The Asymmetrical Brain

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9 Asymmetries in Encoding Spatial Relations

Bruno Laeng, Christopher F. Chabris, and Stephen M. Kosslyn

Our phenomenology seems to respect the Newtonian distinction between matter and space, in contrast with the view of modern physics (since Einstein) of space and matter as two indissoluble aspects of a whole (Smart, 1964). Intuitively, space appears as either an all-pervading stuff or some sort of receptacle filled by material bodies. In cognitive neuroscience, evidence has accumulated that the brain processes space and form as two independent aspects of reality; indeed, a ventral neuroanatomical pathway running from the occipital lobe to the inferior temporal lobe processes shape, color, and other "object properties," whereas a dorsal pathway running from the occipital lobe to the posterior parietal lobe processes location and other "spatial properties" (e.g., Ungerleider & Mishkin, 1982). Such a division of labor between brain areas appears to be a pervasive principle of neural organization, and since the 1800s (cf. Harrington, 1987, 1995) evidence has been growing within the neurosciences that complex mental abilities fractionate into sets of subsystems, each devoted to a specific computational task (Kosslyn & Koenig, 1995).

At the root of our spatial knowledge is the ability to register *locations*. Our proposal is that at least two different properties can be extracted from specifications of location. These properties may be logically independent; that is, knowledge of one may be neither necessary nor sufficient to know the other. Because the properties we are referring to essentially define relations between locations, we shall refer to them as different types of *spatial relations*. According to its original formulation (Kosslyn, 1987), there is an early split within the dorsal stream of visual information into two subnetworks that process qualitatively different types of spatial information. These two networks within the dorsal

system are each concerned with one type of computation, and each type describes a different kind of spatial relation.

COORDINATE SPATIAL RELATIONS

One type of spatial relations representation captures coordinate relations. These sorts of relations occur within a metric space; that is, an order or collection of points on which distance between points is defined. A point could be the lowest level of resolution of the visual system. An order of such points creates a continuum. In other words, this form of representing space is analog or dense (Goodman, 1976), in the sense that two spatial forms can transform into one another through intermediate orders of points.

For example, orders of points constitute lines and areas in two dimensions, or volumes in three, and all possible objects of this kind can transform continuously into one another by simply adding or deleting intermediate points. Thus, the ability to encode coordinate relations would allow the perception and expression of space in a quantitative sense. Distance, size, and orientation between two locations or sets of locations (such as volumes) could be represented integrally in such an encoding system.

This coordinate mode of coding interrelations is most suitable for the control of movement of the body and its parts. Thus, although visual, this type of coding appears to be motor-based, in the sense that it provides a form of representation that can be used to guide movements, such as navigating within the near-to-the-body physical medium, tracking, reaching, and manipulating other external bodies. In general, spatial action would seem to be supported by encodings that specify distal locations as the end points of actions. At first glance, this formulation might seem to exclude the mappings of places and objects that are unreachable or not navigable (e.g., flying birds and stars). Many classes of spatially located objects imply a lack of bodily contact; however, we can point to or look at any visible object. Hence, anything in the line of vision can constitute a specific external target of a directed movement for the index finger or the eye.

CATEGORICAL SPATIAL RELATIONS

As proposed by Piaget and Inhelder (1956), there may be modes of perception that are alternative and qualitatively different from the one

Figure 9.1 Contorted human body. (From Lois Greenfield, *Breaking Bounds*. London: Thames and Hudson, 1992.)

necessary to guide action, and each of these different formats may uniquely enrich the cognitive system's analysis of space. We have good reason to believe that for some tasks where spatial information seems useful, coordinate information is irrelevant and in fact may be counterproductive. For example, some problems of object recognition would seem to require integration of visual information about shape with spatial information about the arrangement of the object's parts. In particular, the recognition of nonrigid objects, when their parts are positioned in novel ways (e.g., a contorted human body; see figure 9.1), may depend heavily on being able to recover their spatial structure. Because the flexible object's parts may not be in their usual locations, a novel view could radically change an object's familiar global geometry and become, in essence, an unknown shape. If some parts are visible in the image and these suggest the presence of a specific object, then stored information about the spatial arrangement of the parts (i.e., a stored structural description) could guide a search for other parts of the object and confirm or discard such a perceptual hypothesis (e.g., Kosslyn, 1987).

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However, using metric information would be irrelevant for such a recognition task, because nonrigid objects flex and bend, and therefore do not preserve constant metric relations between their parts. Therefore, another type of spatial description of the object's geometry seems more useful, one that preserves invariant spatial information by ignoring metric information. Indeed, many contemporary theories of object identification (e.g., Marr, 1982; Biederman, 1987) assume that objects are represented using such structural descriptions, which use abstract types of spatial representations to specify relations among parts (e.g., top-of, end-to-middle-connected, left-side-connected).

To offer another example (see figure 9.2), we can see a human hand as composed of many parts: the palm, the fingers, each finger with its nail and knuckles. Obviously, a hand can make gestures (that is, flex its fingers in several ways) and therefore assume many shapes, while only its boned parts remain rigid across all the transformations. Yet, the way the parts are arranged, or the specific constraints dictated by the structure of connectivity, remains invariant across these transformations and it is inherently spatial, albeit in an abstract sense. Consider that nails are the endpoint and topside of fingers and arc on the backside of the whole hand. When looking down at your hands' palms, the right hand is distinguishable from its left companion because the thumb (easily recognizable by the two, instead of three, phalanges) is attached to the right side of the palm. It is the specification of these connectivity relations that we believe provides a stable representation of the object's shape. The adaptive value of a spatial system that can provide encodings of such relations is not trivial. Its ability to aid the recognition of flexible objects (e.g., other living beings), especially in nonoptimal viewing conditions (when their bodies are contorted in novel ways), has obvious biological significance.

In addition, recognizing contorted objects may not be the only function of abstract, nonmetric, spatial encodings. Generally speaking, nonmetric relations can be described for completely disjointed objects or meaningless visual stimuli (e.g., two dots can be seen above or below a line). Within the more general account, whatever appears to be occupying space (i.e., a figure on a background) can in principle be encoded as being in some reciprocal spatial relation. Categorical encodings are mappings of abstract relations between locations; such processes can occur independently from, and in parallel with, the recognition or identification of shapes, objects, and parts of objects. Nevertheless, if the

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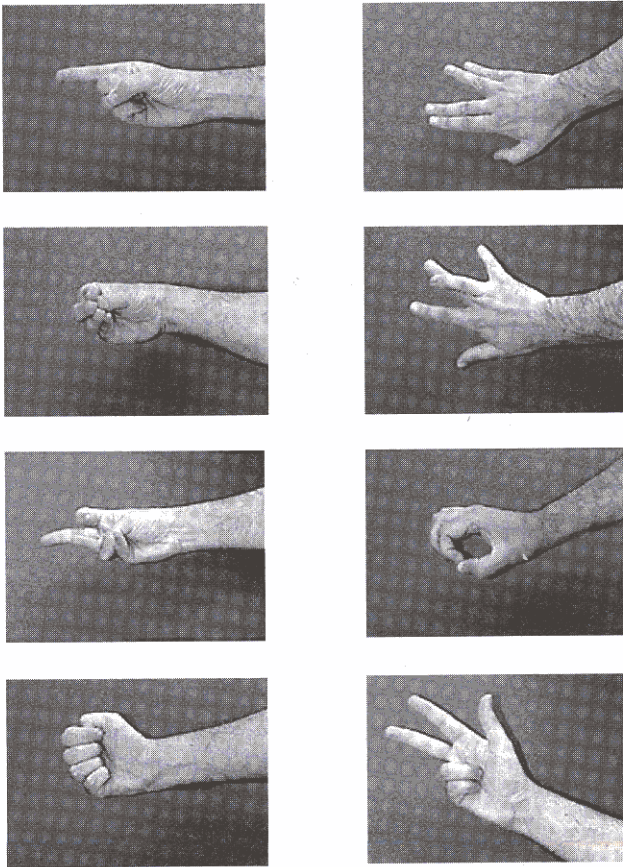
Figure 9.2 Hand contortions (Photos by Bruno Laeng.)

objects viewed have a complex geometry, higher-order spatial relations can emerge between them and can also be encoded (consider all the relations determined by the surfaces of the human body: front/back, top/bottom, and left/right sides).

Thus, close to Kosslyn's original formulation (1987), we define categorical encodings as groupings of locations that define an equivalence class. At the root of such encodings is the ability to delineate patches of space or to discover boundaries or limits that separate bins of space. Categorical encodings are abstract compared to coordinate ones, because a greater number of the latter can be comprised within a position

described by the former (e.g., "anything to the left of that point"). Different categorical spatial relations are qualitatively disjoint, and therefore cannot transform into another (e.g., the relation "inside" cannot map onto "left of" in any formal sense); it is important that these spatial representations cannot support continuous rigid transformations of objects (e.g., spatial rotations), as can occur within a coordinate framework.

