How Do the Cerebral Hemispheres Contribute to Encoding Spatial Relations?

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Early models of cerebral laterality often tended to ascribe entire congeries of complex mental abilities to one or the other cerebral hemisphere. For example, many theorists conceived of the left hemisphere as "verbal" and the right as "spatial"; others distinguished the two halves of the brain according to style or type of information processing, some characterizing the left hemisphere as analytic and the right as holistic (for a review, see Springer & Deutsch, 1998). Such models were at once too broad in ignoring important differences among tasks and abilities and too narrow in being unable to offer unique distinct predictions for novel tasks (see Marshall, 1981).

Recommended Reading

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.

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For example, consider the problems of (a) assessing whether one object is above or below another and (b) assessing whether two objects are greater or less than 1 foot apart. Both are spatial tasks, so early theories might have predicted that the right hemisphere would be superior at both. Yet both require a verbal response involving a categorization, so perhaps the left hemisphere would be better suited in each case. But if the left hemisphere is better, could this instead be because of the "analytical" processing required to compare two elements? It is clear that the coarse conceptualizations offered by early theories shed little light on even such apparently simple tasks as these.

In recent years, the use of computational theories in neuropsychology has increased. Such theories make explicit how different processes work together to transform input to output in a given behavioral task, and thus must be both specific enough to be implemented in a computer program and broad enough to accomplish well-defined tasks. An example of such a theory is the proposal (Kosslyn, 1987) that separate processes in the visual system encode and represent two distinct types of spatial relations between objects,[2] and that the hemispheres differ in the relative efficacy of these two processes (see also Kosslyn, 1994). In this article, we discuss the subsequent development of this theory as an example of how concepts and approaches from cognitive science can be usefully incorporated into theorizing in neuropsychology.

EVIDENCE FOR TWO TYPES OF SPATIAL RELATIONS

According to this theory, *categorical* spatial relations (such as "above/below," "left/right," or "inside/outside") place objects or parts of objects in broad categories of location with respect to each other. For example, two parts of an object can remain "connected to" each other even when the parts are in a wide range of positions. Hence, representations of categorical spatial relations would be useful for tasks in which precise locations can or must be ignored. In particular, recognizing an object whose parts are in an unusual configuration could be accomplished by recognizing the individual parts and the categorical spatial relations among them, then matching this built-up description to a stored description of the object. The same description will be produced for an object when its parts are in a large number of configurations. Categorical spatial relations, especially the most fundamental ones like above/below and left/right, are frequently called simply "spatial relations."

In contrast, *coordinate* spatial relations have the opposite property: They retain precise metric information about the distance between objects, ignoring the categorical spatial relations between them. Such relations are required for tasks like navigation and reaching. If you had only categorical spatial information, you would continually bump into objects or reach for them in the wrong places. For example, an object may be "in front" of you in a wide range of positions on a table, but only if you know its precise coordinates (relative to the body, in this case) will you be able to grasp it.

The theory proposed that the two types of spatial relations are computed by separate subsystems in the brain, and hypothesized that the brain's left hemisphere is more effective than its right hemisphere at encoding and using categorical spatial relations, and that the right hemisphere is better than the left at encoding and using coordinate spatial relations. According to the original theory, the left hemisphere excels at categorization generally, particularly in language, and thus it is useful for the left hemisphere to process spatial relations in a similar way. In contrast, the right hemisphere plays a key role in navigation, and hence metric spatial relations are more useful for it. The theory also proposed that small initial differences between the hemispheres could compound during development, ultimately producing a wide range of functional asymmetries, via a "snowball" mechanism: to the extent that a process received useful input, it "reinforced" the process that sent that input, thereby making the sending process operate more efficiently in the future (Kosslyn, Sokolov, & Chen, 1989).

Empirical support for the distinction between categorical and coordinate spatial relations and its hemispheric basis was offered by several groups. For example, Hellige and Michimata (1989) compared categorical and coordinate judgments using identical stimuli. Adult subjects were shown a small dot and a horizontal bar. In the categorical task, they were asked whether the dot was above or below the bar; in the coordinate task, they were asked whether the dot was greater or less than 2 cm from the bar. This display could appear either to the left of a central point, in place of it, or to its right (the left, center, and right visual fields, respectively) on each trial. Stimuli presented very briefly—for less than 200 ms—in the left or right visual field are registered initially by the opposite hemisphere. Thus, for example, if the left hemisphere is superior at performing a given task, a subject's performance should be faster and more accurate when stimuli are presented briefly in the right visual field (and hence are encoded initially by the left hemisphere) than when they are presented briefly in the left visual field. (For a review of this methodology, see Beaumont, 1982.) Hellige and Michimata reasoned that if their two tasks were performed by a single process (and thus categorical relations were not distinct from coordinate relations), then either the process should be more effective in one hemisphere than the other or there should be no difference between the hemispheres. The results showed, however, that the coordinate task was performed better by the right hemisphere, whereas the categorical task was performed better by the left hemisphere. These findings were replicated in a study that also demonstrated similar asymmetries when categorical judgments of on/off and inside/outside were compared with distance judgments (Kosslyn, Koenig, et al., 1989).

