

# Visuospatial processing and the right-hemisphere interpreter

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## Abstract

Popular views of hemispheric asymmetry hold that the left hemisphere is specialized for linguistic and cognitive processes and fine motor control, whereas the right is specialized for visuospatial processing. Although this dichotomy contains more than a grain of truth, it is an oversimplification. Experiments with split-brain patients have demonstrated that the left hemisphere retains relatively sophisticated visuospatial abilities, and that the asymmetries that favor the right hemisphere are subtler than those that favor the left. A consideration of the constructive nature of visual perception, and the organization of the visual system in the two hemispheres suggests that asymmetries are likely to arise relatively late in visual processing in areas that represent both sides of visual space. I present evidence in favor of the view that the right hemisphere can be considered more “visually intelligent” than the left, and postulate the existence of a “right-hemisphere interpreter” dedicated to constructing a representation of the visual world.

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## 1. Introduction

The idea that the two hemispheres of the human brain differ in their psychological functions has long been a central theme in the cognitive neurosciences. Although the concept can be traced back at least to ancient Greece (see Lokhorst, 1982), it was not until the clinical observations of Dax and Broca in the nineteenth century that the effort to understand cerebral asymmetries really assumed any importance in the study of brain function. These reports, along with those of Wernicke, cemented the notion that the left hemisphere has a special role to play in language production and comprehension. They are also the origin of the notion that the left hemisphere is, in most people, the dominant hemisphere, and that the right hemisphere plays a secondary role.

At roughly the same time as Broca and Wernicke were illustrating the importance of the left hemisphere in language production and comprehension, John Hughlings Jackson (1874, 1876) described patients suffering from the “loss or defect of memory for persons, objects, and places.” He termed this deficit “impercption,” and associated it with damage to the right hemisphere. Jackson’s reports challenged the notion of left hemisphere dominance, and instead suggested that both hemispheres possess specialized abilities of their own.

Jackson noted that the left frontal lobe developed earlier than the right frontal lobe, and that the posterior lobes developed earlier in the right hemisphere. He also observed that the psychological functions that were lateralized to the left hemisphere tended to be associated with the frontal lobe, and the perceptual functions he attributed to the right hemisphere were associated with more posterior brain regions. Accordingly, Jackson suggested, “The ‘important side’ of the left hemisphere is the anterior lobe, and the important side of the right the posterior lobe” (Jackson, 1874/1915).

These neurological observations laid the groundwork for the popular view of hemispheric organization that emerged in subsequent years that the left hemisphere “controls” language, while the right hemisphere is responsible for visuospatial perception. Although this notion clearly contains an element of truth, research with callosotomy (or “split-brain”) patients has demonstrated that it is equally clearly an oversimplification. The right hemisphere is capable of some limited language comprehension, and the left hemisphere must be capable of reasonably sophisticated visuospatial processing to support tasks such as reading and object recognition, at which it excels. Nevertheless, this dichotomy continues to motivate research in cognitive neuroscience (e.g., Kelley et al., 1998).

## 2. The split-brain

Callosotomy surgery involves the surgical sectioning of the corpus callosum, and in some cases the other forebrain commissures, for the relief of pharmacologically intractable epilepsy. The result is that the cerebral hemispheres are effectively isolated at the cortical level (although subcortical connections remain intact). In addition to the clinical benefits, this procedure offered the first opportunity to interrogate each hemisphere in isolation, since information presented to one hemisphere is typically not available to the other.

The first systematic studies of split-brain patients in the 1960s dramatically confirmed the dominance of the left hemisphere in controlling speech. Patients were unable to describe visual stimuli presented to the left visual hemifield, and thus to the right hemisphere (e.g., Gazzaniga, Bogen, & Sperry, 1965a; Gazzaniga, Bogen, & Sperry, 1965b). The right hemisphere was able to indicate that it had processed the stimuli by using the left hand to select from a number of items. Subsequent studies with split-brain patients have confirmed that stimuli that are restricted to the right hemisphere cannot generally be verbally articulated, while those that are presented to the left hemisphere can be described with ease. The isolated right hemisphere, however, is able to understand written words and follow simple verbal instructions. More detailed experiments have demonstrated that the left hemispheres of split-brain patients are capable of producing and comprehending all aspects of language. By contrast, although the right hemisphere often knows the meanings of words, it seldom shows much evidence for grammar or generative syntax (see Gazzaniga, 2000).

The dominance of the left hemisphere for linguistic abilities extends to other aspects of cognitive function. After callosal disconnection, the verbal IQ of patients remains intact (Nass & Gazzaniga, 1987; Zaidel, 1990) and the capacities for problem-solving and hypothesis formation remain unchanged for the left hemisphere (LeDoux, Risse, Springer, Wilson, & Gazzaniga, 1977). The right hemispheres of these patients, however, are seriously impoverished in cognitive tasks involving problem solving as well as many other mental activities (Gazzaniga, 2000).