A Model of Spatial Relations Encodings: Lateralized Processing

In recent years, the use of computational theories in neuropsychology has become increasingly influential. Such theories make explicit how different processes work together to transform input to output in a given behavioral task, and thus have the advantage of being both specific enough to be implemented in a computer program and general enough to accomplish well-defined tasks (e.g., Kosslyn, 1987; Shallice, 1988; Farah, 1990; Behrmann et al., 1991; Humphreys et al., 1992; Kosslyn, 1994; Ivry & Robertson, 1998). We can distinguish the two hemispheres of the brain according to the type of information processing or computations that they support. A computational theory of cerebral asymmetry specifies what type of representation each hemisphere encodes most effectively. Thus, it differs from other theories of hemispheric specialization (cf. Bradshaw & Nettleton, 1983; for a review, see Springer & Deutsch, 1998) that either (1) focus on ill-defined distinctions, such as "cognitive style" or "strategies" (e.g., holistic versus analytical), or (2) equate each hemisphere's preferred function with specific tasks (e.g., spatial versus verbal versus musical).

Nevertheless, because all theories of cerebral lateralization must provide an account for the same data, there are analogies between different theories. For example, the present theory's distinction between categorical and coordinate encoding shows some relationship to the traditional verbal/nonverbal distinction between the processing of two hemispheres. Specifically, because we posit categorical spatial relations to be qualitative and discrete (often expressed in binary oppositions; e.g., on/off), we would expect that they should easily map onto spatial concepts and words. Indeed, all natural languages seem to have a special class in their grammar (i.e., prepositions) devoted to the expression of categorical spatial relations (cf. Miller & Johnson-Laird, 1976). In contrast, because we posit coordinate spatial relations to be quantita-

tive and continuous, we would expect these relations to be difficult to verbalize (e.g., telling how many inches apart two objects are and verbally describing someone's face are notoriously difficult tasks).

Kosslyn (1987, 1994) hypothesized that although both hemispheres embody computational subsystems that encode the two types of spatial relations representations, the subsystem that encodes categorical spatial relations is more efficient in the left hemisphere, whereas the one that encodes coordinate spatial relations is more efficient in the right hemisphere. The theory is grounded on the idea that the two types of spatial relations are most efficiently computed by separate subsystems, a hypothesis that has been independently supported by computational simulations. For example, Kosslyn et al. (1992) showed that model neural networks encode the two types of spatial relations better if the networks are split, so that different partitions encode categorical and coordinate relations, than if a single, undifferentiated network must encode both types of relations (figure 9.3). One study with a large cohort of brain-damaged patients (Laeng, 1994) has shown that lesions to one hemisphere result in more impairment in one type of spatial encoding than in the other, and lesions to the other hemisphere result in the reverse impairment. This finding lends support to the idea that the human neural substrate separates the computations underlying each spatial encoding into split neural networks, each in one cerebral hemisphere.

DIFFERENCES IN RECEPTIVE VISUAL FIELDS

The theory has evolved over time, and the computational models have been developed in more detail (cf. Jacobs & Kosslyn, 1994; Kosslyn & Jacobs, 1994). In the current version of the theory, different processes accomplish the two kinds of spatial encoding, but these processes in turn regulate attention to facilitate encoding the appropriate aspects of the input. Specifically, according to this theory, 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, and neurons can differ in the sizes of their receptive fields. In addition, the receptive fields of different neurons may overlap to differing degrees.

Computational simulations showed that categorical spatial relations are encoded more effectively if the outputs being attended come from
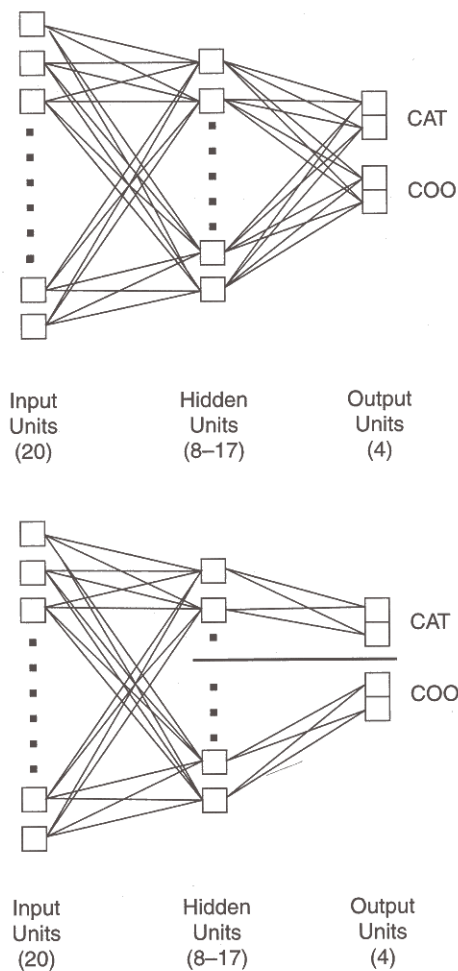
Asymmetries in Spatial Relations

Input   Hidden   Output
Units   Units   Units
(20)   (8–17)   (4)

Input   Hidden   Output
Units   Units   Units
(20)   (8–17)   (4)

Figure 9.3 The architecture of the unsplit (*top*) and split (*bottom*) networks. (Numbers in parentheses indicate the size of the layers.) CAT, categorical spatial relations; COO, coordinate spatial relations. (From Kosslyn et al., 1992.)

neurons with relatively small, nonoverlapping receptive fields, as opposed to relatively large, overlapping receptive fields. For categorical relations, an observer can attend to one object and group the receptive fields for the surrounding space into "bins" that have specific spatial relations relative to the object being focused upon; it is then a small step to categorize the relation of a second object that falls into one of

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these bins. Moreover, the models showed that coordinate spatial relations representations are encoded more effectively if the outputs from neurons with relatively large, overlapping receptive fields are attended, facilitating coarse-coding (e.g., Hinton et al., 1986; O'Reilly et al., 1990). According to this account, outputs from neurons with large, overlapping receptive fields allow a system to localize a stimulus precisely.

Empirical evidence from human studies has shown that the left cerebral hemisphere (LH) has a bias to filter visual input through small attended areas (or high spatial frequency processing), whereas the right cerebral hemisphere (RH) has a bias to filter visual input through large attended areas (low spatial frequencies; for a thorough review of the evidence, see Ivry & Robertson, 1998; see also Kitterle et al., 1990; Kitterle & Selig, 1991; Sergent, 1991a). For example, when "striped" stimuli, such as sinusoidal gratings with wide stripes (e.g., at a low spatial frequency of 1 cycle/degree) and narrow stripes (e.g., at a high spatial frequency of 9 cycles/degree) are presented in the left visual field (LVF) or in the right visual field (RVF), subjects identify the wide-striped stimuli better in the LVF than in the RVF. In contrast, narrow-striped stimuli are better identified in the RVF than in the LVF. This processing asymmetry appears to be mediated by attentional mechanisms, not hardwired differences in the population of receptors feeding into each hemisphere (Kosslyn et al., 1994; Ivry & Robertson, 1998).

The convergence and combination of outputs from neurons involved in early visual processing within each hemisphere could promote the encoding of higher-order spatial properties. However, these later encodings would be more or less easily computed, depending on properties of the early encodings. Specifically, we would expect that the large, overlapping receptive fields of the neurons in the RH would promote encoding fine-grained, precise, coordinate spatial relations through a coarse-coding strategy. In contrast, filtering visual input through small, nonoverlapping receptive fields in the LH would help to divide space around the center of attention into categorically distinct regions, which would promote encoding categorical spatial relations. Moreover, these hemispheric encoding biases should also affect the way each hemisphere process shapes (cf. Delis et al., 1986; Robertson & Delis, 1986; Robertson & Lamb, 1991; Jacobs & Kosslyn, 1994). Accordingly, we would expect exemplar or individual-level representations of shapes to be encoded more efficiently in the RH (Marsolek et al., 1992; Marsolek, 1995). In contrast, the LH's ability to focus attention over

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H     H      H H H H H     H H H H H     O O O O O
H     H      H     H       H             O
H     H      H     H       H             O
H H H H H    H     H       H H H H H     O O O O O
H     H      H     H             H               O
H     H      H     H             H               O
H     H      H H H H H     H H H H H     O O O O O



S     S      S S S S S     S S S S S     O         O
S     S      S     S       S             O         O
S     S      S     S       S             O         O
S S S S S    S     S       S S S S S     O O O O O
S     S      S     S             S       O         O
S     S      S     S             S       O         O
S     S      S S S S S     S S S S S     O         O
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Figure 9.4 Hierarchical visual stimuli used by Van Kleeck (1989).

distinct and discrete regions may be better suited for "carving out" patterns contained within other patterns, or the extraction of parts from a global shape (Van Kleeck, 1989; figure 9.4).

The receptive field biases of the cerebral hemispheres may in part reflect differences in the use of information from two neural pathways: the transient, or magnocellular (M), and the sustained, or parvocellular (P). 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 (Livingstone & Hubel, 1988). Kosslyn and colleagues (1992) proposed that the M pathway may provide more input to the RH than to the LH, whereas the P pathway has more connections with the LH than the RH. Alternatively, it may be that the LH is biased to encode information from the P pathway, and the RH 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.

