gether, as our intellectual paths first crossed 18 years ago in graduate school, when we each began to study issues related to lateralization of function. The topic was in its heyday then, but even after it became less popular, we continued to pursue work in this area of research. Thus, it is especially satisfying for us to see that with an increased interest in understanding how the neurological organization of the brain affects mental capabilities, issues of lateralization of function are once again being given serious thought. We thank our contributors for helping us to provide a perspective on what this fundamental, dynamic aspect of human brain organization can add to the understanding of the relationship between brain and mind.

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Complementary Right- and Left-Hemisphere Language Comprehension

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The importance of the left hemisphere of the brain for language processing and control of speech was first established by 19th-century neurologists, who investigated the correlation between left-hemisphere injury and obvious language disorders. Yet a few of these pioneers also speculated on a complementary role for the right hemisphere (e.g., Jackson, 1874/1932, p. 130: "... as regards the use of words, the brain is double in function . . . [but] the two hemispheres are not mere duplicates in this function"). Certainly, language deficits are far more dramatic following left-hemisphere than following right-hemisphere lesions. But careful study of patients with right-hemisphere damage has revealed language-specific deficits.

A striking example is provided by right-hemisphere stroke patient D.B., who related that he found it difficult to follow conversations, stating, "I understand words, but I'm missing the subtleties, the complex mosaic of meaning that is language" (Beeman, 1993). Given this articulate description, one could wonder whether he was truly impaired. Standardized testing revealed little cognitive impairment. Furthermore, he responded accurately when questioned about factual information conveyed in short stories. But D.B. did have difficulty answering questions that required inferences from the stories. It is not uncommon to observe, after brain damage, cognitive impairments limited to specific components of language processing. D.B. and similar patients demonstrate that an isolated impairment in one component of language comprehension can result from damage in the right hemisphere; conventional wisdom, of course, ascribes total control of language to the left hemisphere.

As aptly described by D.B., language comprehension and production is a "complex mosaic," composed of multiple components and processes. Each component may be somewhat distinct, and is often studied in isolation. Yet all the components must function together for full comprehension. We contend that most, if not all, language components include complementary right- and left-hemisphere processes. These

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complementary processes are not strictly isolated from each other, because information can be shared and the hemispheres clearly interact; but language processing in the two hemispheres is parallel in the sense that each performs its own computation on information at every level of processing.

The existence of complementary—distinct, but parallel and mutually supportive—processes may confer additional benefits: When one hemisphere is injured or removed at an early age, the remaining hemisphere may be able to compensate for the injured hemisphere's function, with minor adjustments. Children can learn language relatively well after removal of the entire left hemisphere at a much later age than previously reported (Vargha-Khadem et al., 1997). This suggests that the hemispheres begin with similar potentialities, and later develop complementary (though still similar) processing, and is inconsistent with the notion that a hard-wired language module exists solely in the left hemisphere. Further evidence against this idea comes from at least one patient whose hemispheres were surgically separated (in a complete commissurotomy). This split-brain patient "acquired" speech in his previously mute right hemisphere 15 years following the surgery (Baynes, Wessinger, Fendrich, & Gazzaniga, 1995). A radical rewiring of the brain seems an unlikely source of such recovery; it is more likely that corresponding contralateral areas undergo a slight shift in neural circuitry (which may differ across hemispheres; see, e.g., Jacobs, Schall, & Scheibel, 1993), shifting from a focus on one aspect of complementary language processing to attempting another aspect.

In this review, we briefly outline just a few of the language processes for which the two hemispheres have been shown to play complementary roles. In addition to data from brain-injured patients, we consider studies of neurologically normal persons in whom stimuli were directly transmitted to the left and right hemispheres,[2] or in whom regional variations in the brain's activity were measured. These studies confirm that the normal right hemisphere processes language in a distinct fashion, and contributes meaningfully to language comprehension.

SPEECH PERCEPTION

It is by now well established that the right hemisphere does indeed process speech input, and that its processing style is conducive to extracting paralinguistic information, such as speech melody and intonation (Ross, 1981), and to identifying a speaker. So, clearly, the right hemisphere processes verbal information, although much of its processing could relate to the acoustic properties of the signal, rather than to its linguistic function.