### 2.1. The left hemisphere interpreter

Split-brain patients will often confabulate when asked to explain choices made by the right hemisphere. For example, patient J.W. was shown a picture of a bell tower in his left visual hemifield. He was then asked to choose between four pictures by pointing with his left hand. The pictures depicted four musical instruments, one of which was a bell. J.W. chose the bell, and when asked to explain why he said that he “must have heard a

bell ringing on [his] way into the lab.” The speaking left hemisphere, observing the response controlled by the mute right, interpreted the response in a context consistent with its knowledge. Since it had no knowledge of the picture of the bell tower it found a feasible reason to account for the selection of the bell. Gazzaniga has postulated that this confabulation reveals the existence of an “interpreter” that elaborates upon perceptual information to create a “story” or schema (e.g., Gazzaniga, 2000). He has further suggested that the mechanism responsible for this elaboration is lateralized to the left hemisphere.

Although the left hemisphere seems driven to interpret events, the right hemisphere shows no such tendency. This difference in cognitive styles can be observed in the performances of the two hemispheres in recognition memory tasks. When asked to decide whether a stimulus was presented in a study set, the left hemisphere tends to falsely “recognize” items that are thematically similar to studied stimuli, but that had never been presented. The right hemisphere is no more prone to make false alarms to related than to unrelated new items (Metcalf, Funnell, & Gazzaniga, 1995; Phelps & Gazzaniga, 1992). These observations are consistent with the existence of a left hemisphere interpreter that is not present in the right hemisphere. The elaboration by the interpreter has a deleterious effect on accuracy in the recognition task, but in general makes it easier to cope with new information. Because patterns in the world often have discernible, deterministic causes, the interpreter’s drive to find patterns of causation and regularity in the world usually has adaptive value.

### 2.2. Asymmetries in visuospatial abilities

Research with split-brain patients has reinforced the nineteenth-century notion that the left hemisphere is dominant in most people. The left hemisphere controls speech and dominates language functions, has greater fine motor control, and superior cognitive abilities in general. Split-brain researchers have suggested that the left hemisphere often over-rules the right, even when it does not possess task-relevant information, and that it is “in control” most of the time (see Gazzaniga, 2000). So what does the right hemisphere contribute? Initial studies with split-brain patients provided intriguing confirmations of Jackson’s idea that visual perception may be stronger in the right hemisphere. For example, a group of right-handed patients were asked to copy simple line drawings with either the right or left hand. The copies produced by the left hand were better than those produced with the dominant right hand. Similarly, the left hand performed better than the right on a block design task that required the patient to assemble colored blocks to reproduce a pattern (Bogen & Gazzaniga, 1965; Gazzaniga et al., 1965a, 1965b). These findings

suggested that the visuospatial abilities of the right hemisphere may exceed those of the left. The nature of the right hemisphere's superiority remained unclear, however.

More recent investigations of visuospatial asymmetries in split-brain patients using lateralized, tachistoscopically presented stimuli have revealed that the right hemisphere outperforms the left on a variety of visual tasks. The right hemisphere is better able to detect whether two images are identical or mirror reversed (Funnell, Corballis, & Gazzaniga, 1999). Likewise, the right hemisphere is better than the left at performing fine spatial discriminations such as detecting small differences in line orientation or vernier offset (Corballis, Funnell, & Gazzaniga, 2002). These observations and others invite the speculation that the left hemisphere may process visual stimuli preferentially for identity information, at the expense of spatial precision. Corballis, Funnell, and Gazzaniga (1999b) tested this hypothesis explicitly by asking split-brain patients to perform either a spatial- or an identity-matching task using the same stimuli. When the task required an identity match, the two hemispheres performed similarly. In the spatial matching version, however, the right hemisphere performed significantly better than the left. This implies that the asymmetry in visuospatial processing is not in the low-level processing of the stimulus information, but in the tasks that information is used to perform.

