Psychological Bulletin
1994, Vol. 116, No. 2, 195–219

How and Why Do the Two Cerebral Hemispheres Interact?

Matthew J. Hoptman and Richard J. Davidson

Research on the anatomical bases of interhemispheric interaction, including individual differences in corpus callosum (CC) anatomy, is reviewed. These anatomical findings form the basis for the discussion of two major themes. The first considers interhemispheric transfer time (IHTT) and related issues. These include varieties of IHTT and possible directional asymmetries of IHTT. Evidence suggests that pathological variations in IHTT may have cognitive consequences. The second involves conditions under which interhemispheric interaction is necessary and beneficial. The data suggest that when both hemispheres have some competence at a difficult task, there is a benefit to interhemispheric interaction. The role of the CC in the dynamic distribution of attention may be particularly relevant to this advantage. Throughout the article reference is made to individual differences and developmental changes associated with interhemispheric interaction.

How and under what conditions do the cerebral hemispheres integrate and coordinate their disparate abilities? Researchers in fields as diverse as neurophysiology (Bremer, 1958) and psychoanalysis (Hoppe, 1977) have been intrigued by this question. In the past 30 years, a major research effort has been made to investigate differences in the functions of the cerebral hemispheres. This work has shown, for instance, that the left hemisphere (LH) is specialized for speech and phonetic analysis, motor functions, and certain forms of emotion and that the right hemisphere (RH) is specialized for some visuospatial functions, prosody, components of attention, and other forms of emotion (for reviews, see Benson & Zaidel, 1985; Davidson, 1984). As compelling as these differences are, the brain does not consist of two isolated hemispheres. For this reason, work is beginning to focus on how the hemispheres work together.

Although an obvious candidate for such integration is the corpus callosum (CC), the largest fiber tract in the brain, for centuries its function was a mystery. Most early studies suggested that cutting it had few significant long-term behavioral consequences (e.g., Akelaitis, 1941). Thus, McCulloch (1949) facetiously suggested that the CC served only to permit the spread of epileptic seizures from one side of the brain to the other, and Lashley (1951) humorously proposed that it prevented the two hemispheres from sagging.

This skepticism was apparent despite isolated findings as early as the 17th century that callosal sections affected behavior (see Harris, in press, for a discussion). Not until 1953 did a better understanding of the functions of the CC begin to emerge. It was then that R. E. Myers and Sperry demonstrated the critical role of the CC in the transfer of visual discrimination learning in cats.

Sperry's group (e.g., Gazzaniga, Bogen, & Sperry, 1962; Levy, Trevarthen, & Sperry, 1972) was among the first to clearly show the effects of complete forebrain commissurotomy on human behavior.[1] Their studies showed that information of a variety of types presented to one hemisphere was inaccessible to the other, causing a *disconnection syndrome*. Geschwind and Kaplan (1962) demonstrated a similar syndrome in a patient whose CC was split by a tumor. Since that time, a number of hypotheses have emerged regarding the nature of interhemispheric interaction.

Although many of these hypotheses seem mutually exclusive, with some emphasizing either inhibitory or excitatory roles for such interaction, the heterogeneity of interhemispheric connections allows for a variety of functions. Because some seeming contradictions in the literature may arise from a failure to consider this heterogeneity, it is a recurring topic in our review.

In this article, we discuss two major themes: (a) issues related to the timing of interhemispheric interaction, especially interhemispheric transfer time (IHTT), and (b) the cognitive processes for which interhemispheric interaction is necessary or beneficial. The role of interhemispheric interaction in motor behavior is beyond the scope of this review. Interested readers are referred to reviews by Geffen, Jones, and Geffen (in press) and Preilowski (1990). Before these themes are developed, we

---

Matthew J. Hoptman and Richard J. Davidson, Department of Psychology, University of Wisconsin—Madison.

This work was supported by Public Health Service, National Research Service Award F32 AG05538 from the National Institute on Aging to Matthew J. Hoptman and by National Institute of Mental Health (NIMH) Grants MH43454, MH40747, and P50-MH52354; by a grant from the March of Dimes Birth Defects Foundation; and by an NIMH Research Scientist Award (MH00875) to Richard J. Davidson.

Matthew J. Hoptman wishes to thank Jerre Levy, his dissertation advisor, for providing the inspiration for many of the ideas in this article. He thanks Karen Luh, Marie Banich, Peter Spear, Yoshio Nakamura, and Mary P. Grattan for their many helpful comments and discussions both recently and over the years. We thank Lauren Harris and Linda Rueckert for reviewing an earlier draft of this article. Clifford Saron deserves a very special thanks for his many insightful comments and suggestions on a previous draft of this article. We also thank Theodore Bashore and four anonymous reviewers for their helpful comments.

Correspondence concerning this article should be addressed to Richard J. Davidson, University of Wisconsin, Department of Psychology, 1202 W. Johnson Street, Madison, Wisconsin 53706.

[1] *Commissurotomy* refers to section of the corpus callosum (CC) and other commissures; *callosotomy* refers only to section of the CC.

discuss some of the anatomical bases of interhemispheric interaction. This discussion forms the basis for the functional issues examined later in this article.

Gross Anatomy, Phylogeny, and Ontogeny of Interhemispheric Transfer

In addition to the CC, other commissures in the central nervous system may play important roles in interhemispheric interaction. Other forebrain commissures include the anterior commissure, the dorsal and ventral hippocampal commissures, and the basal telencephalic commissure (identified in the rhesus monkey by LaMantia & Rakic, 1990a). Di- and mesencephalic connections are mediated by hypothalamic, supraoptic, and habenular commissures, the massa intermedia (mediating thalamic connections), the posterior commissure, and the collicular commissures. The spinal cord likewise is replete with commissures.

There are reasons, however, for thinking that the CC plays the dominant role in interhemispheric interaction (see, e.g., Levy, 1985). It is the largest fiber tract in the brain. The CC appears late in phylogeny, as indicated by its presence only in placental mammals, which evolved more recently than other animals. It appears late in ontogeny as well, becoming evident only in the 4th gestational month (Rakic & Yakovlev, 1968). The CC myelinates slowly and, in humans, approaches adult levels of myelination only in the teens (Yakovlev & Lecours, 1967). This development of the CC may be mirrored by reductions in its size in aged humans (e.g., Cowell, Allen, Zalatimo, & Denenberg, 1992), consistent with Hughlings Jackson's (1884/1958) notion that later developing structures are more vulnerable to functional loss. Among placental mammals, its complexity increases with increasing complexity of the organism. For example, Curtis (1940) used electrophysiological methods to show that (a) the magnitude of callosally mediated evoked potentials is smaller in cats than in monkeys and (b) CC connectivity is more circumscribed in monkeys than in cats. Kennedy, Meisserel, and Dehay (1991) also discussed anatomical evidence that increasing brain size is associated with more limited callosal connectivity.