Recent evidence, however, suggests that even one of the most fundamental linguistic processes, phonetic perception, may have complementary right-hemisphere and left-hemisphere components. When normal subjects hear speech sounds against a background of white noise, phonetic discriminations depending on voice onset time (the onset of vocal chord vibrations; e.g., "ba" and "pa" are virtually identical except that voicing doesn't begin until the vowel in "pa") are made more efficiently for stimuli presented to the left ear (right hemisphere) than the right ear (left hemisphere). In contrast, phonetic discriminations depending on place of articulation (i.e., the precise position of the tongue and lips when articulating a sound: "ba" vs. "da") are made more efficiently for right-ear (left-hemisphere) than for left-ear (right-hemisphere) presentations (Ivry & Lebby, 1998).

In each case, subjects were making phonetic discriminations, clearly a linguistic process. What stimulus features dictate whether the left hemisphere or right hemisphere will be more efficient? One proposal is that the right hemisphere is biased to amplify the relatively low frequencies of the speech signal (Ivry & Lebby, 1998). Because voicing is carried predominantly in these frequencies, the right hemisphere efficiently distinguishes speech pairs that differ only in voicing. In contrast, place of articulation is carried predominantly in the higher frequencies of speech sounds, which may account for the greater left-hemisphere efficiency in distinguishing such contrasts.

Complementary hemispheric processing of voicing versus place of articulation has been documented only recently and needs to be confirmed. However, differential processing of relatively low and high auditory frequencies appears to be consistent with electrophysiological (Molfese, 1980) and other evidence (for a review, see Ivry & Lebby, 1998). The right-hemisphere advantage for processing paralinguistic information could also be due to this proposed asymmetry, because such information is carried predominantly in the lower speech frequencies. Thus, the hemispheres appear to perform complementary processing of the speech signal, with each attuned to different components of the auditory spectrum.

DECODING OF PRINT

Both hemispheres also make unique contributions when people decode written text. The isolated right hemisphere of most split-brain patients can comprehend written words. This implies that the right hemisphere is able to access stored knowledge about words when words are presented visually (Baynes & Eliassen, 1998). It appears that the hemispheres differ both in the kinds of visual representations initially constructed from the printed word and in the manner in which letter- and word-level information interact.

People read material faster the second time a word or text is presented. When a word is shown in the left visual field, therefore going directly to the right hemisphere, readers benefit more from the second reading when the word is shown in the original font and case than when font or case is changed. Yet when a word is presented to the right visual field, thereby going directly to the left hemisphere, the second reading benefits equally regardless of the font and case used for the repetition (Marsolek, Kosslyn, & Squire, 1992). This finding implies that the right-hemisphere processing of printed words tends to preserve information related to the visual details of the words, whereas left-hemisphere processing results in more abstract representations.

In addition, letter and word identification appear to interact less within the right hemisphere than within the left hemisphere. When words are presented to the left visual field (right hemisphere), performance always deteriorates as the number of letters in the word increases. In contrast, under some conditions, word recognition in the right visual field (left hemisphere) is independent of word length. It seems, then, that right-hemisphere word recognition depends on identification of each component letter, whereas left-hemisphere word recognition can proceed in parallel with letter identification. Similarly, when the task is to identify a letter, presenting the letter within a word context enhances performance in the left hemisphere, but not in the right hemisphere. This finding likewise suggests that the left hemisphere rapidly accesses stored word knowledge, and that this knowledge assists in the identification of component letters (for a review, see Chiarello, 1988).

One important component of reading involves the conversion of print to a sound-based (i.e., phonological) code. Testing of split-brain patients at one time indicated that only the left hemisphere could accomplish this print-to-sound mapping (Zaidel & Peters, 1981). However, it was recently demonstrated that certain regions of the right hemisphere are especially active during reading in individuals who are most sensitive to phonological influences in reading tasks (Pugh et al., 1997). This observation implies that the right hemisphere, as well as the left hemisphere, plays some role in computing phonology from print (see also Chiarello, Hasbrooke, & Maxfield, in press), although additional research will be needed to determine just how each hemisphere accesses sound codes for printed words.