### 2.3. *The architecture of the visual system*

To understand the nature of perceptual asymmetries, it is worth considering whether the organization of the visual system in the brain offers any clues about where asymmetries might arise. Vision scientists often find it useful to distinguish between low-level and high-level vision, although the boundaries between them are often somewhat fuzzy. This distinction maps roughly onto the cortical architecture of the visual system in the occipital, temporal, and parietal lobes. Visual processing proceeds hierarchically from the primary visual cortex (V1) at the occipital pole through a cascade of visual areas. Neurons in "low-level" or "early" visual areas have small receptive fields that respond to stimulation in small areas of the contralateral visual hemifield and get progressively larger through the visual processing hierarchy (Zeki, 1978). Processing in these areas appears to be dedicated to the extraction of features from the retinal image. Early visual areas maintain a retinotopic organization, so that adjacent cortical columns tend to respond to adjacent areas of the visual field. At higher levels of visual processing in the temporal and parietal lobes, the retinotopic organization breaks down, and neurons respond to increasingly abstract aspects of visual stimuli. In these visual areas the receptive fields are

large and extend across the vertical midline. Thus, neurons in high-level areas are responsive to stimuli in both the contralateral and ipsilateral visual hemifields (e.g., Desimone & Gross, 1979; Gross, Rocha-Miranda, & Bender, 1972). The representation of ipsilateral space in these higher visual areas depends on commissural connections between these areas. Lesions of the fore-brain commissures eliminate the ipsilateral response of these neurons but leave the contralateral response intact (Rocha-Miranda, Bender, Gross, & Mishkin, 1975; Seacord, Gross, & Mishkin, 1979). Although the majority of the studies of the functional architecture of the visual system have been conducted with macaque monkeys, recent neuroimaging studies suggest that the hierarchical organization of visual areas and receptive fields is essentially the same in humans (e.g., Smith, Singh, Williams, & Greenlee, 2001).

The architecture of the visual system is such that at early levels of processing the representation of visual space in each hemisphere is unique. That is, each hemisphere represents the contralateral visual hemifield. At higher levels of the processing hierarchy, however, the representation of the visual world in one hemisphere is redundant with the representation in the other hemisphere. This suggests that asymmetries in visual processing are likely to arise relatively late in the visual system, in areas with bilateral receptive fields. Although earlier asymmetries are not logically impossible, they would result in one visual hemifield (or both) being relatively insensitive to some kinds of stimuli, which would presumably be maladaptive. Asymmetries arising in visual areas with bilateral receptive fields could be compensated by the redundant representation in the opposite hemisphere, so could evolve at no overall cost (see Corballis et al., 1999b; Gazzaniga, 1970; Kosslyn, 1987 for similar arguments).

### 2.4. *Visual perception as an intelligent process*

The task of the visual system is to represent objects and surfaces in the environment so as to allow interaction with, and navigation through, the world. The visual system faces a serious challenge in representing a three-dimensional world on the basis of a two-dimensional retinal image. Because there are an infinite number of possible three-dimensional configurations that could give rise to a given retinal image, visual perception is a mathematically ill-defined process. This problem has been a fundamental one in perception research at least since it was described in Berkeley's *New Theory of Vision* (Berkeley, 1709/1963). In keeping with the empirical tradition, von Helmholtz (1909/1962) proposed that visual perception proceeds by unconscious inference from the information in the retinal image. That is, the process of perception is fundamentally a cognitive one, driven as much by the experience and goals of the perceiver as by

the information in the retinal image. This view formed the basis for the idea that our perceptual worlds are internal constructions constrained by the retinal image. Hoffman (1998), one of the modern champions of this constructivist view, describes vision as an intelligent process akin to problem solving in which the visual system creates a representation from the retinal image. This representation is then tested and updated as the perceiver scans the visual field and interacts with the environment.

Low-level vision can be considered as a largely data-driven process. That is, the responses of neurons in early visual areas are determined by the stimulation that falls within their receptive fields—although feedback from higher-level areas undoubtedly modulates these responses. At higher levels of visual processing the neural responses are somewhat more abstract and can be more readily influenced by the observer's goals, experiences, and expectations. It thus seems reasonable to suggest that those aspects of visual perception that can be deemed intelligent, or constructive, tend to be higher-level visual processes. There is some evidence to suggest that although activity in early visual areas is necessary for perceptual awareness of a visual stimulus, it is not sufficient to sustain a conscious percept of that stimulus (Crick & Koch, 1995). Furthermore, it appears that observers rely on high-level representations of visual stimuli to perform visual search tasks, even when lower-level representations might in fact allow for more efficient performance (He & Nakayama, 1992; Suzuki & Cavanagh, 1995). These findings imply that observers typically do not have access to the outputs of low-level visual areas, and that the phenomenology of visual perception arises fairly late in visual processing.

### 2.5. Is there a right-hemisphere interpreter?

The foregoing reasoning suggests two conclusions: (1) those aspects of visual processing that can be considered intelligent are likely to be high-level processes, and (2) high-level visual processes are more likely to be lateralized than lower-level processes. Thus, it is reasonable to consider hemispheric asymmetry in visual processing as an asymmetry in visual intelligence. Just as the left hemisphere can be described as more cognitively intelligent than the right, the right hemisphere can be conceived as more perceptually intelligent than the left. From this perspective, the specialized functions of the right hemisphere could also be considered as an “interpreter” dedicated to resolving the ambiguities inherent in spatial vision.