THE "SNOWBALL" MECHANISM

At the initial formulation of the present theory (e.g., Kosslyn, 1987), other theoretical considerations had led us to expect that a specific

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spatial encoding subsystem could develop more strongly in one hemisphere than in the other. Namely, the original idea was that an effective computational architecture will "yoke" subsystems that often operate together, facilitating their joint operation (cf. Jacobs & Kosslyn, 1994). Another way to express this relation between different but interdependent subsystems is that they exert reciprocal feedback training (Van Kleeck & Kosslyn, 1991); that is, to the extent that a process receives useful input, it reinforces the process that sends that input, thereby making the sending process operate more efficiently in the future (Kosslyn, Sokolov, et al., 1989). An interesting implication of this theory is that small initial differences between the hemispheres could compound during development, ultimately producing a wide range of functional asymmetries, via a "snowball" mechanism.

Of particular relevance for this account is the evidence that the speech output control system is genetically constrained to develop in the LH (Corballis, 1991). This constraint may derive from the fact that "action" in general may best originate from a unilateral source of control, as opposed to several potentially interfering, bilateral executive centers. Indeed, the evidence from neuropsychology indicates LH's dominance in speech as well as other complex motor behaviors or praxis (Heilman & Valenstein, 1985).

Our proposal is that LH's initial bias for the speech output control system may constitute the "seed" for the development in the same hemisphere of other interdependent, yoked subsystems. In turn, the knowledge database (semantic and verbal, containing facts and words) could become more dependent on processing in the LH than in the RH (cf. De Renzi et al., 1969; Warrington & Taylor, 1978; Gazzaniga, 1983; Gainotti et al., 1995; Damasio et al., 1996; Caramazza & Shelton, 1998). Moreover, if the LH generally possesses a richer representation of the lexical and semantic information than does the RH, then these systems in the LH will also exert better feedback training of the pattern recognition and spatial encoding subsystems in the same (LH) hemisphere, thereby providing them with the optimal input for access to conceptual and lexical representations of space.

In summary, according to the theory, complementary encoding subsystems develop in different hemispheres under the influence of different sources, such as early spatial frequency biases and unilateral feedback training from the speech control system. These sources con-

tribute to channeling and grouping compatible types of information processing within one hemisphere while splitting and dividing, across the corpus callosum, the less compatible types.

EMPIRICAL EVIDENCE FOR CATEGORICAL AND COORDINATE SPATIAL RELATIONS ENCODING IN SEPARATE CEREBRAL HEMISPHERES

The theory is consistent with a large and varied body of empirical findings that rely on different methodologies and different subject populations. In this section, we briefly review these results.

Divided Visual Field Studies

Most of the evidence garnered for the theory relies on divided-visual-field studies (for a review of this methodology, see Beaumont, 1982, or Bryden, 1982). Specifically, the theory predicts an interaction between the visual field in which stimuli are presented and the way in which spatial relations must be encoded to perform the task: Subjects should be faster and more accurate when stimuli are presented in the LVF (to the RH initially) and coordinate spatial relations must be encoded, and faster and more accurate when stimuli are presented in the RVF (to the LH initially) and categorical spatial relations must be encoded.

In one of Kosslyn's (1987) initial experiments, subjects were shown stimuli like the blob and dot in figure 9.5. In one condition, the subjects were asked to verify whether the dot was on or off the blob, and in another condition they were asked whether the dot was within 2 mm of the blob (including being on its contour) or farther than 2 mm. As predicted, the on/off, categorical, spatial judgment was easier when the stimuli were presented initially to the LH, whereas the less/more than 2 mm, coordinate, judgment was easier when the stimuli were presented initially to the RH.

Hellige and Michimata (1989; see also Kosslyn, Koenig, et al., 1989) replicated these complementary hemispheric advantages for categorical and coordinate judgments with another simple perceptual task (figure 9.6). In the categorical condition, subjects were asked whether the dot was above or below the bar; in the coordinate condition, they were asked whether the dot was at a distance greater or less than 2 cm from the bar.

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Figure 9.5 Blob and dot stimuli used in the original near/far, on/off task.
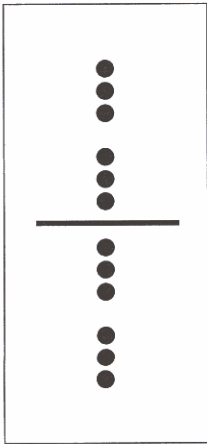

Figure 9.6 The standard dot-above/below-bar stimuli used by Hellige and Michimata (1989).

Several researchers criticized these initial experiments on both methodological and conceptual grounds. Sergent (1991a) had difficulty replicating Kosslyn and colleagues' findings, even with similar stimuli, unless the stimuli were presented with relatively low levels of luminance. She also challenged the validity of the categorical/coordinate distinction on methodological and conceptual grounds by proposing that a single, coordinate spatial representation was sufficient and logically prior to computing any other type of spatial relation. Specifically,

if the exact locations of two objects in two-dimensional space are known, then it should be trivial to deduce which object is above the other. By contrast, knowing only that one object is above another does not provide the information needed to find the distance between them.

Kosslyn et al. (1992) replied by proposing a computational mechanism that could underlie the encoding of the two types of spatial relations. In these computational simulations (see also Jacobs & Kosslyn, 1994; Kosslyn & Jacobs, 1994), metric (coordinate) distance relations could be extracted directly from visual arrays by filtering visual input through large overlapping receptive fields, which enable coarse coding. In contrast, as we noted earlier, they showed that outputs from units with small, nonoverlapping receptive fields can divide visual space into patches corresponding to simple categorical relations. Moreover, they showed why these effects would be evident only at low levels of illumination, assuming that at higher levels the quantitative differences in the proportions of units with large vs. small receptive fields becomes irrelevant (due, essentially, to ceiling effects).

Cowin and Hellige (1994) used, together with the standard dot-above/below-bar paradigm of Hellige and Michimata (1989), a modified condition in which the stimuli were blurred. They found that blurring impaired categorical but not coordinate judgments. As Ivry and Robertson (1998) point out, it is not intuitive how a theory based on categorical and coordinate spatial relations accounts for such a selective effect. The key idea is that blurring does not affect the outputs from neurons with large receptive fields, but it degrades distinctions usually registered by neurons with small receptive fields. Hence, the theory does make the counterintuitive prediction 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.

As noted earlier, information from the transient, or magnocellular (M), pathway may be tapped primarily by the coordinate spatial relations encoding process, whereas information from the sustained, or parvocellular (P), pathways may be used primarily by the categorical spatial relations encoding process (Kosslyn et al., 1992). One way to differentially activate the two pathways is to alter the color of stimuli: Diffuse red light reduces the response of some M pathway neurons, from the retina through the lateral geniculate nucleus, to primary visual cortex (Dreher et al., 1976). Accordingly, if the RH preferentially

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uses information from the M pathway, including red in a display should reduce LVF performance relative to a control condition with no red. Roth and Hellige (1998) directly tested this idea in two tasks, asking whether a line is above or below a pair of dots and whether it is short enough to fit between them (cf. Rybash & Hoyer, 1992). Critically, they varied the color (red/green) of the stimuli or the background. The results were consistent with Kosslyn and colleagues' (1992) predictions: The red background, which as the dominant color in the stimulus should inhibit the M pathway and reduce RH detection performance, slowed coordinate processing. Also, when red was the only color present in the display, coordinate processing was impaired and categorical processing was not.

Several other experiments, described below, have overall converged on finding the expected visual field differences. In some of these studies, the effects have been transient (e.g., Kosslyn et al., 1989), and there have also been clear failures to replicate some of the single visual field differences (cf. Sergent, 1991a; Rybash & Hoyer, 1992; Kogure & Hatta, 1999; Wilkinson & Donnelly, 1999). However, most important, the reverse pattern of dissociations has never been reported.

In addition, some studies have produced results that could not have been predicted by the theory. For example, Banich and Federmeier (1999) replicated the basic dot-bar task asymmetry only when the bar appeared unpredictably at one of several different vertical positions on each trial. Horner and Freides (1996) replicated the hypothesized asymmetries when stimuli were presented at 3 degrees of visual angle, but not at 1 or 9 degrees.

Bruyer et al. (1997) have shown that, at least with the standard dot-below/above-line paradigm, the expected task-by-visual-field interaction is fragile and influenced by several methodological factors. Bruyer and colleagues varied, in a series of experiments, either the mode of response (vocal versus manual), the presence or absence of feedback, whether there was a binary versus continuous response, and the age of the subjects. They were able to reveal the expected visual field effects and their double dissociation, but across all the experiments some of the single visual field differences appeared unstable.

Parrot et al. (1999) varied the level of difficulty of each spatial judgment, and observed an LH advantage for categorical spatial relations as well as "easy" coordinate processing, in contrast to an RH advantage

for "difficult" coordinate decisions. Interestingly, other researchers have reported that the RH advantage for coordinate encoding may disappear before the end of the testing session (Kosslyn, Koenig, et al., 1989; cf. Rybash & Hoyer, 1992). Coordinate spatial relations encoding in the LH appears to improve over time, and eventually "catches up" with the RH. A possible explanation for this phenomenon is that new spatial categories get formed that allow the LH-based processes to perform more effectively. Consistent with this view, Koenig et al. (1992) have shown that the more complex and novel the categories a task calls for, the more time the LH needs to match the RH in performance. Chabris and Kosslyn (1998) have reported that practice in the coordinate task transfers to the categorical judgment, but not vice versa, again suggesting that the categorical system is gradually "tuned" when one performs a new coordinate task (and is thereby "primed" for operation).