The data summarized here are consistent with the view that the right hemisphere and left hemisphere subserve complementary processes when decoding print. The end product of right-hemisphere text processing may allow people to recover greater detail about visual features, whereas the left hemisphere rapidly categorizes input into more abstract representations. By enhancing different aspects of printed words within each hemisphere, the human brain may be able to select and utilize highly processed information, while still retaining potentially useful details about the stimulus.

UNDERSTANDING WORD MEANINGS

Investigations of semantic processing have demonstrated that both hemispheres process the meanings of words, but they do so in characteristically different ways. Most of these studies have employed semantic priming methods, examining whether subjects respond to target words more quickly (or accurately) when they are preceded by semantically related, than by unrelated, prime words or sentences (e.g., *dog* is more easily recognized following *cat* than following *cap*). Semantic priming (better performance when the prime and target are related) indicates that word meanings have been accessed. In this section, we show that distinct patterns of semantic priming for target words presented in the left and right visual fields imply that different semantic information is most accessible within each hemisphere at various moments during language processing.

The consensus of this literature is that the two hemispheres have access to similar mental dictionaries, which operate somewhat independently. The hemispheres do not appear to differ in semantic knowledge, but in how that knowledge is activated by words that are heard or read. In general, the right hemisphere seems to maintain activation of distant semantic relations of words, multiple meanings of ambiguous words, and metaphoric interpretations, whereas the left hemisphere selects closely related meanings and a single interpretation for each word (Chiarello, 1998). For example, summation priming—facilitation derived from three prime words, each only weakly related to the target (e.g., *shuttle-ground-space: launch*)—is more robust within the right hemisphere than within the left hemisphere. In contrast, direct priming—from one prime word strongly related to the target (e.g., *scissors: cut*)—is more robust in the left hemisphere (Beeman et al., 1994). Similarly, the right hemisphere maintains facilitation for related words that do not share many semantic features (e.g., *arm-nose*), and for the less frequent meaning of an ambiguous word (*bank-river*), at moments in processing during which no left-hemisphere priming is observed (Chiarello, 1998; Koivisto, 1997).

The precise mechanisms responsible for divergent semantic processing are not yet fully determined. Superior semantic processing by the left hemisphere is most likely when subjects pay attention to the meaning relation between words, and when suppression of alternate meanings or selection of a single best response from many choices is required (e.g., when the subject generates a verb strongly related to a presented noun: *hammer* → *pound;* Posner, Petersen, Fox, & Raichle, 1988). Conversely, evidence for unique right-hemisphere semantic processing is most likely when measuring more passive semantic processes, and when multiple interpretations are considered (e.g., when the subject generates a secondary and novel verb in response to a presented noun: *hammer* → *throw,* after previously responding with *pound;* Abdullaev & Posner, 1997). Some recent evidence suggests that initial semantic processing in the left hemisphere may resemble later semantic processing in the right hemisphere (Koivisto, 1997), but it is clear that at some important moments in processing, the right hemisphere has available a broader range of word meanings than the left hemisphere. Given that natural language processing extends over seconds, it is clear that complementary semantic processing of word meanings has implications for understanding discourse (for a review, see Beeman, 1998).