Two recent examples serve to illustrate the interpretive nature of the specialized functions of the right hemisphere. Firstly, Corballis, Fendrich, Shapley, and Gazzaniga (1999a) investigated the perception of shape by either modal or amodal boundary completion in two

split-brain patients. Fig. 1a shows a “Kanizsa square,” which most people see as a white square superimposed on four black circles. The process that leads to this percept is termed “modal completion,” because the contours of the square appear to be visibly present (i.e., the square is completed in the visual mode). There is evidence that modal completion is accomplished early in visual processing (e.g., von der Heydt, Peterhans, & Baumgartner, 1984) and, accordingly, both hemispheres were able to perform a modal completion task. In contrast, Fig. 1b shows a square that must be perceived by “amodal completion.” In this case, most observers see a square that is occluded by a surface with four holes in it. The contours of the square do not seem to be visible, but must instead be inferred (i.e., the square is completed outside the visual mode). The right hemisphere was considerably better than the left at perceiving the squares in this configuration, and Corballis and colleagues postulated that amodal completion relied on a higher-level visual mechanism than modal completion, and that this mechanism was lateralized to the right hemisphere.

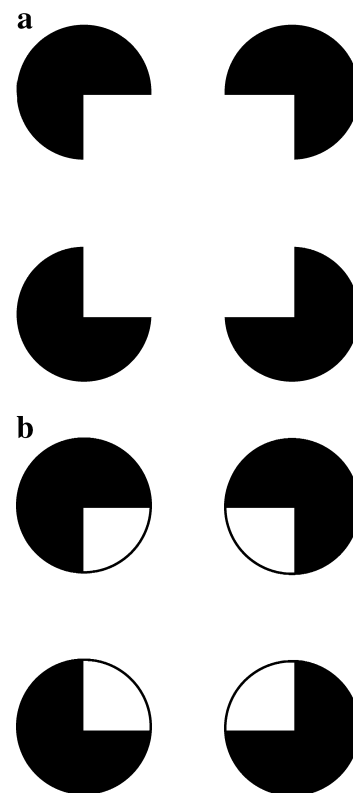


Fig. 1. (a) A “Kanizsa square.” Most people see this as a white square that partially occludes four black circles. Because the square appears to be visibly present the process underlying the percept is termed modal completion. (b) A modified version of the Kanizsa square that appears to most people as a square viewed through four circular holes in an occluding surface. Because the contours of the square do not appear to be visible the process underlying the percept is called amodal completion (see text).

A second example concerns studies of illusory line motion in a split-brain patient (Corballis, Barnett, & Corballis, submitted; Corballis, Funnell, & Gazzaniga, in press). Illusory line motion occurs when a line is presented instantaneously on a visual display, but appears to propagate from one end, as if being drawn. The manifestation of the illusion can be influenced by both low-level and higher-level manipulations of the stimulus configuration. For instance, if a dot flashes at one end of the line just before the line appears, it looks as though the line propagates away from the flashed dot (e.g., Hikosaka, Miyauchi, & Shimojo, 1993). By the same token, if the line flashes between two dots of different colors or widths, a match between the color or width of the line and one of the dots will bias the illusion such that the line appears to propagate from the matching dot (e.g., Tse, Cavanagh, & Nakayama, 1998). The manifestation of the illusion in both hemispheres can be influenced by a flashing dot (a low-level manipulation), but the right hemisphere is more likely to be influenced by a match in width or color (a higher-level manipulation). These results suggest that at least two dissociable mechanisms can contribute to the illusion of motion, and that there is right-lateralized mechanism that is playing an interpretive role in determining the likely origin of motion.

### 3. Conclusions

Although it has long been recognized that the right hemisphere possesses superior visuospatial skills than the left in most people, the nature of this asymmetry has remained unclear. Because the left hemisphere is dominant for controlling actions and language, and is generally seen as cognitively superior to the right, it has traditionally been regarded as the “major” or “dominant” hemisphere, with the right hemisphere relegated to a minor, supporting role. This conceptualization overlooks the fundamentally ambiguous nature of visual perception, and the profound “intelligence” required to create a veridical representation of the world from the information provided by the retinal image. In this paper I have argued that the right hemisphere can be meaningfully described as more visually intelligent than the left, and I have postulated the existence of a right hemisphere “interpreter” as a counterpoint to the superior interpretive capacities of the left hemisphere in other cognitive domains.

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### Further reading

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