A few divided-fields studies have made use of more "natural" stimuli than the initial studies. Michimata (1997) used figures of clocks and asked subjects to make categorical and coordinate decisions about the positions of the two hands. Laeng and Peters (1995) presented figures of animals that, given their geometric complexity, allow the testing of several high-order categorical relations (figure 9.7). Moreover, although studies have typically used distance for the coordinate judgments, Laeng and Peters (1995) tested other coordinate relations, such as size and tilt. Interestingly, this study revealed large visual field differences in response times for both spatial relation decisions (circa 100 ms), in contrast to the majority of studies in which differences between the hemispheres are on the order of a few tens of milliseconds. Possibly the increased computational complexity arising from the inferred 3-D geometry of depictions of natural objects, and the absence of a single, systematic relation manipulation in each spatial task, could have contributed to increase the strength of each hemisphere's encoding advantage and in reducing practice effects.

Servos and Peters (1990) used line drawings of objects in depth (such as the cubes of Shepard & Metzler, 1971) and asked subjects to decide whether the top or bottom part of the figure was closer to the observer (i.e., an in-front/behind categorical decision). They found a strong LH advantage, and also found such an advantage when the judgment involved simple flat figures occluding one another. The latter finding is in contrast to a study by Kogure and Hatta (1999), who also used flat, occluding stimuli, resembling playing cards, and a task that involved

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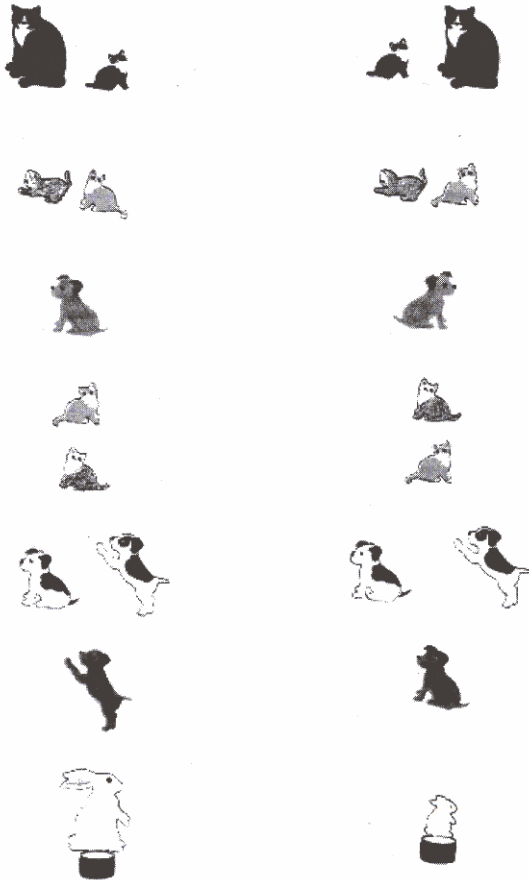
Sample　　　　　　　　　　　　**Match**

Figure 9.7 Stimuli used by Laeng and Peters (1995).

reporting the number written on the leftmost/rightmost or front/rear card. An RH advantage was found with this task. The discrepancy between the two studies may arise from the fact that the latter experiment required subjects to find a number located on a specific card, which could have benefited from coordinate information.

Kosslyn et al. (1995) have tested the effects of categorical and coordinate processing within the imagery domain (see also Michimata, 1997). Subjects were asked to form images of uppercase letters and to judge whether a letter shape would cover a laterally presented probe. They

found that in a condition where a grid was provided on which to form images, there was an RVF advantage, whereas in a condition without a grid there was an LVF advantage. They suggest that the grid supports arranging the parts according to categorical spatial relations (such as "left column, attached at top to right row"), whereas with no grid, subjects would have to rely on more precise metric information in order to generate the visual images.

Laeng et al. (1997) tested the hypothesis that the LH categorizes space into regions by studying the strength of each cerebral hemisphere's memory bias toward prototypical locations or centers of parsed regions of a display. They used a task developed by Huttenlocher et al. (1991) in which a dot appears within a circle at variable angular and radial positions, and subjects are later asked to indicate the dot's position on an empty circle. Huttenlocher and colleagues found that subjects make precise estimates but at the same time show a bias toward prototypical/canonical locations within regions of space (namely, the estimates regress toward the angular and radial center of each invisible quadrant in the circle). These effects demonstrate a double spatial coding of a point's location: (a) in terms of metrics (exactly where) and (b) in terms of the categorical location (where in relation to classes of locations corresponding to parsed regions of space). Laeng et al. (1997) found, in a divided-fields paradigm, that the regressions of spatial estimates toward each quadrant's canonical position were stronger after RVF presentation than LVF presentation, supporting the view that the LH is specifically engaged in parsing space into regions or classes of locations, and stores this spatial information.

Laeng, Shah, et al. (1999) have specifically tested the hypothesis that the LH's categorical spatial processing facilitates the recognition of difficult views of objects, particularly contorted poses of nonrigid objects (figure 9.8). Marr (1982) proposed that the brain stores "structural descriptions" composed of primitives such as generalized cones; Biederman (1987, 1995) has developed a theory of edge-based structural descriptions that specify the components (i.e., geons) of a shape and the qualitative (categorical) spatial relations between these parts (e.g., left-of, top-of, larger-than, end-to-end-connected). One key advantage conferred by the abstractness of these perceptual descriptions is that an object's structure can be captured in a way that remains invariant across a potentially infinite number of shapes or variations of projections.
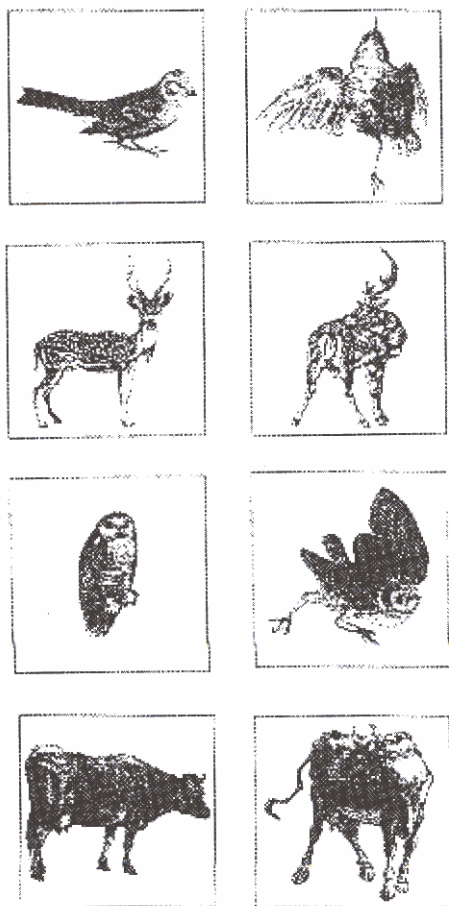
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Figure 9.8 Conventional (*left*) and contorted poses (*right*) of animals. (From Laeng, Shah, et al., 1999.)

Based on the ideas that (a) overall shapes are encoded better by the RH, (b) categorical spatial relations are encoded better by the LH, and (c) categorical relations are used in structural descriptions, Laeng, Shah, et al. (1999) predicted and confirmed an RVF advantage when one first encodes the contorted pose of an animal and an LVF advantage for encoding the same shapes after they are familiar. Moreover, when correlation analyses between the time to match pictures of contorted animals to names and the time to encode categorical spatial relations (in an independent nonverbal task) were performed, they revealed that

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the degree and polarity of lateralization of categorical spatial encoding predicted the LH's initial advantage in the recognition of contorted shapes. This latter finding specifically supports the idea that the LH's categorical spatial encodings play a functional role in the recognition of nonrigid objects.

Divided visual field effects apply not only to lateral hemifields' differences but also to differences between the upper and lower visual fields (cf. Efron, 1990; Previc, 1990). The up/down asymmetry could derive from a greater accessibility of the cortical representations of the lower versus upper visual field with the specialized subsystems within the ventral versus dorsal stream (cf. Andersen et al., 1990; Rubin et al., 1996). The representation of these visual fields is split into disjoint portions of the cortical surface "sheet" so that, topographically, the upper visual field is represented near temporal areas and the lower field near parietal areas. Niebauer and Christman (1998) reasoned that if the upper visual field is specialized for visual search, whereas the lower visual field is specialized for visuomotor manipulations (see Previc, 1990), then it should be possible to observe an upper visual field advantage for categorical judgments and a lower visual field advantage for coordinate judgments. By using the standard dot-above/below-line task they were able to confirm these longitudinal, instead of lateral, differences.