UNDERSTANDING SENTENCES AND DISCOURSE

The message conveyed by a sentence as a whole is more than just the sum of the individual words' meanings. The relations between words in a sentence modify their meaning and allow listeners or readers to construct a unified, unambiguous interpretation. Research conducted by M. Faust (1998) indicates that the left hemisphere is much better at using sentence structure to arrive at this message-level interpretation, whereas the right hemisphere also plays a unique role, by maintaining activation of the individual words' meanings with less modification by the sentence context. For example, greater priming is obtained from a sentence than from a single word in the right visual field (left hemisphere), but not the left visual field (right hemisphere). Similarly, for the left hemisphere, normal sentences are more effective primes than the same words presented in scrambled order, whereas priming for the right hemisphere is not altered by scrambled word order. Thus, the right hemisphere appears to be sensitive to semantic relations between words, rather than to sentence-level constraints. These distinctly different ways of processing sentences are highlighted by examining how ambiguous words are interpreted. Following a sentence such as "He dug with the spade," concepts related to the sentence-biased meaning of *spade* (shovel) are facilitated in the right visual field (left hemisphere), and those related to the unbiased meaning (ace) are suppressed (M.E. Faust & Gernsbacher, 1996). However, unbiased meanings can be facilitated in the left visual field (right hemisphere), suggesting that the availability of word meanings is less affected by sentence-level constraints in the right hemisphere than in the left hemisphere.

There is also strong evidence for complementary hemispheric processing of more complex input, such as discourse (e.g., stories and conversations). Most work on hemispheric differences in discourse comprehension has focused on patients who, like D.B., have right-hemisphere damage. Such patients usually do not appear to have grossly impaired language abilities, but may miss the gist of stories or conversations, and may report difficulty following any complex dialogue or plot. Experimentally, such patients have been shown to have difficulty understanding, imparting organization to, or deriving themes of stories (Hough, 1990); recognizing appropriate story or joke continuations (Brownell, Michel, Powelson, & Gardner, 1983); and understanding metaphors (Brownell, Potter, Michelow, & Gardner, 1984). Moreover, brain-imaging studies reveal increases in right-hemisphere activity in response to sentences containing metaphors (Bottini et al., 1994).

The right hemisphere's importance to discourse comprehension has been variously attributed to social or emotional processing, construction of mental models, or global organization. Although these may all play a role, much discourse comprehension in the right hemisphere can also be parsimoniously attributed to its unique processing of word meanings (see Beeman, 1998). According to this view of right-hemisphere semantic processing, maintaining diffuse semantic activation of numerous related concepts that are seemingly only distantly related to the input words may often be inefficient (hence the left-hemisphere advantage for most language processing), but may provide additional information that aids in integrating new information, or in reinterpreting a word or the general context when needed.

As a case in point, some patients with right-hemisphere damage, like D.B., have difficulty drawing inferences that are necessary to connect two parts of a story (e.g., the shuttle that was on the ground is now in space, so comprehenders infer that it was launched; Brownell, Potter, Bihrle, & Gardner, 1986). Normal comprehenders make such inferences routinely, but these patients seem impaired in activating the information that forms the basis for such inferences. While listening to stories that promoted connective inferences and simultaneously responding to visual test words that described the inferences, these patients showed no priming for inference-related test words (Beeman, 1993).

A follow-up study (in Beeman's lab) revealed complementary hemispheric contributions when normal subjects drew inferences. At an early point in the stories, when just enough information had been given for the subjects to predict what might happen, but before the outcome was certain (e.g., just after "The shuttle sat on the ground, waiting for the signal . . ."), inference-related priming was obtained. That is, subjects responded faster to inference-related words (*launch*) than to unrelated test words, suggesting that the inference concept was activated. However, priming was obtained only for test words presented to the left visual field (right hemisphere), not for words presented to the right visual field (left hemisphere). Later, at the time the inference became necessary to connect the story together (following "After a huge roar, the shuttle disappeared into space . . ."), inference-related priming was observed primarily for presentations to the right visual field (left hemisphere).

These data suggest that the hemispheres play complementary roles in drawing connective inferences: The right hemisphere diffusely activates information distantly related to the input words—hence inference-related priming initially occurs only in the right hemisphere—but the activation is too weak to be acted upon. When a break in the story's coherence occurs, this weak activation provides a good cue to search for information that would fill the gap. At this point, the left hemisphere—taking its cue from the right hemisphere—strongly activates the appropriate inference and its connections to the discourse, causing inference-related priming to be stronger on right-visual-field presentations than on left-visual-field presentations. To simplify: In a complementary fashion, the right hemisphere may activate predictive inferences, whereas the left hemisphere selects and incorporates connective inferences. Such an approach decomposes a broad language behavior—drawing inferences—that some researchers think depends on the left hemisphere (see Reuter-Lorenz & Miller, this issue) and reveals that some components may benefit from unique right-hemisphere processing.