The complexity of callosal anatomy has important functional significance. For this reason, we discuss background anatomical information to provide a foundation for the behavioral studies discussed later.

Topography of Callosal Fibers

The CC typically is divided into four parts; in rostral to caudal order, they are the rostrum, genu, body, and splenium. The main commissures and overlying cortical structures are shown in Figure 1.

Data From Monkeys

Most callosal fibers connect homologous regions of the two hemispheres (homotopic fibers), although there also are connections between nonhomologous areas (heterotopic fibers; see Kennedy et al., 1991, for a discussion). Autoradiographic studies of callosal connections in the macaque brain summarized by Pandya and Seltzer (1986) have revealed a well-ordered topography. Prefrontal callosal fibers cross in the rostrum and genu, premotor and supplementary motor fibers in frontal cortex cross just posterior to those of the prefrontal area, in the rostralmost part of the body of the CC, and sensorimotor fibers cross still farther posteriorly. Running caudally to these fibers are those from the posterior parietal area. Still farther caudally, fibers from the temporal lobe cross the midline. Superior temporal fibers cross dorsally to those from the inferior temporal area. Peristriate callosal fibers cross in the splenium (Pandya & Seltzer, 1986; see Figure 2). Fibers from the cingulate cross dorsally throughout the extent of the CC, whereas those of the insula cross ventrally. There is some controversy regarding whether primary visual cortices are callosally connected, but S. Clarke and Miklossy (1990) found afferent callosal fibers in these regions in humans.

Callosal fibers connecting different regions are not strictly segregated; overlap of fibers that connect separate regions is thought to occur between architectonically similar regions. Overlap also occurs between regions that share considerable intrahemispheric connectivity, for instance, frontal and cingulate cortices.

The density of callosal connectivity increases from primary to association cortex for all sensory modalities, suggesting that interhemispheric transfer may be delayed beyond registration of information in primary cortex. This implies that information is usually at least partially processed before it is transferred (see Kennedy et al., 1991, for a discussion).

Data From Humans

Callosal topography differs somewhat between monkeys and humans. For example, Degos et al. (1987) found degeneration in occipital and superior parietal cortex in a human subject with an infarction affecting the posterior CC (including the splenium and posterior body). In contrast to Pandya and Seltzer's (1986) results in macaques, Degos et al. did not find degeneration in the temporal cortex. This suggested to Degos et al. that in humans, temporal fibers cross rostral to fibers of the superior parietal cortex. Also, Risse, Gates, Lund, Maxwell, and Rubens (1989) found a disruption of auditory, but not somatosensory, information transfer in partial callosotomy patients in whom the splenium and up to the posterior one third of the body were intact. These results also differ from Pandya and Seltzer's findings in macaques. Risse et al. suggested that their own results represent an overlap of fibers from different cortical regions in the CC. In summary, these studies suggest differences between macaques and humans in the location of fibers connecting temporal and parietal cortices and may have implications for the locus of information transfer in macaques versus humans.

Summary

Despite these species differences, callosal connections have a well-ordered topography, the functional significance of which has been shown in findings that anterior and posterior callosal

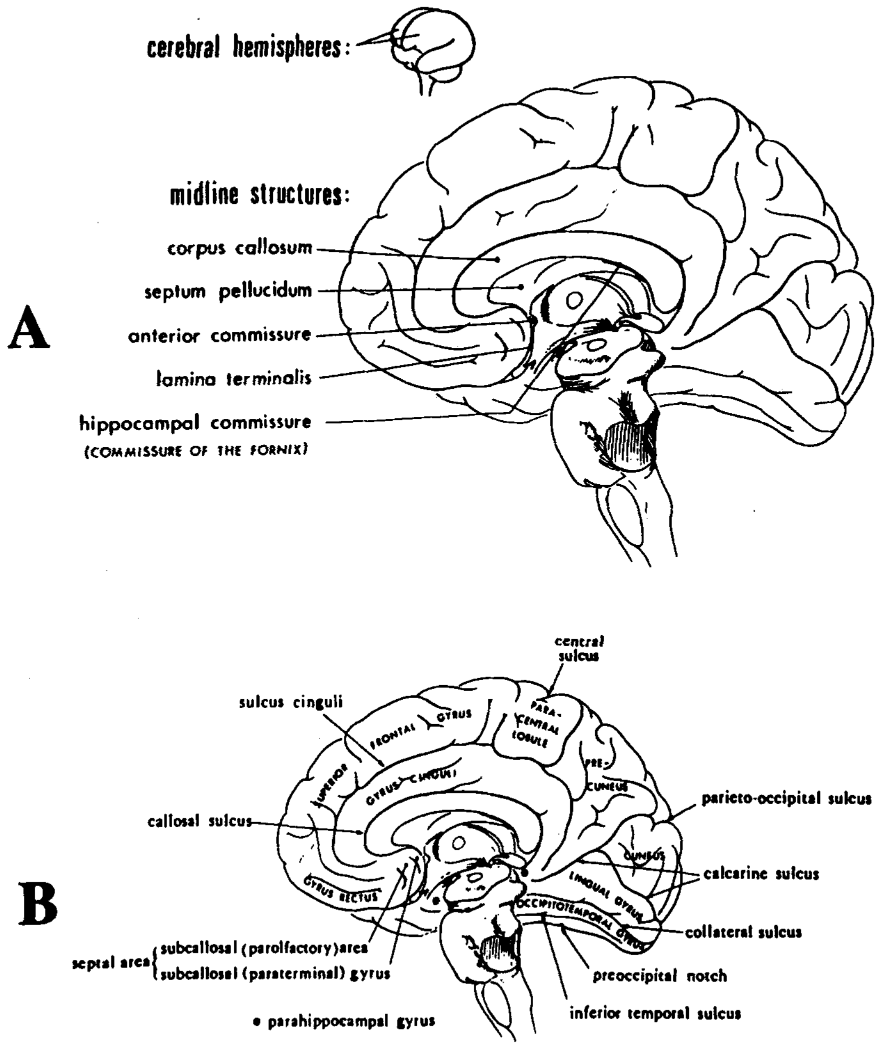

Figure 1. Panel A: Midsagittal view of the brain including the corpus callosum and other forebrain commissures. Panel B: Overlying cortical regions. From *A Basic Atlas of the Human Nervous System* (pp. 101 and 107) by G. B. Dunkerley, 1975, Philadelphia: F. A. Davis. Copyright 1975 by F. A. Davis. Reprinted by permission.

lesions have different consequences for behavior in humans (see Pandya & Seltzer, 1986, for a discussion). An additional determinant of interhemispheric interaction is the size of callosal fibers, as discussed in the next section.