A few divided visual field studies have examined specific subject populations. Koenig et al. (1990) replicated the visual fields' dissociations with children as young as 5 years of age. Hoyer and Rybash (1992) and Bruyer et al. (1997) have tested elderly subjects. Bruyer and colleagues found that the categorical, easier, task showed a visual field difference, whereas there was no field advantage for the coordinate task. They surmised that the disappearance of the LVF effect results from asymmetric aging effects on the brain. Kosslyn (1987), Hellige and colleagues (1994), and Laeng and Peters (1995) converged in showing a failure to reveal laterality effects in left-handers for either spatial relation encoding. Indeed, left-handers would not be expected to show the same pattern and degree of cerebral lateralization for spatial information as right-handers, if we assume that the localization of language areas as well as behavior asymmetries are highly variable in this group of subjects (cf. Bryden, 1982; Geschwind & Galaburda, 1987). Finally, Emmorey and Kosslyn (1996) found that deaf subjects who use American Sign Language as their primary language exhibited a strong RH

advantage for image generation using either categorical or coordinate spatial relations representations. They suggested that the enhanced RH image generation abilities observed in deaf signers may be linked to a stronger RH involvement in processing imageable signs and linguistically encoded spatial relations.

To conclude this section, we present a meta-analysis of existing divided visual field experiments on the topic. To be included, an experiment had to test the encoding of both a categorical and a coordinate spatial relation using identical stimuli with normal human subjects (of any age group), and had to report sufficient information about the results to enable extraction of mean response times. Experiments testing categorical judgments that did not involve encoding a well-defined simple spatial relation under normal viewing conditions (e.g., the studies by Horner & Freides, 1996, and Cowin & Hellige, 1994) were not included. For many experiments, detailed accuracy data were not reported, usually because there were few errors, especially on categorical judgments. Although effects were sometimes found for error rates but not response times, speed-accuracy trade-offs were almost never reported.

The results of 24 experiments (with a total of 887 degrees of freedom) were considered. Twenty of these experiments used the above/below categorical judgment; of these, 16 used the distance coordinate judgment (with distances varying from 3 to 25 mm). For uniformity, we shall report only results based on response-time analyses from these 16 experiments (536 degrees of freedom), although the results from the other paradigms showed the same, predicted pattern. For the categorical judgments, subjects responded 8 ms faster when stimuli were presented initially to the LH (529 ms) than to the RH (537 ms), whereas for coordinate judgments subjects responded 14 ms faster when stimuli were presented initially to the RH (636 ms) than to the LH (650 ms). The overall effect size for this interaction was $d = .47$, the combined Z-value was 6.93, and the associated p-value was much smaller than .0001 (all calculations based only on experiments for which variability estimates could be extracted). Therefore, it is reasonable to conclude that although the hemispheric asymmetries predicted by the theory are small in absolute terms, they do exist.

Clinical Studies Laeng (1994) provided converging evidence for the distinction between the two types of spatial relations encoding on the

basis of results from the study of patients with brain lesions. If categorical spatial relations are computed primarily in the LH, then damage to this hemisphere should cause the patient to become insensitive to changes in categorical relations between objects; in contrast, if coordinate spatial relations are computed primarily in the RH, then damage to this hemisphere should cause the patient to become insensitive to changes in the metric relations among the same objects. The experiment confirmed a "double dissociation" between the spatial impairments of the two neurological patient groups.

Specifically, 30 patients with damage confined to the LH, 30 with damage confined to the RH, and 15 controls matched by age and education saw a drawing of one or more versions of the same object (typically, animals; e.g., a large cat to the left of a small cat). After a short delay, they were asked to decide whether another drawing was the same or different. Half of the drawings were changed so that they incorporated either a different categorical spatial relation (e.g., a large cat to the left of a small cat) or a different coordinate spatial relation (the large cat was still to the left of the small cat but the distance separating them had changed; see figure 9.7).

In another task, the same subjects initially saw one drawing and, after a delay, two variations of the sample drawing: one that had altered categorical relations and one that had altered coordinate relations. They were asked to indicate which of the two drawings looked more similar to the sample one. Both tasks confirmed that LH-damaged patients had more difficulty in perceiving that categorical relations were altered, since they committed more errors on the first task in categorical than in coordinate trials, and showed an abnormal increase of choices for the categorical alterations in the second task (figure 9.9). In contrast, in both tasks RH-damaged patients showed the opposite pattern of difficulty, now having problems in perceiving alterations of coordinate relations.

This study also provided some information about the underlying functional neuroanatomy of the two types of spatial processing. Each stroke patient had been included in the study if clinical brain imaging evidence indicated a lesion within the parietal lobe area, which was relevant because Kosslyn's (1987) original hypothesis assigned each function to the dorsal area of each hemisphere (e.g., posterior parietal, Brodmann area 40). However, for some of these patients, the lesions included parts of the parietal lobe together with parts of neighboring
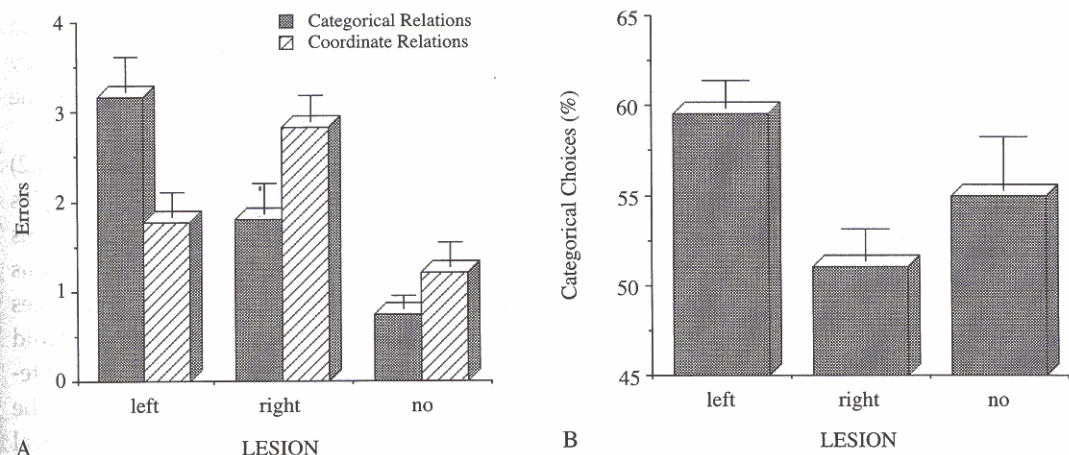
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Figure 9.9 Performance of individuals with left or right unilateral lesions and without cerebral lesions in tasks requiring the encoding of categorical and coordinate spatial relations. (*A*) Error rates in a task requiring subjects to determine whether a drawing shown a short time after another one had categorical or coordinate relations, or was unchanged. (*B*) Percentage of choices in another task where the most similar picture to a sample picture had to be chosen from two versions, one showing a categorical relation change and another a coordinate relation change. (From Laeng, 1994.)

lobes, such as the frontal or temporal lobes. Thus patients could be subdivided into smaller groups and the relative contribution of parietal lobe lesions only could be compared with that of mixed lesions. The selective deficits in both tasks were largest for patients with damage to the parietal lobes per se.

LH patients were also given tasks to assess their language abilities (i.e., aphasia tests). There was no correlation between the language or verbal impairment and the degree of impairment in the spatial relations task. This evidence refutes the possibility that categorical spatial relations are simply easily labeled configurations (using prepositions and locatives), and that the categorical task could therefore be reduced to a verbal strategy of mentally naming and memorizing the verbal description (cf. Goodglass et al., 1974; Hannay et al., 1981). Indeed, if coordinate encodings are to support motor activity, they do not seem readily available to language. Although we are clearly able to discriminate quantitative differences in distance and we possess the ability to think and verbally express numerical quantities, we do not seem to be able to map these two types of knowledge onto one another. In contrast, a

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consequence of perceiving categorical relations is that verbal labels can be "directly" provided after a simple visual inspection and, in fact, they constitute much of our daily communications (e.g., "the book is on the table").

In addition, results on the "token test" (De Renzi & Vignolo, 1962) did not correlate with the degree of categorical spatial impairment. This aphasia test requires the patient to observe a display of wooden tokens of different colors and shapes, and to follow simple requests, such as "Point to the square to the left of the blue circle." Although sentences like these contain spatial predicates, several of the LH patients could follow these commands while showing clear impairments in the categorical spatial memory test, and some of the patients who failed the requests of the token test showed no impairment in the categorical spatial memory test. This situation suggests that for these posterior LH patients, the spatial problem is best characterized as affecting an encoding (bottom-up) stage; in contrast, these patients can access categorical spatial information in a top-down manner, possibly by translating the spatial predicative into a motor-based procedure (e.g., by looking leftward of the blue circle; see also Laeng, Kosslyn et al., 1999). Kemmerer and Tranel (2000) have also reported a subject with LH damage who was impaired in tasks requiring the assignment of the appropriate spatial prepositions but not in visual tasks hypothesized to require the encoding of categorical spatial information.

Sergent (1991b) used the divided visual field paradigm with three split-brain patients (N.G., A.A., and L.B.). These epileptic patients had their cerebral hemispheres surgically separated to relieve their seizures (cf. Trevarthen & Sperry, 1973). The patients were shown displays consisting of a dot within a circle, either at its center position or in 4 different angular and 2 different radial positions. The coordinate tasks were judging whether the dot was exactly on or off the circle's center, or in a near/far radial position from center. The categorical tasks consisted in judging whether the dot was above/below the circle's center or to the left/right of the center. One patient (N.G.) showed an LH advantage for the categorical tasks and an RH advantage for the coordinate tasks. However, another patient (L.B.) showed the reverse pattern—an RH advantage for the categorical task and an LH advantage for the coordinate tasks. The third patient (A.A.) showed no significant differences between visual fields.