SYNTAX

As we have discussed, there is evidence for right-hemisphere processing of linguistic meaning at various levels. But all languages additionally employ grammatical devices (such as word ordering and altering word forms to reflect number, gender, and role in the sentence) to structure the way words are interrelated within sentences. Linguists consider this syntactic knowledge to be highly rule governed, and it is frequently argued that such knowledge is hardwired within the left hemisphere. Certainly, dramatic impairments in the use of grammar occur following left-hemisphere, but not right-hemisphere, injury, and early research with split-brain patients demonstrated little or no grammatical competence within the right hemisphere. Hence, very few investigations have examined grammatical processing within the right hemisphere. However, patients with right-hemisphere damage are somewhat impaired (although less so than patients with left-hemisphere damage) at determining sentence meaning if that meaning depends in part on complex syntactic structure (Caplan, Hildebrandt, & Makris, 1996). They can also have difficulty manipulating the syntactic structure of sentences (Schneiderman & Saddy, 1988). A recent study conducted by Stella Liu in Chiarello's laboratory implies that the right hemisphere may be sensitive to some types of grammatical agreement. In that study, participants read nouns (e.g., "ducks") in the right visual field (left hemisphere) or left visual field (right hemisphere) after reading centrally presented contexts that were syntactically consistent ("all brown") or inconsistent ("each brown"). Participants read the nouns faster following consistent than inconsistent contexts for both right- and left-visual-field presentations of nouns. This result may indicate that the right hemisphere has some ability to process number agreement, at least when tested in a priming paradigm.

It would be premature to conclude that unique right-hemisphere grammatical processing supplements the syntactic analyses known to be computed within the left hemisphere. However, because it is our view that the right hemisphere and left hemisphere conjointly process language at all levels, we strongly suspect that future investigations will verify that the right hemisphere does process syntactic information, and contributes to complete grammatical processing.

CONCLUSIONS

This sampling of results demonstrates that the right hemisphere uniquely processes linguistic input, probably at all levels of analysis. Moreover, under certain conditions, unique right-hemisphere processing contributes significantly to overall language comprehension, and could mediate long-term language recovery after left-hemisphere damage.

As always in laterality research, caution is warranted before positing a simple dichotomy of "processing styles." Right- and left-hemisphere processing may differ somewhat within each domain (i.e., phonological vs. semantic vs. syntactic). Nevertheless, there does appear to be some commonality. Language input is inherently ambiguous and continuous (e.g., shades of meaning, the acoustic continuum from "ba" to "da"). The left hemisphere appears particularly adept at categorizing input quickly and selecting the most plausible interpretation given the context—skills that form the very basis of language processing. Left-hemisphere processing could be characterized as relatively fine coding, resulting in sharp activation patterns and categorical representations (see Beeman, 1998). In contrast, the right hemisphere appears to maintain multiple possible interpretations, allowing for the extraction of specific information such as letter case or relatively precise voice onset time, as well as semantic reinterpretation. Right-hemisphere processing could be characterized as relatively coarse coding, resulting in diffuse activation patterns and analogical representations.

In sum, a great deal of scientific research supports D.B.'s insight about his own subtle disorder. Even after a relatively small right-hemisphere stroke, some significant pieces of the language mosaic will be missing. To fully appreciate language in all of its nuanced complexity requires putting together the various complementary pieces contributed by the right, as well as the left, hemisphere.

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Notes

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2. Because of the structure of the nervous system, stimuli presented to one ear or visual hemifield (i.e., the left or right half of a person's field of vision) are input directly to the contralateral hemisphere, requiring relay across the callosum (the primary pathway connecting the hemispheres) to reach the ipsilateral hemisphere.

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How Do the Cerebral Hemispheres Contribute to Encoding Spatial Relations?

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

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

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

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EVIDENCE FOR TWO TYPES OF SPATIAL RELATIONS

According to this theory, *categorical* spatial relations (such as "above/below," "left/right," or "inside/outside") place objects or

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