Cytology of the CC

Data From Monkeys

LaMantia and Rakic (1990a) examined the cytology of the macaque's CC by dividing it into tenths along its length and sampling myelination, axonal density, and axonal diameter in each tenth. Across sections, they found that areal measurements did not predict callosal fiber number in the macaque. Within sections, they found huge variation in axonal diameters (see Figure 3). All regions had a preponderance of small fibers, but they varied in the proportion of myelinated axons and larger fibers they contained. The smallest mean fiber diameter and the lowest percentage of myelinated fibers were found in the anterior CC. Higher proportions of large, myelinated fibers were found more posteriorly, especially in regions connecting homologous somatosensory and visual extrastriate cortices.

These variations in cytology may be important because large-diameter fibers transmit information faster than smaller fibers. The higher proportion of small fibers connecting association cortices implies that, on average, information transfer may be slower between those regions than between primary cortices.

Another important aspect of callosal cytology is the finding of massive axonal loss during embryological and early postnatal development. Both cats (Innocenti, 1986) and macaques (LaMantia & Rakic, 1990b) lose about 70% of their callosal axons

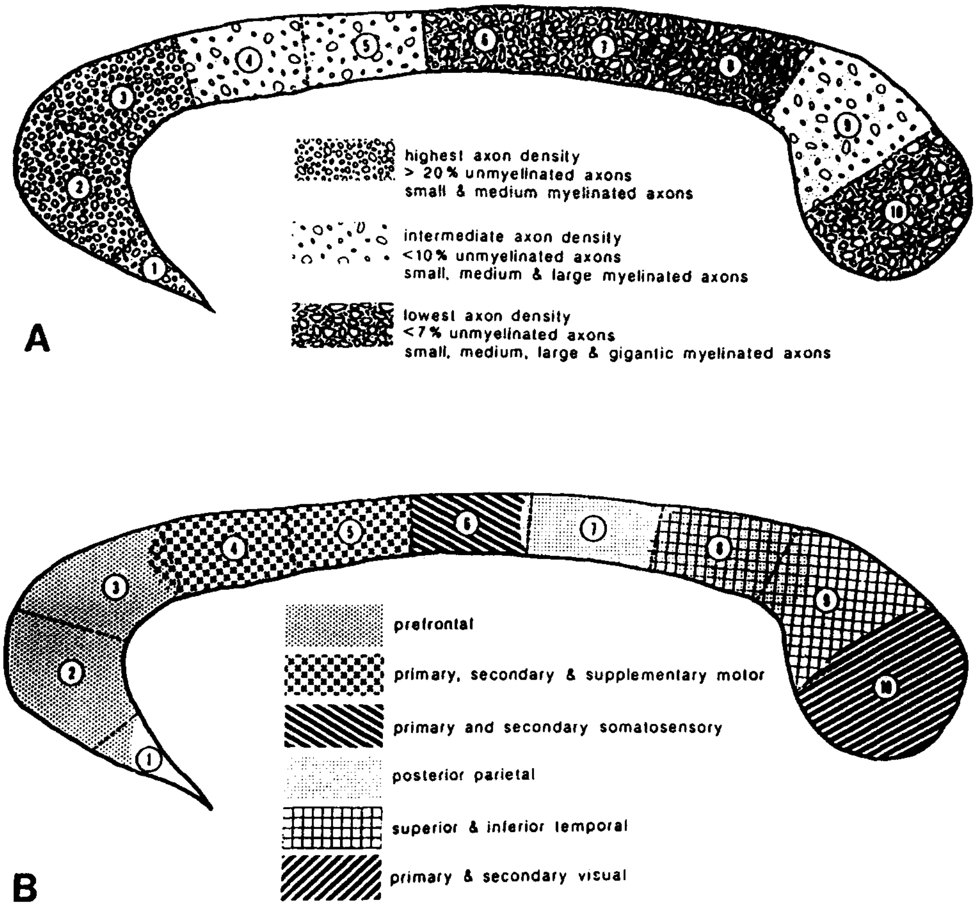

Figure 2. Panel A: Average fiber size, degree of myelination, and fiber density for each successive tenth of the macaque corpus callosum. Panel B: Topography of the macaque corpus callosum. From "Cytological and Quantitative Characteristics of Four Cerebral Commissures in the Rhesus Monkey" by A.-M. LaMantia and P. Rakic, 1990, *Journal of Comparative Neurology, 291,* p. 531. Copyright ©1990 by John Wiley and Sons, Inc. Reprinted by permission of Wiley-Liss, a division of John Wiley and Sons, Inc.

during early development. This loss of callosal axons may be related to synaptic loss in other cortical regions (e.g., Huttenlocher, 1979; Rakic & Goldman-Rakic, 1982). The topography of the CC appears to be established in primates before this period of axonal loss (see LaMantia & Rakic, 1990b for a discussion). However, individual differences in the extent of callosal axonal loss may relate to findings of Sex × Handedness differences in callosal anatomy (see the later section).

Data From Humans

There may be a species difference in the location of the largest callosal fibers. Whereas LaMantia and Rakic (1990a) found that mean axonal diameter was largest in the middle of the body of the CC (see Figure 2A, Sector 6) in macaques, Aboitiz, Scheibel, Fisher, and Zaidel (1992a) found the greatest number of large fibers more caudally in humans, in the posterior midbody. This finding may be related to species differences in topography discussed previously, which suggest that in humans, in contrast to macaques, fibers from the temporal lobe cross anteriorly to those from occipital and superior parietal regions.

Aboitiz et al. (1992a) found that CC area predicted fiber number in humans when small to intermediate fibers were included in the counts (Tomasch, 1954, obtained similar findings). The relation did not hold when only large fibers were included in the count. Machiyama, Watanabe, and Machiyama (1987) also found more fibers in human CCs with larger areas. These findings contrast with those of LaMantia and Rakic (1990a), who found that CC area did not predict fiber number in macaques and may mean that larger CCs have more fibers only in humans. This relation between fiber number and CC area may have relevance for the individual differences in callosal area.