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Sergent concluded from these findings that the two hemispheres are equally competent at representing categorical and coordinate spatial relations. However, there are a few caveats to this conclusion. First, the findings showed the presence of significant complementary functional specialization, or division of labor between hemispheres, in two of the three patients. Moreover, none of the patients' performance supported a model in which the two spatial functions are performed by a single hemisphere (i.e., the RH). Second, and perhaps most important, localization data from a few split-brain patients cannot necessarily be generalized to the normal population. For example, some split-brain patients can respond verbally to stimuli presented to the RH; however, as pointed out by Gazzaniga (1983), the evidence for language function in the RH of a few split-brain patients exists for only 3 out of 28 cases (and it turns out that N.G. and L.B. are among these three "unusual" split-brain subjects). The variability in localization of function in these patients is interesting in other respects, but should not be incorrectly generalized to imply that RH language is a common feature of either the whole group of split-brain patients or of the normal population.

Animal Studies   It is well known that species other than man show asymmetries, either behaviorally (e.g., in handedness; Corballis & Morgan, 1978) or in terms of brain structure (e.g., songbirds; Nottebohm, 1979) as well as external body structures (e.g., the chela of crabs). In connection with the present topic, a few studies have investigated the processing of spatial information in nonhuman primates. For example, Hamilton and Vermeire (1988) proposed a complementary hemispheric specialization, on the basis of investigation on split-brain macaques (*Macaca mulatta*), between discriminations of line orientation and face identification. It would also seem that several species learn to distinguish spatial abstract relations. For example, Herrnstein et al. (1989) taught pigeons to distinguish two spatial categories, between a closed line and a dot, corresponding to the inside/outside relations. Depy et al. (1999) investigated the processing of above/below spatial relations in baboon subjects. The monkeys were able to transfer learning of the relation in a line-dot task to a task using a letter above/below a digit. However, in these studies, neither the pigeons nor the monkeys were tested for hemispheric differences.

Depy et al. (1998) specifically assessed the presence of lateralization in baboons (*Papio papio*) when processing distance categories. A matching-to-sample task was used with the divided visual field paradigm in which subjects, both human and baboon, had to decide whether the distance between a line and a dot belonged to one of two spatial categories. Humans initially showed an LVF advantage, which vanished with practice, but overall performance in this task was better for RVF presentations than for LVF ones. The same bias was found in baboons, but in a weaker way. Depy and colleagues concluded that initially distance is judged more efficiently by the RH than the LH, but the effect vanishes after practice—possibly because of a progressive involvement of the LH for spatial categorization (cf. Kosslyn, Koenig, et al., 1989; Chabris & Kosslyn, 1998).

Baboons do not possess a verbal system like humans. Yet, baboons seem to show the same LH specialization seen in humans for categorical spatial relations. If this finding is replicated and stable, it would clearly imply that lateralization models for categorical processing that are based on "feedback training" from lexical representation or spatial language (as we sketched it earlier) are inadequate to account for the development of laterality for categorical processing. Possibly hemispheric differences in receptive field size (spatial frequency filtering) could provide a more comprehensive explanation of hemispheric specialization of function for both human and nonhuman species.

Neuroimaging Studies   Kosslyn et al. (1998) measured regional cerebral blood flow with PET while subjects performed separate blocks of categorical and coordinate spatial relations judgments on identical stimuli. In the control task, subjects simply viewed the stimuli (an X above/below a bar) without making any decision, whereas in the experimental task subjects viewed the X and the bar, and were requested to make categorical or coordinate spatial relations judgments. When subtracting measurements in the experimental tasks from those in the control task, Kosslyn and colleagues found activation within the RH's parietal lobe when subjects performed a coordinate decision, and within the LH's parietal lobe when subjects performed a categorical decision. Therefore, these results provide some converging evidence to those of Laeng (1994) on the effects of unilateral lesions to the parietal lobes on these same types of spatial judgments.

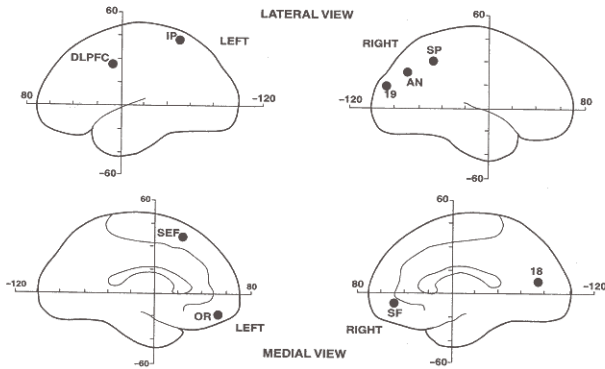B. Laeng, C. F. Chabris, and S. M. Kosslyn

However, the subtractions of the activation patterns for the two tasks revealed differences in several additional areas. Particularly compared to each other (not to the baseline), the coordinate task appeared to activate areas in both the right and left parietal lobes, whereas the categorical task did not activate either parietal lobe (when the results from the two experimental tasks were subtracted from each other, rather than from a baseline). These effects are illustrated in figure 9.10.

One explanation for these results is that the categorical task, judging whether an X is above or below a large horizontal bar, is too easy to cause blood flow changes in the parietal lobes, whereas the coordinate task, judging whether the X is within a certain distance from the bar, is quickly converted into a categorical task as the brain gains practice with the stimuli and judgment involved (see Kosslyn, Koenig, et al., 1989; see also Goel et al., 1998), and thus both parietal lobes are activated within the duration of a single PET scan. However, there were clear lateralized differences in the dorsolateral prefrontal cortex, which is intimately connected with parietal cortex (Burnod et al., 1999).
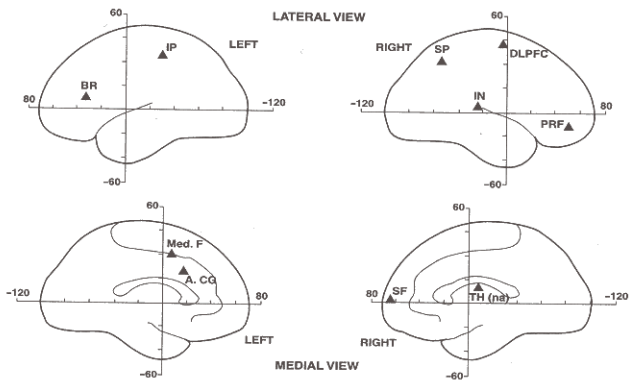
A currently strong candidate area for the localization of the spatial relations encoding processes is the angular gyrus. Baciu et al. (1999) reported an fMRI study in which subjects first performed the categorical, then the coordinate, task with the dot-bar stimuli. Throughout the categorical task, the left angular gyrus was more active than the right, whereas over the course of the coordinate task, right angular gyrus activity decreased and left angular gyrus activity increased. Although these results are consistent with the predictions developed above (and, as Baciu and colleagues note, with the characteristics of lesions that cause Gerstmann's syndrome; cf. Heilman & Valenstein, 1985), it is important to note that no other brain regions were examined.

In another PET study, Kosslyn, Alpert, et al. (1994) found that subjects performing a picture-name matching task of canonical and non-canonical views of rigid objects showed massive activation of areas in the dorsal systems. Specifically, the inferior parietal lobe in the RH was active when objects were shown in noncanonical views. This brain-imaging evidence converges with the fact that brain damage has corresponding effects on the encoding of noncanonical views of rigid objects (e.g., Warrington & Taylor, 1973, 1978). In addition, Kosslyn and colleagues found no selective activation in the LH's parietal lobe when subjects saw noncanonical views of rigid objects in compar-
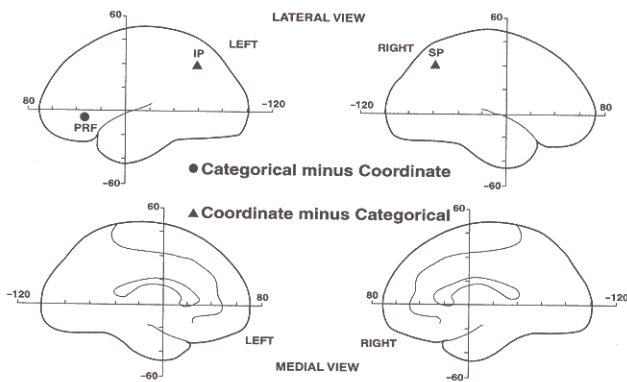
Panel A

LATERAL VIEW

MEDIAL VIEW

Panel B

LATERAL VIEW

MEDIAL VIEW

Panel C

LATERAL VIEW

● Categorical minus Coordinate

▲ Coordinate minus Categorical

MEDIAL VIEW

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ison to the activation while judging the canonical views of the same objects.

If the brain uses a top-down hypothesis-testing process based on structural descriptions when recognizing objects seen in difficult views, and if structural descriptions involve the encoding of categorical spatial relations (cf. Laeng, Shah, et al., 1999), then we would expect to see activation of the LH's parietal areas when identifying noncanonical views. One possible way to account for the lack of activation in these subtractions is that top-down processing mechanisms run virtually all the time, reflexively and in parallel, even when their engagement is not essential, and other mechanisms terminate the processing before the top-down mechanisms can contribute to object recognition. If the whole visual system truly operates in such "cascade" manner, then brain imaging studies based on the subtraction method may fail to distinguish the activation of a cerebral area in conditions in which its processing is essential and contributes to the decision from those conditions in which it is not.