Such findings constitute evidence that the two types of spatial relations are encoded by two different processes, with the categorical encoding process more effective in the left hemisphere and the coordinate encoding process more effective in the right hemisphere. Note that, as Sergent (1991) pointed out, this *relative specialization* model is more reasonable and conservative than an *absolute localization* model in which each hemisphere computes only one type of spatial relation.

Since 1989, many additional studies of spatial relations encoding have been conducted, most offering support for the theory. For example, the pattern of complementary hemispheric asymmetries has been replicated using the original dot-bar paradigm (Hellige et al., 1994, Experiment 3) and using the same task with 5- and 7-year-old children (Koenig, Reiss, & Kosslyn, 1990). Most important, Laeng (1994) found that stroke patients with left-hemisphere damage were impaired more on categorical than on coordinate encoding tasks, and similar patients with right-hemisphere damage were impaired more on coordinate than on categorical tasks. However, some studies have produced results that could not have been predicted by the theory. For example, Banich and Federmeier (1997) replicated the basic dot-bar task asymmetry, but only when the bar appeared unpredictably at one of several different vertical positions on each trial.

COMPUTATIONAL MODEL

The original theory assumed that two separate processing subsystems exist, one that encodes categorical spatial relations and one that encodes coordinate spatial relations. This idea was supported, for example, by the finding that model neural networks encode the two types of spatial relations better if the networks are "split," so that different portions encode categorical and coordinate relations, than if a single undifferentiated network must encode both types of relations (Kosslyn, Chabris, Marsolek, & Koenig, 1992, Study 1). The theory has evolved over time as such computational models have been developed in more detail. We now propose that the two kinds of judgments are made by different processes, but that these processes in turn regulate attention to facilitate encoding the appropriate aspects of the input. Specifically, we argue that the efficiency with which spatial relations are encoded depends critically on the receptive fields of the neurons that are being attended.

A visual neuron's receptive field is the region in space from which that neuron receives stimulation. In other words, a stimulus will activate only those neurons whose receptive fields include the location of that stimulus. Neurons differ in the sizes of their receptive fields. In addition, the receptive fields of different neurons may overlap to differing degrees. We argue that categorical spatial relations are encoded more effectively if the outputs being attended come from neurons with relatively small, nonoverlapping receptive fields, as opposed to relatively large, overlapping receptive fields. This situation allows the observer to attend to one object and group the receptive fields for the surrounding space into "bins" that have specific categorical spatial relations relative to the object being focused on; it is then a small step to categorize the relation of a second object that falls into one of these bins.

We also propose that coordinate spatial relations are encoded more effectively if instead the outputs from neurons with relatively large, overlapping receptive fields are attended, facilitating a *coarse-coding* solution (e.g., Hinton, McClelland, & Rumelhart, 1986). The classic example of coarse coding is the role of the three types of cones in color vision (one most sensitive to red wavelengths, another most sensitive to green wavelengths, and the third most sensitive to blue wavelengths). The brain can extract precise wavelength information by combining signals from the three types of cones. The crucial information is not simply the presence or absence of activation in any particular type of cone, but rather the relative proportions of activation. This information allows the brain to "zero in" on precisely what wavelength would produce that specific profile of activation. Similarly, outputs from neurons with large, overlapping receptive fields can allow a system to localize a stimulus precisely.

The theory also claims that the left hemisphere is biased toward encoding outputs from neurons with relatively small, nonoverlapping receptive fields, whereas the right hemisphere is biased toward encoding outputs from neurons with relatively large, overlapping receptive fields. These biases are largely under attentional control, and thus the nature of the task can alter the way the hemispheres encode spatial information. This revised theory, by adding roles for receptive-field properties and attentional control, can account for a wider range of data than the original two-subsystem model. Next, we consider some results that address critical aspects of the theory.