Summary

Callosal cytology varies both within and across regions. Across species, anterior regions have the smallest fibers. There

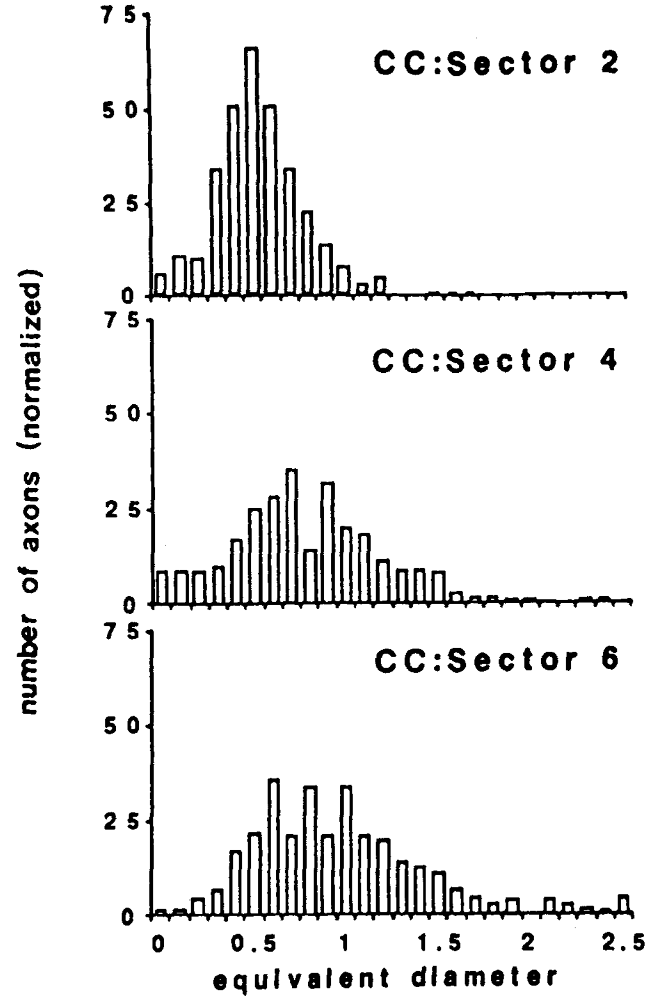

Figure 3. Histogram of fiber sizes of three regions of the macaque callosum. Sectors are as described in Figure 2. From "Cytological and Quantitative Characteristics of Four Cerebral Commissures in the Rhesus Monkey" by A.-M. LaMantia and P. Rakic, *Journal of Comparative Neurology, 291,* p. 528. Copyright ©1990 by John Wiley and Sons, Inc. Reprinted by permission of Wiley-Liss, a division of John Wiley and Sons, Inc.

may be species differences in the location of the largest fibers and in the relation between fiber number and CC area. Potentially important individual differences in CC area have been found in humans, as we discuss in the next section.

Individual Differences

Many researchers have investigated individual differences in CC anatomy. De Lacoste-Utamsing and Holloway (1982) found sex differences, and Witelson (1985) found handedness differences in the CC. Witelson determined handedness using an adaptation of Annett's (1967) handedness inventory. Handedness effects were found only when subjects were divided into consistent right-handers (CRHs), who preferred their right hands for all items on the inventory, and nonconsistent right-handers (NCRHs), who showed more variable hand preferences, a handedness classification based on work by Annett (1967). For both sex and handedness effects, there have been many nonreplications (e.g., Byne, Bleier, & Houston, 1988; Demeter, Ringo, & Doty, 1988; Kertesz, Polk, Howell, & Black, 1987). However, recently there have been consistent findings of Sex × Handedness interactions.

Sex × Handedness Effects

Witelson (1989) accumulated material from 50 autopsy cases, including subjects from her earlier reports (Witelson, 1985). She extended her previous findings of a larger total CC area, isthmus (defined by Witelson, 1985, as the posterior one third minus the posterior one fifth of the CC) and posterior midbody of the CC in NCRHs than CRHs, but this held only for men. The isthmus, relative to total CC area, was larger for both NCRH and CRH women than CRH men. Witelson suggested that the axonal elimination that takes place in the CC during the prenatal and early postnatal period may be greater in CRH men than in the other groups (Witelson, 1989; Witelson & Nowakowski, 1991).

Witelson and Goldsmith (1991) increased Witelson's (1989) sample of male brains from 15 to 22. They extended her earlier findings and found a negative correlation between relative isthmal area and score on their handedness questionnaire in men, implying that fewer right-handed men had larger isthmal areas. However, the absolute value of the handedness score also correlated significantly with isthmal area, so it was unclear to them whether the magnitude or direction of handedness correlated with isthmal area.

Several researchers using magnetic resonance imaging (MRI) have replicated these findings, suggesting that they generalize across methods. J. M. Clarke and Zaidel (1993; $N = 60$) found that relative isthmal area was larger in female than male CRHs, with no differences between other groups. However, this region was nearly significantly larger in mixed-handers (who have variable hand preferences) than CRH men. The interaction was not significant when consistent left-handers and mixed-handers were combined, emphasizing that consistency of hand use, rather than handedness per se, determines Sex × Handedness effects.

Habib et al. (1991; $N = 53$) likewise showed that isthmal area was larger in NCRH than CRH men. They also found that the posterior body (posterior midbody and posterior isthmus) was larger in CRH women than men, replicating Witelson (1989) and J. M. Clarke and Zaidel (in press). Finally, Denenberg, Kertesz, and Cowell (1991; $N = 104$) did a factor analysis on the Kertesz et al. (1987) data and found that in the factors representing the isthmus, CRH men and both female groups had smaller widths than did NCRH men, consistent with Witelson.

Steinmetz et al. (1992; $N = 52$) failed to find a Sex × Handedness interaction in CC anatomy, finding instead that women had larger relative isthmal areas than men. However, Witelson (1992) suggested that the analytic method they used may be of insufficient resolution to reveal individual differences in small callosal regions. Although there is some variability among studies, they are, except for the Steinmetz et al. study, consistent in showing a Sex × Handedness interaction in relative isthmal area.

The meaning of these effects is unclear, especially because of the handedness classification method used. Most studies of the incidence of handedness, using a variety of criteria, show that about 90% of the population is right-handed (Benson & Zaidel, 1985). If Witelson's (1989) subjects were classified only by writing hand, 88% of her subjects were right-handers, a group that is homogeneous for language lateralization (e.g., Harris, 1992). Her NCRH group, which made up 36% of the sample, included people who would have been classified as right-handers in most studies. Because many NCRHs would fall into a group that is homogeneous for language lateralization, Witelson's claim that male NCRHs have cognitive bilateralization must be taken with caution (for a more detailed discussion of handedness classification, see Harris, 1992). The lack of consistent behavioral evidence of sex or handedness differences in interhemispheric interaction (e.g., Banich, Goering, Stolar, & Belger, 1990; Burton, Pepperell, & Stredwick, 1991) also suggests that more work is necessary to determine whether these relations have functional significance and, if so, what it is.