CONCLUSIONS

The value of a new theory must be measured by its ability to provide a systematic framework for organizing findings and to make new predictions that lead to additional empirical observations. To the extent that those predictions are counterintuitive, the theory accrues greater value. Partial reviews of the interrelations between previous theories of spatial relations encoding and the current theory are available in earlier

Figure 9.10 (A) Areas in which there was significantly greater blood flow in the categorical spatial relations encoding condition than in the baseline condition. 18 and 19, the respective Brodmann's areas; AN, angular gyrus; DLPFC, dorsolateral prefrontal cortex; IP, inferior parietal; OR, the orbital gyrus; SEF, supplementary eye fields; SF, superior frontal; SP, superior parietal. (B) Areas in which there was significantly greater blood flow in the coordinate spatial relations encoding condition than in the baseline condition. A.CG, anterior cingulated gyrus; BR, Broca's area; DLPFC, dorsolateral prefrontal cortex; IN, insula; IP, inferior parietal; TH(na), thalamus (nucleus accumbens); Med.F, medial frontal; PRF, prefrontal area; SF, superior frontal; SP, superior parietal. (C) Areas in which there was significantly greater blood flow in the categorical spatial relations encoding condition than in the coordinate spatial relations encoding condition (circles) or vice versa (triangles). IP, inferior parietal; PRF, prefrontal area; SP, superior parietal. (From Kosslyn et al., 1998.)

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publications (e.g., Kosslyn, 1994; Laeng, 1994; Chabris & Kosslyn, 1998). The theory proposed here would seem to have the benefit of being sufficiently general to allow us to make sense of a wide range of findings, without the failing of being vague or unsubstantiated; moreover, the theory has generated a large number and variety of empirical tests and findings.

The meta-analysis of results from divided visual field studies provides strong evidence for the distinction between categorical and coordinate encoding of spatial relations, as do the basic dissociations that have been replicated with a variety of types of visual material, types of judgments, modes of response, subject populations, and measurement methods. The theory has also proved compatible with facts about neuroanatomy and neurophysiology, as well as results from simulation modeling and neuropsychological experimentation. Such converging factors have extended the model to account for otherwise unpredictable results, and apply it to other hemispheric asymmetries. Hence, the model outlined here goes far beyond the initial proposal (Kosslyn, 1987) and is certainly now more complex than one based on a direct assignment of subsystems or modules to encoding tasks. The incremental development of the theory is a good sign; if the foundations were not firm, it would not have been possible to build upon them.

ACKNOWLEDGMENTS

REFERENCES

Note: References marked with an asterisk indicate studies included in the meta-analysis.

Andersen, R. A., Asanuma, C., Essick, G., & Siegel, R. M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *Journal of Comparative Neurology, 296*, 65–113.

B. Laeng, C. F. Chabris, and S. M. Kosslyn

Baciu, M., Koenig, O., Vernier, M.-P., Bedoin, N., Rubin, C., & Segebarth, C. (1999). Categorical and coordinate spatial relations: fMRI evidence for hemispheric specialization. *NeuroReport, 10,* 1373–1378.

*Banich, M. T., & Federmeier, K. D. (1999). Categorical and metric spatial processes distinguished by task demands and practice. *Journal of Cognitive Neuroscience, 11,* 153–166.

Beaumont, J. G. (Ed.). (1982). *Divided visual field studies of cerebral organisation.* London: Academic Press.

Behrmann, M., Moscovitch, M., & Mozer, M. C. (1991). Directing attention to words and nonwords in normal subjects and in a computational model: Implications for neglect dyslexia. *Cognitive Neuropsychology, 8,* 213–248.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review, 94,* 115–147.

Biederman, I. (1985). Human image understanding: Recent research and a theory. In S. M. Kosslyn and D. N. Osherson (Eds.), *Visual cognition: An invitation to cognitive science* (pp. 121–165). Cambridge, MA: The MIT Press.

Bradshaw, J. L., & Nettleton, N. C. (1983). *Human cerebral asymmetry.* Englewood Cliffs, NJ: Prentice-Hall.

Bruyer, R., Scailquin, J. C., & Coibon, P. (1997). Dissociation between categorical and coordinate spatial computations: Modulation by cerebral hemispheres, task properties, mode of response, and age. *Brain and Cognition, 33,* 245–277.

Bryden, M. P. (1982). *Laterality: Functional asymmetry in the intact brain.* New York: Academic Press.

Burnod, Y., Baraduc, P., Battaglia-Mayer, A., Guigon, E., Koechlin, E., Ferraina, S., Lacquaniti, F., & Caminiti, R. (1999). Parieto-frontal coding of reaching: An integrated framework. *Experimental Brain Research, 129,* 325–346.

Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience, 10,* 1–34.

Chabris, C. F., & Kosslyn, S. M. (1998). How do the cerebral hemispheres contribute to encoding spatial relations? *Current Directions in Psychological Science, 7,* 8–14.

Corballis, M. C. (1991). *The lopsided ape. Evolution of the generative mind.* New York: Oxford University Press.

Corballis, M. C., & Morgan, M. J. (1978). On the biological basis of human laterality: I. Evidence for a maturational left-right gradient. *Behavioral and Brain Sciences, 2,* 261–336.

*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.

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature, 380,* 499–505.

*David, A. S., & Cutting, J. C. (1990). Categorical-semantic and spatial-imagery judgments of non-verbal stimuli in the cerebral hemispheres. Unpublished manuscript, Institute of Psychiatry, London.

Delis, D. C., Robertson, L. C., & Efron, R. (1986). Hemispheric specialization of memory for visual hierarchical stimuli. *Neuropsychologia, 24,* 205–214.

Depy, D., Fagot, J., & Vauclair, J. (1998). Comparative assessment of distance processing and hemispheric specialization in humans and baboons (*Papio papio*). *Brain and Cognition, 38,* 165–182.

Depy, D., Fagot, J., & Vauclair, J. (1999). Processing of above/below categorical spatial relations by baboons (*Papio papio*). *Behavioural Processes, 48,* 1–9.

De Renzi, E., Scotti, G., & Spinnler, H. (1969). Perceptual and associative disorders of visual recognition. *Neurology, 19,* 634–642.

De Renzi, E., & Vignolo, L. (1962). The token test: A sensitive test to detect receptive disturbances in aphasics. *Brain, 85,* 665–678.

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.

Efron, R. (1990). *The decline and fall of hemispheric specialization.* Hillsdale, NJ: Lawrence Erlbaum Associates.

Emmorey, K., & Kosslyn, S. M. (1996). Enhanced image generation abilities in deaf signers: A right hemisphere effect. *Brain and Cognition, 32,* 28–44.

Farah, M. (1990). *Visual agnosia.* Cambridge, MA: MIT Press.

Gainotti, G., Silveri, M. C., Daniele, A., & Giustolisi, L. (1995). Neuroanatomical correlates of category-specific semantic disorders: A critical survey. *Memory, 3,* 247–264.

Gazzaniga, M. J. (1983). Right hemisphere language following brain bisection. *American Psychologist, 38,* 525–549.

Geschwind, N., & Galaburda, A. M. (1987). *Cerebral lateralization: Biological mechanisms, associations, and pathology.* Cambridge, MA: MIT Press.

Goel, V., Gold, B., Kapur, S., & Houle, S. (1998). Neuroanatomical correlates of human reasoning. *Journal of Cognitive Neuroscience, 10,* 293–302.

Goodglass, H., Denes, F., & Calderon, M. (1974). The absence of covert verbal mediation in aphasia. *Cortex, 10,* 264–269.

Goodman, N. (1976). *Languages of art: An approach to a theory of symbols.* Indianapolis, IN: Hackett.

Hamilton, C. R., & Vermeire, B. A. (1988). Complementary hemispheric specialization in monkeys. *Science, 242,* 1691–1694.

Hannay, H. J., Dee, H. L., Burns, J. W., & Masek, B. S. (1981). Experimental reversal of a left visual field superiority for forms. *Brain and Language, 3,* 54–66.

Harrington, A. (1987). *Medicine, mind, and the double brain: A study in nineteenth century thought*. Princeton, NJ: Princeton University Press.

Harrington, A. (1995). Unfinished business: Models of laterality in the nineteenth century. In R. J. Davidson & K. Hughdahl (Eds.), *Brain asymmetry* (pp. 3–27). Cambridge, MA: MIT Press.

Heilman, K. H., & Valenstein, E. (1985). *Clinical neuropsychology*. New York: Oxford University Press.

*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.

Herrnstein, R. J., Vaughan, W., Mumford, D. B., & Kosslyn, S. M. (1989). Teaching pigeons an abstract relational rule: Insideness. *Perception and Psychophysics, 46,* 56–64.

Hinton, G. E., McClelland, J. L., & Rumelhart, D. E. (1986). Distributed representations. In D. E. Rumelhart & D. L. McClelland (Eds.), *Parallel distributed processing: Explorations in the microstructure of cognition.* Volume 1: *Foundations* (pp. 77–109). Cambridge, MA: MIT Press.