Sizes of Receptive Fields

According to the theory, filtering visual input through small, nonoverlapping receptive fields efficiently divides space around the center of attention into categorically distinct regions; large, overlapping receptive fields promote encoding precise coordinate relations through a coarse-coding strategy. Sergent (1991) challenged the validity of the distinction between categorical and coordinate encoding on methodological and conceptual grounds. She had difficulty replicating earlier results (Kosslyn, Koenig, et al., 1989), even with similar stimuli, unless the stimuli were presented with relatively low levels of luminance. She also argued that "a coordinate representation conveys information about the two types of spatial relations" (p. 763)—that is, a coordinate representation ought to contain enough information for the subsequent computation of a categorical representation. For example, if you know the exact locations of two objects in two-dimensional space, it is trivial to deduce which object is above the other. By contrast, knowing only that one object is above another does not give you the information to find the distance between them.

We (Kosslyn et al., 1992; see also Jacobs & Kosslyn, 1994) replied to these objections by proposing a computational mechanism that could underlie and differentiate between the encoding of the two types of spatial relations. Sergent (1991) conceived of coordinate relations as little more than lists of points within "a frame of reference, with axes specifying . . . the position (absolute and relative) of the objects in space" (p. 763). We showed that distance relations can be extracted directly from visual arrays or maps without such intermediate representations of points by filtering visual input through large, overlapping receptive fields, which enable coarse coding. In contrast, as we noted earlier, outputs from neurons with small, nonoverlapping receptive fields can divide visual space into regions representing simple categorical relations. (A model of categorical-relations encoding with similar features has been independently proposed by Logan and Sadler, 1996.) In addition, Logan (1994) provided evidence that attention plays a role in encoding categorical relations. For example, in a visual search task, he found that response time increased steeply with number of additional distractors when targets differed from distractors only in a categorical spatial relation, either above/below or left/right, between their elements. If attention were not required for categorical encoding, subjects should have been able to process all the stimuli in parallel instead of one by one, as his results showed.

We (Kosslyn et al., 1992) tested the importance of receptive-field size with neural network simulations. In our most important experiment (Study 3, Part 2), networks were trained using a standard procedure to perform either a categorical or a coordinate encoding with their input filtered through either small, nonoverlapping or large, overlapping receptive fields. The input patterns were simplified visual arrays, each consisting of a bar and dot. These arrays and the number of receptive fields were the same in all four conditions (defined by crossing the type of encoding and the size of receptive field). As predicted, on the coordinate task, the networks performed better (produced less error after a given amount of training) with large, overlapping receptive fields than with small, nonoverlapping receptive fields; on the categorical task, there was a slight advantage for small over large receptive fields.[3]

A crucial prediction derived from these models was tested by Cowin and Hellige (1994), who tested subjects in the standard dot-bar paradigm (e.g., Hellige & Michimata, 1989) but varied the overall appearance of the stimuli. In one condition, the stimuli were presented normally; in another, they were blurred. Intuitively, one might think that blurring would make precise distances hard to extract without affecting perception of gross relations like above/below, but the models make the opposite prediction: Blurring should not affect the outputs from neurons with large receptive fields, but should degrade distinctions usually registered by neurons with small receptive fields. This prediction has the counterintuitive implication that judgments of metric distance should be affected less by blurring than judgments of categorical relations, if in fact judgments of metric distance rely on outputs from neurons with large, overlapping receptive fields. And in fact, Cowin and Hellige found that blurring impaired categorical but not coordinate judgments.

Hemispheric Biases for Outputs From Neurons With Large or Small Receptive Fields

According to the theory, at stages of visual processing beyond simple detection and grouping of stimuli, the left hemisphere is biased toward input from neurons with smaller receptive fields, and the right hemisphere is biased toward input from neurons with larger receptive fields. Besides being consistent with the asymmetries discussed thus far, this property could be the mechanism behind the common finding (e.g., Sergent, 1982) that the left hemisphere is better than the right hemisphere at processing details of objects, whereas the right hemisphere is better than the left hemisphere at processing overall shapes of objects. Results consistent with this idea have been obtained in experiments using stimuli consisting of many small capital letters arranged in the shape of a different capital letter (e.g., a set of *S*s arranged in the shape of an *H*). Subjects are asked to identify either the global shape (*H*) or the local shape (*S*) while ignoring the other shape. The left hemisphere is generally superior at processing the local shapes, and the right hemisphere is superior with global identification (see Van Kleeck, 1989, for a meta-analysis); moreover, blurring the stimuli selectively slows responses to the local shapes (Lovegrove, Lehmkuhle, Baro, & Garzia, 1991), exactly as would be predicted if small stimuli must be identified using information processed through small receptive fields. By contrast, removal of low spatial frequencies[4] slows global responses and eliminates the typical overall superiority of global identification (Badcock, Whitworth, Badcock, & Lovegrove, 1990), also as predicted.