Recent work by Aboitiz, Scheibel, Fisher, and Zaidel (1992b) and Aboitiz, Scheibel, and Zaidel (1992) on autopsy material showed sex differences in relations between CC anatomy and anatomical asymmetries in the planum temporale. The left planum temporale is implicated in language function and was found to be larger on the left than right by Geschwind and Levitsky (1968). Aboitiz et al. (1992a) found that larger numbers of fibers in posterior callosal regions (isthmus in men, anterior splenium in women) correlated with smaller anatomical asymmetries in both men and women and Aboitiz, Scheibel, and Zaidel (1992) found that larger posterior callosal areas correlated with smaller asymmetries only in men. However, handedness data were not reported. Given the possible Sex × Handedness interaction for isthmal area, the Aboitiz et al. findings may have to be qualified.

Summary

Studies of individual differences suggest that the relative isthmal area is larger in NCRH men than in CRH men, with no handedness effect in women. Although some studies showed that relations between callosal area and anatomical cerebral asymmetries vary according to sex, handedness was not always reported, making interpretation difficult.

More generally, some important features of callosal anatomy are its sheer size, topographic distribution of fibers, and regional differences in cytology. The topographic organization means that localized lesions to the CC will have different effects. Similarly, regional variation in cytology of the CC has implications for the speed and type of information transfer among various cortical areas.

Heterogeneity of the Callosal Connections

A review by Kennedy et al. (1991) emphasized similarities between CC connections and intrahemispheric association pathways. These authors discussed both anatomical and neurophysiological bases for their model.

Anatomy

Although Hedreen and Yin (1981) reported that callosal connections are less dense between hetero- than homotopic sites, Kennedy et al. (1991) suggested that this may result from the fact that heterotopy entails a divergence of connectivity of callosal fibers from source to recipient cortex. Thus, there may be as many hetero- as homotopic fibers, but, because of divergence, the former are lower in density. Kennedy et al. argued that heterotopic fibers play an important role in *feedforward* and *feedback* pathways in the cortex. Feedforward pathways link ascending levels of the processing hierarchy (e.g., from primary to secondary visual cortex), whereas feedback pathways link descending levels (e.g., from secondary to primary visual cortex).

Kennedy et al. (1991) cited data showing that heterotopic callosal fibers show convergence and divergence similar to that of other corticocortical association fibers (i.e., connections between cortical areas). For homotopic callosal fibers, they argued, the situation resembles that of intrinsic connections (i.e., connections within a cortical area). They noted that callosal connections further resemble association pathways between cortical regions and long-range intrinsic connections (within a cortical region) in that they are primarily excitatory and distributed in patches.

Neurophysiology

Kennedy et al. (1991) also argued that "callosal connections exhibit many if not all of the characteristics of association projections and that this indicates that both pathways fulfill a common integrative role which precludes a unique psychophysical function such as perceptual continuity across the midline" (p. 347).

Since the 1960s (e.g., Whitteridge, 1965), it had been stressed that callosal connections served to unify the visual (and other sensory) hemifields. Kennedy et al. (1991) argued that since then, evidence has accumulated that the CC is involved in functions beyond the unification of sensory hemifields, although they agreed that this must be a critical function of callosal neurons in primary sensory areas. Thus, Kennedy et al. took issue with Berlucchi, Tassinari, and Antonini's (1986) position—the vertical midline rule—that afferent and efferent callosal projections are limited to cortical neurons with receptive fields on or near the vertical midline.

In support of their argument, Kennedy et al. (1991) discussed evidence that in the macaque, there are callosal connections in areas that represent the peripheral field in motor, somatosensory, and visual cortex. However, the interpretation of these data has been debated. Berlucchi et al. (1986) argued that although receptive fields have been found away from the vertical midline, they are large enough to contact that meridian. To evaluate the Kennedy et al. claim, it must be shown that the receptive fields in question neither contact the midline nor are callosally connected to receptive fields that do.

Kennedy et al. (1991) further suggested that heterotopic, homotopic, and association connections play an integrative function and that callosal fibers may facilitate performance both within and between hemispheres. They argued that the latter point is supported by Lassonde's (1986) finding that callosal agenic patients show deficits in both intra- and interhemispheric conditions of simple visual discrimination tasks.

Kennedy et al.'s (1991) emphasis on heterotopic connections and on the merging of association and callosal terminations provides a novel framework for understanding a role for the CC in neural networks that involve feedback and feedforward connections. Their model provides a mechanism for the right parietal cortex to influence activity in left frontal regions directly and vice versa. This kind of connectivity may have important consequences for the distribution of attentional resources for environmental stimuli for which right parietal regions play a crucial role (e.g., Heilman & Van Den Abell, 1979; Levy, Wagner, & Luh, 1990; Tucker & Williamson, 1984) and for the distribution of attentional resources devoted to motor readiness for which left anterior regions may be critically involved (Tucker & Williamson, 1984).[2] The model also may provide a mechanism for understanding the inverse relations between arousal asymmetries in frontal and parietal regions that have been reported in patients with mood disorders and in healthy control subjects (e.g., Davidson, Schaffer, & Saron, 1985; Wood, Flowers, & Naylor, 1991).

Kennedy et al.'s (1991) model also reinforces the notion that the CC may be involved in high-level functions, including the dynamic allocation of attention in response to task demands. Levy and Trevarthen (1976) argued that the determinant of which hemisphere takes control of processing depends on task and instructional demands as well as some sort of evaluation by each cerebral hemisphere of its capacity for the task. Levy and Trevarthen (1976) used the term *metacontrol* to denote "the neural mechanisms that determine which hemisphere will attempt to control cognitive operations" (p. 300). Levy et al. (1972) and Levy and Trevarthen (1976) found evidence for the disruption of these mechanisms in split-brain patients. Both studies showed that split-brain patients sometimes used the hemisphere that was less suited for a given task, despite detrimental effects on performance. Electroencephalographic (EEG) data suggest that in healthy subjects, the hemisphere specialized for a task is the one that is typically more active during that task (e.g., Davidson, Chapman, Chapman, & Henriques, 1990). It is not known, however, whether the less skilled hemisphere can dominate performance in healthy subjects. Metacontrol is a topic to which we return; its importance in the context of this article lies in the demonstration that section of the forebrain commissures profoundly impair allocation of information processing resources, with the implication that in normal situations they play a key role in this allocation.

