detect significant effects

Another potential concern, given that no predicted significant correlations were observed between different task asymmetry scores, is whether the study had sufficient statistical power to detect significant correlations with small effect sizes. It is important to note that power was not of concern for the majority of correlations (see Figs. 2–4), which were in the opposite directions to those predicted by the relevant theories. The only viable exception across all response-time and accuracy correlations was the small negative correlation of $r_1 = -.10$ ($p > .40$) between the raw response time asymmetry scores for abstract and specific shape-recognition tasks (see Fig. 1), which is in the direction predicted by causal-complementarity theory. However, for an effect that small, 384 subjects would be required to reject the null hypothesis with only a modest power of .5. Thus, the single correlation in line with any theory besides statistical complementarity is extremely small, and although we cannot rule out that it might be statistically significant given enough power, we conclude that it is unlikely to be of theoretical significance. Also, when that correlation was calculated on normalized asymmetry scores, it was positive (not negative). Furthermore, even if a significant negative correlation were to be observed between those tasks, the theory

it would support (causal complementarity) was disconfirmed by the observation of a trend toward a *positive* correlation between the asymmetry scores for abstract and specific spatial-relations encoding (see Fig. 2). Because we replicated the sample-level asymmetries established in this literature, by using common stimuli in four tasks that were modeled directly on tasks used in the relevant published literature, our tasks apparently engaged the visual processes of interest. Yet, the power analysis and the trends in the correlations indicate no support for the theories positing significant correlations.

5. Discussion

Two important results were obtained. First, in a single experiment using the same stimuli and participants across four different tasks, we replicated the typical abstract (LH advantage) and specific (RH advantage) processing asymmetries that have been shown previously using spatial-relations encoding tasks (e.g., Hellige & Michimata, 1989; Kosslyn et al., 1989; Laeng, 1994) and shape recognition tasks (e.g., Beeri, Vakil, Adonsky, & Levenkron, 2004; Marsolek, 1995, 1999; Marsolek, Kosslyn, & Squire, 1992). This replication is important because it validates that the tasks and stimuli used in this experiment were appropriate for revealing the relevant functional asymmetries, and therefore should also be useful for revealing any relationships between the functional asymmetries, of the subsystems supporting the tasks.

Second, by correlating the asymmetry scores from the four tasks, we found no support for theories positing a causal relationship between the asymmetries of the four visual subsystems. In fact, most of the correlations were in the opposite directions of those predicted by the theories. The theory largely supported by the present pattern of results was statistical complementarity, which posits that no causal relationship exists between the asymmetries of different visual subsystems, but rather that different, independent sources influence the asymmetries (see Bryden, 1986). An important ramification of these findings is that the typical pattern of hemispheric asymmetries observed when performance is averaged across a sample of participants may not be indicative of the pattern of asymmetries observed within a particular participant or even within a number of participants. Although somewhat counterintuitive, this finding is exactly what one would expect if there were independent probabilistic biases for certain independent subsystems to be lateralized to particular hemispheres. We suggest that analyses of asymmetries that are averaged across a sample are useful for testing hypotheses about the neural architecture of the “average” individual (an important goal, indeed), but correlational analyses of asymmetry scores are needed to test hypotheses about any relations between asymmetries of subsystems (also an important goal).

We should emphasize that statistical complementarity does not predict only null correlations for any pair of possible asymmetry scores. It predicts significant correlations between the asymmetry of a subsystem and any measure that reflects or is influenced by a cause of that asymmetry (as long as that source is independent of sources for the asymmetries of the other subsystems of interest). Of course, strictly speaking, this sort of independence of sources must have limits; presumably, some of the relevant sources of asymmetries (e.g., genetic factors influencing handedness) do affect more than one asymmetric neural subsystem, essentially ruling out a strong version of statistical complementarity. For the purposes of the present study, however, we were interested in examining the asymmetries of the four previously investigated visual subsystems in particular, which have been implicated previously in theories of causal complementarity and input asymmetry, and hence in testing statistical complementarity as applied just to those four subsystems. It is likely that factors related to the asymmetry of one of those subsystems may also influence the asymmetry of another neural subsystem (although apparently not the other three visual subsystems of present interest, given our findings).

Interestingly, the common finding of population-level asymmetries suggest that there must be factors responsible for producing the asymmetries in the “average” individual, even though our results suggest there are no causal relations between these asymmetries within an individual. One interesting possibility is that the population-level asymmetries are consistent due to pressures of appropriate social interactions between members of a species (Vallortigara & Rogers, *in press*). The asymmetry of one function in one individual may be influenced by the asymmetry of that function in other individuals with which he or she has social interactions (e.g., consider shaking hands, right hand to right hand in our society). In this way, functional asymmetries may arise at the population level without an influence of causal relations between asymmetries of functions within an individual (Deason, Andresen, & Marsolek, *in press*).

Our conclusions also are supported by data from a split-brain patient (J.W.). J.W. appears to exhibit the typical asymmetry in ventral visual processing (a LH advantage for abstract shape recognition, and a RH advantage for specific shape recognition; e.g., Funnell, Corballis, & Gazzaniga, 1998, 1999; Metcalfe, Funnell, & Gazzaniga, 1995), however he also exhibits an asymmetry in dorsal visual processing that is opposite compared to people with intact commissures (he exhibits a RH advantage for abstract spatial-relations encoding and a LH advantage for specific spatial-relations encoding; see Kosslyn & Koenig, 1992, Chap. 9). Taken together, these findings are consistent with statistical complementarity but inconsistent with predictions from input asymmetry, in that a positive correlation was not observed for asymmetries in

abstract shape recognition and abstract spatial-relations encoding nor for asymmetries in specific shape recognition and specific spatial-relations encoding.

We also should note that the method of comparing multiple asymmetry measures to uncover patterns of asymmetries within individuals has been used in other studies. Some researchers have used such a method to conclude that a global relationship exists in which all asymmetries load on the same factor in a principal-components analysis, perhaps due to an asymmetry in a central process like arousal (Kim & Levine, 1992; Kim, Levine, & Kertesz, 1990; Luh, Rueckert, & Levy, 1991). However, Boles (1998a) pointed out that, in those cases, the component does not reflect observed null or negative correlations between some tasks, and he argued that the component may be a statistical artifact that does not reflect a psychological reality. In addition, Boles (1998b) provided direct evidence against a global relationship using tasks with acceptable reliability estimates for the task asymmetry scores. The results did support local relationships between two or a small number of task asymmetries, but it is important to note that these relationships were observed using tasks that likely required processing in the same neural subsystem. For example, positive relationships were observed between visual recognition of digits, visual recognition of words, and visual recognition of words that name numbers, which makes sense given that these tasks likely were supported by an (abstract) visual shape recognition subsystem. In addition, positive relationships were observed for auditory recognition of digits and auditory recognition of words, and these tasks likely were supported by an auditory-form recognition subsystem. The general method of measuring relations between different task asymmetries should continue to prove useful for testing questions about the nature of functional differentiation in the brain.

By investigating the relations between four asymmetric visual subsystems, we found that the typical sample-level patterns of asymmetries may not be indicative of the patterns of asymmetries found within individuals. These results suggest that the typical sample-level asymmetries reveal probabilistic population level biases that are more independent from one another than typically hypothesized.

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