The theory also posits that underlying the receptive-field biases of the cerebral hemispheres is differential use of information from two neural pathways, the magnocellular (M) and parvocellular (P) pathways. These pathways both begin at the retina and continue to high levels of the visual system;

one of the differences between them is that neurons in the M pathway have larger receptive fields than those in the P pathway (see Livingstone & Hubel, 1988). We (Kosslyn et al., 1992) proposed that the M pathway may provide more input to the right hemisphere than the left, whereas the P pathway has more connections with the left hemisphere than the right. Alternatively, it may be that the left hemisphere is biased to encode information from the P pathway, and the right hemisphere is biased to encode information from the M pathway, rather than that there are actual anatomical distinctions between the connections of the two pathways in the two cerebral hemispheres.

To test the theory's prediction about differential use of the M and P pathways, Roth and Hellige (1997) used tasks in which the categorical judgment is whether a line is above or below a pair of dots and the coordinate judgment is whether it is short enough to fit between them (Rybash & Hoyer, 1992). In their first experiment, the stimuli were either green on a red background or red on a green background. The former display, with red the dominant color, should selectively impede the M pathway (because diffuse red light reduces the response of some M neurons; see, e.g., Dreher, Fukuda, & Rodieck, 1976). Roth and Hellige's results were consistent with our (Kosslyn et al., 1992) models: The red background slowed coordinate processing, whereas the green background slowed categorical processing. These results were confirmed by Roth and Hellige's second experiment, in which either the stimulus or the background was black and the other varied in color. When red was the only color present in the display, coordinate processing was impaired and categorical processing was not.

Attentional Control

The theory posits that the left hemisphere is biased to attend to smaller regions of space than the right hemisphere. We asked whether the left hemisphere is better able than the right hemisphere to adjust (i.e., move, expand, or contract) the scope of attention in response to demands of the task. In a study consistent with this possibility (Kosslyn, Anderson, Hillger, & Hamilton, 1994), subjects viewed pairs of line segments shown in succession and judged whether the lines in each pair had the same orientation. When the lines appeared near each other in the same visual field, the left hemisphere was superior to the right hemisphere, but when the lines were farther apart, the right hemisphere was superior. A follow-up experiment showed that this effect could not be explained purely by differences in hard-wired size of receptive fields: When the stimuli were moved farther into the periphery, where there should be fewer small receptive fields than in the center and thus a general improvement in right-hemisphere performance, the left hemisphere was actually superior when the lines were far apart, and there was no hemispheric difference when the lines were near each other. One interpretation of these results is that the left hemisphere prefers to attend to smaller regions, but is more flexible than the right hemisphere in altering its scope and resolution of attention to meet task demands.

The notion that allocation of attention plays a crucial role in modulating the sizes of receptive fields has been supported by Tsal and Shalev (1996). They found that line length was judged more accurately when stimuli were attended, and was consistently overestimated when stimuli were unattended. These results are consistent with their proposal that (a) the processing units involved respond if anything is present within their receptive fields, and (b) attention allows the decision-making process to receive input from units with smaller receptive fields. (For example, a line that covered the diameters of five small receptive fields might extend through three receptive fields that are twice as large; thus, when large all-or-none receptive fields are monitored, the line will appear to be longer than when small fields are monitored.) We would predict that the effect should be greatest for stimuli in the right visual field, because the left hemisphere is better able than the right hemisphere to both allocate attention and take advantage of high-resolution input.

Category Learning

We also predict that the left hemisphere can develop new spatial categories with practice, which should eliminate the right-hemisphere superiority for encoding metric distances. In studies using the dot-bar paradigm, the right-hemisphere advantage for coordinate encoding often disappears before the end of the testing session (Kosslyn, Koenig, et al., 1989; cf. Rybash & Hoyer, 1992). Both hemispheres improve with practice, but the left hemisphere improves more and catches up with the right hemisphere, sometimes after just 36 trials. One interpretation of these results is that new spatial categories can be formed, allowing the left-hemisphere-based processes to perform more effectively.