This concludes our review of callosal anatomy. The anatomy discussed previously has important implications for interhemispheric interaction. Callosal topography suggests that different kinds of information are transferred in different regions of the CC. Variations in CC cytology may influence the rate of information transfer. It is possible that the perinatal loss of callosal axons also plays a role in individual differences in interhemispheric interaction. In addition, individual differences in CC anatomy may have implications for rate and quality of information transfer, as well as for sharing of processing resources between hemispheres. Finally, the heterogeneity of CC connections may allow direct interaction between nonhomologous cortical regions, which could have important effects on processing. Some of these relations could be studied in living humans by combining behavioral methods, psychophysiological methods, or both with structural MRI measures.

Timing of Interhemispheric Interaction

We now turn to a consideration of issues related to IHTT. This topic is important both because IHTT is a commonly measured index of callosal function and because it highlights the implications of the CC's anatomical heterogeneity for information transfer. Thus, individual differences in IHTT may relate to cognitive performance. For instance, Davidson, Leslie, and Saron (1990; Davidson & Saron, 1992) found that in dyslexic subjects, who may have larger splenia than control subjects (Duara et al., 1991), shorter IHTTs from the RH to the LH predicted poorer reading ability. Recognizing that most visual input is bilaterally represented, they proposed that when the LH dominates response execution (as in reading with semantic processing), the representation of the information in the RH is sent to the LH to provide it with redundant data. Such redundancy is used for error checking to maximize accurate responding. This circuit may require tight temporal tolerances. If the RH's representation is sent to the LH either too quickly or too slowly, it will interfere with the LH's ability to smoothly execute response output. Data consistent with this model have been obtained using both reaction time (RT; Davidson et al., 1990) and event-related potential (Davidson & Saron, 1992) measures of IHTT.

IHTT for Simple Tasks

Simple RT Paradigms

The oldest method of estimating IHTT involves the comparison of manual RTs for stimuli briefly presented to the same (ipsilateral) or opposite (contralateral) visual hemifield as the response hand.[3] On ipsilateral trials, one hemisphere both receives the visual signal and controls the motor output, whereas on contralateral trials, one hemisphere receives the visual signal and the other must execute the motor output. To our knowledge, Poffenberger (1912), studying adults, was the first to estimate IHTT. He did this by subtracting RTs for ipsilateral trials from those for contralateral trials. This *crossed–uncrossed*

---

[2] Pribram and McGuiness (1975) proposed two neural systems that mediate different kinds of attentional functions. *Arousal* entails a readiness to incorporate sensory information, whereas *activation* refers to motor readiness. Tucker and Williamson (1984) associated the arousal system with the right hemisphere and the activation system with the left hemisphere.

[3] In these and other divided visual hemifield studies, unless otherwise noted, stimuli are presented briefly (tachistoscopically) at a sufficiently low exposure duration to rule out hemisaccades that could invalidate the lateralized presentation.

difference (CUD) is taken as an estimate of IHTT. Typical CUDs estimated from simple RTs are 2–3 ms for healthy young adults (see Bashore, 1981, for a review).

Transfer times of this magnitude are presumably mediated by large (>2.4 μm), myelinated fibers (e.g., Swadlow, Geschwind, & Waxman, 1979). Aboitiz et al. (1992a) and Tomasch (1954) found that the axons that can mediate this kind of transfer are relatively rare; these may be the only fibers necessary for such simple tasks.

Vocal RT Paradigms

Another way to estimate IHTT is to use the difference between vocal RTs to left visual hemifield (LVF) and right visual hemifield (RVF) stimuli. In the former case, the LVF stimulus must be relayed to speech regions of the LH for spoken output. This is not necessary for RVF stimuli because the connection is intrahemispheric. Although some have found IHTT estimates of 10–30 ms using vocal RT (see, e.g., Filbey & Gazzaniga, 1969; A. D. Milner & Lines, 1982), the validity of this method is questionable because it gives a variety of estimates (usually longer than those obtained by simple RT methods), and an RVF advantage is not always obtained (e.g., Amadeo, Roemer, & Shagass, 1977; Bashore, 1981; St. John, Shields, Krahn, & Timney, 1987). Amadeo et al. even found an LVF advantage for vocal RTs in two of their four experiments. The nature of the stimuli and the vocal response also may influence results, making interpretation of vocal RT paradigms even more difficult (McKeever, Gill, & VanDeventer, 1975).

Electrophysiological Paradigms

Still others have used electrophysiological methods to estimate IHTT. Evoked potentials (EPs) are produced by recording EEG time locked to a stimulus. Across trials, noise averages out and a characteristic waveform emerges. This waveform has early, middle, and late components. Middle components (80–200 ms poststimulus) are thought to reflect cortical activity time locked to the stimulus. These components, particularly a positive-going peak at roughly 100 ms (P100) and a negative-going peak at about 160 ms (N160), have been used to estimate IHTT (e.g., Saron & Davidson, 1989b). The waveform elicited in the hemisphere contralateral to the side of sensory stimulation is produced through a direct pathway, whereas the presence of the EP ipsilateral to the side of sensory stimulation depends on transmission of the signal across the CC (see section *IHTT in Special Populations*). The latency difference between ipsilateral and contralateral peaks gives an estimate of IHTT. These estimates obtained in visual EP (VEP) and somatosensory EP (SEP) modalities have ranged from 8 ms to 26 ms (see Saron & Davidson, 1992b, for a review).

Saron and Davidson (1989b) estimated IHTT using VEPs to lateralized checkerboard flashes presented in a simple RT task. They examined both P100s and N160s from the occipital cortex and obtained IHTT estimates of approximately 12 ms. These estimates have high test–retest reliabilities (rs = .80–.93; Saron & Davidson, 1989a).

Estimates of IHTT derived from VEPs are likely mediated by smaller fibers than those that mediate simple RT estimates. According to Aboitiz et al. (1992a), fibers that could mediate an IHTT of 12 ms are more common than those that could mediate simple RT estimates. Larger axons in the body of the CC may subserve the shorter IHTT estimates found in simple RT tasks, whereas smaller axons in the splenium may mediate the larger estimates obtained with VEP methods. Consistent with this notion, Lines, Rugg, and Milner (1984) found that VEP-based IHTT estimates derived from the N160 were longer at occipital sites than at central sites (see section *Is There More Than One Callosal Transfer?*). These data provide an example of how the heterogeneity of CC anatomy may explain discrepant results in the literature by suggesting that different regions of the CC may subserve the transfer of different kinds of information.