*Horner, M. D., & Freides, D. (1996). Effects of retinal eccentricity on the lateralized processing of categorical and coordinate spatial relations. *International Journal of Neuroscience, 86,* 7–13.

*Hoyer, W. J., & Rybash, J. M. (1992). Age and visual field differences in computing visual-spatial relations. *Psychology and Aging, 7,* 339–342.

Humphreys, G. W., Freeman, T. A. C., & Muller, H. J. (1992). Lesioning a connectionist model of visual search: Selective effects on distractor groupings. *Canadian Journal of Psychology, 46,* 417–460.

Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review, 98,* 352–376.

Ivry, R. B., & 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.

Kemmerer, D., & Tranel, D. (2000). A double dissociation between linguistic and perceptual representations of spatial relationships. *Cognitive Neuropsychology, 17,* 393–414.

Kitterle, F., Christman, S., & Hellige, J. (1990). Hemispheric differences are found in the identification, but not detection, of low versus high spatial frequencies. *Perception and Psychophysics, 48,* 297–306.

Kitterle, F., & Selig, L. (1991). Visual field effects in the discrimination of sine-wave gratings. *Perception & Psychophysics, 50,* 15–18.

Koenig, O., Kosslyn, S. M., Chabris, C. F., & Gabrieli, J. D. E. (1992). Computational constraints upon the acquisition of spatial knowledge in the cerebral hemispheres. Unpublished manuscript, University of Lyon 2, Bron, France.

*Koenig, O., Reiss, L. P., & Kosslyn, S. M. (1990). The development of spatial relations representations: Evidence from studies of cerebral lateralization. *Journal of Experimental Child Psychology, 50*, 119–130.

Kogure, T., & Hatta, T. (1999). Hemisphere specialisation and categorical spatial relations representations. *Laterality, 4*, 321–331.

Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemispheres: A computational approach. *Psychological Review, 94*, 148–175.

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? *Neuropsychology, 8*, 139–147.

Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., & Koenig, O. (1992). Categorical versus coordinate spatial relations: Computational analyses and computer simulations. *Journal of Experimental Psychology: Human Perception and Performance, 18*, 562–577.

Kosslyn, S. M., & Jacobs, R. A. (1994). Encoding shape and spatial relations: A simple mechanism for coordinating complementary representations. In V. Honavar & L. M. Uhr (Eds.), *Artificial intelligence and neural networks: Steps toward principled integration* (pp. 373–385). Boston: Academic Press.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Chabris, C. F., Rauch, S. L., & Anderson, A. K. (1994). Identifying objects seen from different viewpoints: A PET investigation. *Brain, 117*, 1055–1071.

Kosslyn, S. M., & Koenig, O. (1995). *Wet mind.* New York: The 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.

Kosslyn, S. M., Maljkovic, V., Hamilton, S. E., Horwitz, G., & Thompson, W. L. (1995). Two types of image generation: Evidence for left and right hemisphere processes. *Neuropsychologia, 33*, 1485–1510.

Kosslyn, S. M., Sokolov, M. A., & Chen, J. C. (1989). The lateralization of BRIAN: A computational theory and model of visual hemispheric specialization. In D. Klahr & K. Kotovsky (Eds.), *Complex information processing: The impact of Herbert Simon* (pp. 3–29). Hillsdale, NJ: Lawrence Erlbaum Associates.

Kosslyn, S. M., Thompson, W. T., Gitelman, D. R., & Alpert, N. M. (1998). Neural systems that encode categorical versus coordinate spatial relations: PET investigations. *Psychobiology, 26*, 333–347.

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., Kosslyn, S. M., Caviness, V. S., & Bates, J. (1999). Can deficits in spatial indexing contribute to simultanagnosia? *Cognitive Neuropsychology, 16,* 81–114.

Laeng, B., & Peters, M. (1995). Cerebral lateralization for the processing of spatial coordinates and categories in left- and right-handers. *Neuropsychologia, 33,* 421–439.

Laeng, B., Peters, M., & McCabe, B. (1997). Memory for locations within regions. Spatial biases and visual hemifield differences. *Memory and Cognition, 26,* 97–107.

Laeng, B., Shah, J., & Kosslyn, S. M. (1999). Identifying objects in conventional and contorted poses: Contributions of hemisphere-specific mechanisms. *Cognition, 70,* 53–85.

Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240,* 740–749.

Marr, D. (1982). *Vision.* San Francisco: Freeman.

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.

Michimata, C. (1997). Hemispheric processing of categorical and coordinate spatial relations in vision and visual imagery. *Brain and Cognition, 33,* 370–387.

Miller, G. A., & Johnson-Laird, P. N. (1976). *Language and perception.* Cambridge, MA: Harvard University Press.

*Niebauer, C. L. (1996). A possible connection between categorical and coordinate spatial relation representations. Unpublished manuscript, University of Toledo, Toledo, OH.

*Niebauer, C. L., & Christman, S. D. (1998). Upper and lower visual field differences in categorical and coordinate judgments. *Psychonomic Bulletin & Review, 5,* 147–151.

Nottebohm, F. (1979). Origins and mechanisms in the establishment of cerebral dominance. In M. S. Gazzaniga (Ed.), *Handbook of behavioral neurology.* Volume 2: *Neuropsychology.* New York: Plenum Press.

O'Reilly, R. C., Kosslyn, S. M., Marsolek, C. J., & Chabris, C. F. (1990). Receptive field characteristics that allow parietal lobe neurons to encode spatial properties of visual input: A computational analysis. *Journal of Cognitive Neuroscience, 2,* 141–155.

Parrot, M., Doyon, B., Démonet, J. F., & Cardebat, D. (1999). Hemispheric preponderance in categorical and coordinate visual processes. *Neuropsychologia, 37,* 1215–1225.

Piaget, J., & Inhelder, B. (1956). *Le développement des quantités chez l'enfant.* Paris.

Previc, F. H. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences, 13,* 519–575.

Robertson, L. C., & Delis, D. C. (1986). "Part-whole" processing in unilateral brain-damaged patients: Dysfunctions of hierarchical organization. *Neuropsychologia, 24*, 363–370.

Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part-whole organization. *Cognitive Psychology, 24*, 363–370.

*Roth, E. C., & Hellige, J. B. (1998). Spatial processing and hemispheric asymmetry: Contributions of the transient/magnocellular visual system. *Journal of Cognitive Neuroscience, 10*, 472–484.

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science, 271*, 651–653.

Rueckl, J. G., Cave, K. R., & Kosslyn, S. M. (1989). Why are "what" and "where" processed by separate cortical visual systems? A computational investigation. *Journal of Cognitive Neuroscience, 1*, 171–186.

*Rybash, J. M., & Hoyer, W. J. (1992). Hemispheric specialization for categorical and coordinate spatial representations: A reappraisal. *Memory & Cognition, 20*, 271–276.

*Sergent, J. (1991a). Judgments of relative position and distance on representations of spatial relations. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 762–780.

Sergent, J. (1991b). Processing of spatial relations within and between the disconnected cerebral hemispheres. *Brain, 114*, 1025–1043.

Servos, P., & Peters, M. (1990). A clear left hemisphere advantage for visuo-spatially based verbal categorization. *Neuropsychologia, 28*, 1251–1260.

Shallice, T. (1988). *From neuropsychology to mental structure*. Cambridge: Cambridge University Press.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional object. *Science, 171*, 701–703.

Smart, J. J. C. (1964). *Problems of space and time*. New York: Collier Macmillan.

Springer, S. P., & Deutsch, G. (1998). *Left brain, right brain: Perspectives from cognitive neuroscience*. Fifth edition. New York: Freeman.

Teuber, H. L. (1955). Physiological psychology. *Annual Review of Psychology, 6*, 267–296.

Trevarthen, C., & Sperry, R. W. (1973). Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain, 96*, 547–570.

Ungerleider, L., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Engle, M. A. Goodale, & R. J. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Van Kleeck, M. H. (1989). Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of previous studies. *Neuropsychologia, 27*, 1165–1178.

Van Kleeck, M. H., & Kosslyn, S. M. (1989). Gestalt laws of perceptual organization in an embedded figures task: Evidence for hemispheric specialization. *Neuropsychologia, 27,* 1179–1186.

Van Kleeck, M. H., & Kosslyn, S. M. (1991). The use of computer models in the study of cerebral lateralization. In F. L. Kitterle (Ed.), *Cerebral laterality: Theory and research* (pp. 155–174). Hillsdale, NJ: Lawrence Erlbaum Associates.

Warrington, E. K., & James, M. (1991). A new test of object decision: 2D silhouettes featuring a minimal view. *Cortex, 27,* 370–383.

Warrington, E. K., & Taylor, A. M. (1973). The contribution of the right parietal lobe to object recognition. *Cortex, 9,* 152–164.

Warrington, E. K., & Taylor, A. M. (1978). Two categorical stages of object recognition. *Perception, 7,* 695–705.

*Wilkinson, D., & Donnelly, N. (1999). The role of stimulus factors in making categorical and coordinate spatial judgments. *Brain and Cognition, 39,* 171–185.