According to this view, the more complex and novel the categories a task calls for, the more time the left hemisphere needs to catch up to the right in performance. We (Koenig, Kosslyn, Chabris, & Gabrieli, 1992) confirmed this prediction by increasing the number of possible dot locations and thereby lengthening the period of a left-hemisphere disadvantage for coordinate encoding. Also on these grounds, we predicted that performing the coordinate task would improve later performance on the categorical task more than would first performing a nonspatial control task with the same stimuli, but that by contrast, practice on the categorical task would not transfer to the coordinate task. This is what we found in a recent unpublished study. Indeed, the practice on categorical encoding provided by coordinate encoding may be even greater than that provided by first doing the very same categorical task. This pattern of results suggests that in this paradigm, categorical encoding is "mandatory" (once the stimuli are attended to), whereas coordinate encoding requires an explicit decision-making step that does not automatically occur whenever stimuli are presented; if this were not so, coordinate encoding would have improved after practice on the categorical task.

Discrimination Effects

Finally, the theory predicts that better examples of a spatial relation will be assessed more rapidly and accurately than will poorer examples. Results that support this prediction most clearly have been obtained in coordinate-encoding tasks, in which dot locations close to the criterion distance (e.g., 2 cm) from the bar are difficult for subjects to learn to judge accurately (e.g., Koenig et al., 1992). The neural mechanism behind this effect could take various forms. One possible system would be a population of neurons that each come to respond maximally to a preferred target location (relative to a reference point), with the properties that (a) more neurons are tuned to more frequently encountered locations and (b) the system's output depends on the accumulation over time of a sufficient total amount of individual neural responses, with a winner-take-all mechanism (e.g., see Grossberg, 1976) amplifying the first response that dominates. Thus, target locations that are more ambiguous will engender slower and less accurate responses. (For a discussion of related models, see Oram, Földiák, Perrett, & Sengpiel, 1998.)

CONCLUSION

The model we have outlined goes beyond the initial proposal (Kosslyn, 1987) and is more complex than one based on a direct assignment of subsystems or modules to encoding tasks. This emerging hidden complexity of spatial relations encoding tasks is also reflected in the results of positron emission tomography (PET) studies (Kosslyn, Thompson, Gitelman, & Alpert, in press) that found evidence for the predicted hemispheric differences in activity during categorical versus coordinate tasks but also surprisingly large networks of brain areas being activated by each task. Future research with neuroimaging techniques may also explore the interactions between the tasks discussed, as well as the possibility that difficult coordinate judgments may be performed using visual mental imagery (a possibility suggested by the degree of overlap between the areas activated by coordinate and imagery tasks; Kosslyn et al., 1993).

The past decade has seen an acceleration of interest in how the brain encodes, represents, and uses spatial relations. The main theory of hemispheric differences in this area is relatively young but has inspired many studies, which in turn have forced continual reevaluation of the theory. Although the distinction between categorical and coordinate encoding of spatial relations has held up well, we have used ideas from physiological studies, simulation modeling, and neuropsychological experimentation to extend the theory to account for otherwise unpredictable results and apply it to other hemispheric asymmetries. Computational theories are especially suited to this incremental approach, and our theory is sure to undergo further changes as research on spatial processing progresses.

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Notes

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2. We use the term relation in the somewhat ambiguous sense found in the literature under discussion, which does not always require a mapping between two sets of elements. For example, size has sometimes been described as a spatial relation, though it is really more like a property of a single object, unless the sizes of two objects are explicitly put in relation (object A "is larger than" object B).

3. We (Kosslyn et al., 1992) also extended our basic model to explain Sergent's (1991) luminance effect. The interpretation of our simulations was debated in several subsequent articles (see, e.g., Cook, Früh, & Landis, 1995; Kosslyn, Chabris, Marsolek, Jacobs, & Koenig, 1995), but our hypothesis about the benefits of different-size receptive fields for encoding different types of spatial relations was not seriously challenged. Recently, we (Baker, Chabris, & Kosslyn, in press) conducted new simulations that removed the potential confounds of earlier versions, and found again that enlarging receptive fields benefited coordinate more than categorical encoding.

4. Any visual image consists of a distribution of light energy over an

area. When the intensity of the light changes rapidly, such as occurs with alternating light and dark stripes, the visual information is said to be of high spatial frequency. When the intensity of the light changes slowly over an area, the spatial frequency is said to be low. Removing high spatial frequencies from an image results in blurring the image. Removing low spatial frequencies from an image reduces the largest scale light-dark variations.

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