Complex RT Estimates

Complex manual RT tasks also have been used to estimate IHTT. However, there have been relatively few studies, and they are not discussed further, other than to note that some of these methods are influenced by stimulus–response compatibility (e.g., Berlucchi, Crea, Di Stefano, & Tassinari, 1977), suggesting that for these more complex tasks, other factors may take precedence over fixed neural pathways. The reader is referred to Bashore (1981) for a review.

Development of IHTT

EP measures. As mentioned earlier, the CC is slow to myelinate. Because myelination increases neural conduction velocity, it is clear, by this criterion at least, that the CC is not functionally mature until at least the teen years. Salamy (1978) used SEPs to show that IHTT decreases linearly with log age; IHTT was not comparable to adult values until the age of 10 years. Although this study has not been replicated, Davidson and Saron (1992) found that VEP estimates of IHTT were longer in preteens than in adults.

Simple RT measures. Simple RT studies also suggest that IHTT decreases in parallel with callosal myelination. Brizzolara, Casalini, Cioni, and Ferretti (1992) assessed IHTT in 210 children with a simple RT paradigm and reported that IHTT decreases between 7 and 11 years of age. In their review of the literature, they noted that the IHTT of subjects congenitally lacking a CC does not decrease during childhood, with its value resembling that of healthy 7-year-olds.

IHTT in Special Populations

The developmental studies suggest that myelination affects IHTT. Studies in split-brain and acallosal patients suggest that the integrity of the CC is critical to timely information transfer.

Split-brain studies. Split-brain patients have undergone section of the forebrain commissures to treat intractable longstanding epilepsy. Simple RT estimates of IHTT in patients with complete commissurotomy range from 30 ms to 50 ms (J. M. Clarke & Zaidel, 1989; Sergent & Myers, 1985).

Estimates of IHTT derived from VEPs also have been validated in split-brain patients. Mangun, Luck, Gazzaniga, and Hillyard (1991) showed that activity ipsilateral to the side of sensory stimulation is absent in patients with complete commissurotomy.

Acallosal patients. Acallosal patients congenitally lack some or all of the CC; the extent of this deficit depends on when in embryological development the neural event responsible for the agenesis occurs. For instance, many agenic patients have enlarged anterior commissures (see Jeeves, 1990). Jeeves (1969; A. D. Milner, Jeeves, Silver, Lines, & Wilson, 1985; Reynolds & Jeeves, 1974) reported IHTT estimates in acallosal patients of roughly 20 ms. Although Kinsbourne and Fisher (1971) found no CUD difference between an acallosal boy and healthy subjects, this might have been due to relatively few trials (n = 50 per hand) or a poor time resolution in their task (see criticism in Reynolds & Jeeves, 1974).

The validity of VEP estimates of IHTT also has been demonstrated in acallosal subjects. Rugg, Milner, and Lines (1985) showed that clear ipsilateral activity does not appear in acallosal patients.

Summary

The massive increase in IHTT estimates in acallosal patients and split-brain patients suggests that the integrity of the CC is critical for the timely transfer of information in healthy subjects. In addition to these variations in neurological populations, individual differences have been found in healthy subjects, as is discussed in the next section.

Individual Differences in IHTT

Handwriting posture. Differences in IHTT have been found as a function of writing posture. Some left-handers write with the pen pointing above the writing line and the hand below it (normal posture [LN]), whereas others write with the opposite (inverted) posture (LI; Levy & Reid, 1976). Right-handed inverters (RIs) are rare, making up about 1% of dextrals; the rest use the normal posture (RN; Levy, 1984; Levy & Reid, 1976, 1978). Levy and Reid initially proposed that in inverters language functions are mediated ipsilateral to the writing hand, whereas in noninverters they are mediated contralateral to the writing hand.

Later studies revealed that relations were more complex. Studies using visual stimuli found differences between LI and LN subjects (e.g., McKeever & Hoff, 1979; Moscovitch & Smith, 1979), whereas studies using tactile or auditory stimuli or go–no-go tasks did not (e.g., Moscovitch & Smith, 1979). Levy and Wagner (1984) compared LIs and LNs on visual, tactile, and auditory simple RT tasks and found that only on the visual simple RT task did LIs fail to show the positive CUD typical of LNs and RNs. When they examined the more sensitive measure of intraindividual standard deviation, LIs showed a negative CUD, in contrast to LN and RN subjects.

Levy and Wagner (1984) and Levy (1986) concluded that LIs have a defect in within-hemisphere visuomotor integration for control of the contralateral hand. Manual RT estimates of IHTT seem to involve a transfer of motor or sensorimotor information (A. D. Milner & Lines, 1982; see section *Is There More Than One Callosal Transfer?*), implying to Levy that visuomotor integration occurs before callosal transfer of information. Responses were slowed more for uncrossed than crossed reactions, suggesting to Levy that the disorder must be specific for control of the contralateral hand. The hypothesized deficit in within-hemisphere visuomotor integration for the contralateral hand requires LIs to use a transcallosal pathway to write with the left hand.

Although there are problems with the data suggesting that simple RT estimates of IHTT entail a relay of motor or sensorimotor information (see section *Is There More Than One Callosal Transfer?*), a report from Gur, Gur, Sussman, O'Connor, and Vey (1984) also supports the idea that the writing pathway is mediated via the CC in LI people. Gur et al. found that an LI patient with LH language became agraphic with his left hand after commissurotomy. Presumably, LNs control writing contralaterally via the RH. It is not known whether the transcallosal pathway used for writing in inverters is related to differences in callosal anatomy. Thus, anatomical studies would be relevant.

Sex. St. John et al. (1987) found that CUDs that were based on simple RT were longer for women than for men. Dufresne, Lapierre, Chouinard, Daigneault, and Braun (1993) replicated this effect. However, because sex differences in CC anatomy have been found only inconsistently, the neural substrate of this behavioral effect is unclear. The finding that relative isthmal area is larger in CRH women than CRH men seems inconsistent with these results. However, the interpretation depends on the number of large fibers in these larger isthmal regions, especially because Aboitiz et al. (1992a) found that the number of large CC fibers, which would presumably mediate this transfer, did not correlate with CC area in humans. Aboitiz et al. did not report these relations by sex, so it is not known whether the relation between fiber size and area differs in men and women.

Summary

IHTT can be measured in a variety of ways, the most common being simple RT, vocal RT, and EPs. The development of IHTT closely follows the myelination of the CC. Studies on acallosal and split-brain patients provide validation for the RT and EP methods; these populations show prolonged CUDs and deficient ipsilateral EP waveforms. Finally, individual differences in IHTT have been found, especially with regard to hand posture. These results must be qualified by many sources of variance, as discussed in the next section.

Sources of Variance in IHTT

Simple RT Estimates

Despite the support offered by studies of split-brain and callosal agenic patients, there are many sources of variance in measures of IHTT. St. John et al. (1987) tested 6 men and 6 women for IHTT using simple RT in 20 experimental sessions. In all, more than 5,700 trials were given to each subject. All subjects showed a significant CUD. However, for the estimate of IHTT across sessions, the coefficient alpha, a measure of internal consistency, was high for men (approximately .90), but not for women (about .48). Among the possible sources of variance discussed by St. John et al. was stimulus eccentricity. However, although CUDs increased as stimulus eccentricity increased from 2° to 15° from the vertical midline, the effect was small, and the authors noted that it was present in only 4 subjects. Furthermore, the effect is inconsistent with Berlucchi, Heron, Hyman, Rizzolatti, and Umiltà's (1971) finding that simple RT estimates of IHTT were not influenced by retinal eccentricity. Thus, the St. John et al. eccentricity effect may be spurious.

Saron and Davidson's (1989b) results also suggest unreliability in simple RT estimates. In their experiments, VEP estimates of IHTT showed CUDs in the direction predicted by anatomy (i.e., crossed greater than uncrossed) in 94% of their computations, whereas simple RT estimates computed from the identical trials were positive only 70% of the time. Because the assumption is that crossed and uncrossed reactions differ only by a callosal relay, negative CUDs are generally taken to be invalid.[4] Thus, simple RT estimates may be less consistently valid than are VEP measures.

Vocal RT Estimates

St. John et al. (1987) tested the same subjects as in their simple RT experiment on a vocal RT task and found that coefficient alphas were lower for vocal than simple RT measures of IHTT. Although vocal RT estimates of IHTT did not vary with stimulus eccentricity, coefficient alphas increased from only .20 at 2° to .79 at 15°. Finally, estimates of IHTT were longer for vocal than for simple RT measures. St. John et al. concluded that simple RT estimates are more reliable than those from vocal RTs. However, CUDs from vocal and simple RT were uncorrelated, suggesting that they may index transfer of different information (or that the former are too unreliable to allow a significant correlation), making comparisons difficult. The functional significance of this lack of correlation is discussed shortly. Vocal RT estimates of IHTT depend on the possibly faulty assumption that IHTT is symmetrical with respect to the direction of the transfer (Braun & Daigneault, 1994; Marzi, Bisiacchi, & Nicoletti, 1991; see section *Is There an Asymmetry in IHTT?*). The lack of correlation between manual and vocal RT measures of IHTT suggests that there may be more than one kind of IHTT.

Is There More Than One Callosal Transfer?

A. D. Milner and Lines (1982) argued that the difference between simple and vocal RT estimates of IHTT is attributable to differences in the signal that is transferred in each case. Both tasks were used in their experiments. Vocal, but not simple, RT estimates of IHTT were affected by stimulus intensity. A. D. Milner and Lines suggested that for the simple RT task a nonsensory signal was transferred between hemispheres, whereas for the vocal RT task a sensory signal was transferred. They posited that the CUD for simple RTs was nonsensory in nature because it was unaffected by stimulus intensity, whereas the CUD for vocal RTs was thought to be sensory coded because it was affected by such variations. The lack of correlation between vocal and manual RT (St. John et al., 1987) estimates of IHTT also suggests that the two measures may index different processes.

As noted earlier, the validity of vocal RT estimates of IHTT has not been determined. A. D. Milner and Lines (1982) excluded subjects who failed to show an RVF advantage on their vocal RT task; 50% of their recruits were excluded on this basis. Brysbaert's (1992) failure to find effects of stimulus intensity on vocal RT estimates of IHTT also suggests caution in interpreting these data.

Rugg, Lines, and Milner (1984) and Lines et al. (1984) extended A. D. Milner and Lines's (1982) findings using VEPs and showed that at central leads the IHTT estimate was about 3 ms, whereas at occipital sites it was approximately 14 ms. They argued that the nonsensory relay occurs at central leads, suggesting that it may entail a transfer of motor or sensorimotor information, whereas the sensory relay occurs at occipital leads. Thus, stimulus intensity affected IHTT estimates at occipital, but not central, leads. The IHTTs over central sites are similar to simple RT estimates, whereas those over occipital sites are similar to Saron and Davidson's (1989b) VEP results. These findings are consistent with the lack of correlation between estimates of VEPs collected over occipital cortex and manual RT estimates of IHTT (Saron & Davidson, 1989b). Thus, although in Saron and Davidson's study both simple RT and VEP measures were collected concurrently, using identical trials, and did not significantly differ, they were not significantly correlated, implying either that (a) they measure different processes or (b) the error variance of simple RT estimates was too great to allow a significant correlation.

Recent work by J. M. Clarke and Zaidel (1989) also addressed this issue. In their experiments, subjects made simple RT responses to lateralized light flashes. Stimulus intensity was varied in their first experiment, and eccentricity was varied in a second experiment. As expected from A. D. Milner and Lines (1982) and the Berlucchi et al. (1971) work, neither intensity nor eccentricity affected CUDs in healthy subjects. J. M. Clarke and Zaidel attributed these patterns to a nonsensory relay, consistent with Milner and Lines's interpretation.

Special Populations

J. M. Clarke and Zaidel (1989) also tested an acallosal patient and split-brain patients. Stimulus intensity and eccentricity had no effect on CUDs in one of the complete commissurotomy

---

[4] Braun (1992) argued that negative interhemispheric transfer times (IHTTs) are valid and that the varying estimates of IHTT obtained with simple reaction time (RT) measures are due to the presence of fast and slow interhemispheric channels. He argued that information processing can be accomplished more quickly by a fast interhemispheric channel than by an intrahemispheric pathway, presumably via a heterotopic route, leading to negative crossed–uncrossed differences. However, it is likely that processing on ipsilateral and contralateral trials is mediated by similar brain regions, albeit in opposite hemispheres. Consistent with this idea, RTs for ipsilateral and contralateral trials are highly correlated ($r > .95$ in our pilot data). Therefore, it is unclear how adding a callosal relay could fail to increase RT.

patients or in the acallosal boy. The CUDs of other complete commissurotomy patients were affected by stimulus eccentricity, but not intensity. J. M. Clarke and Zaidel suggested that subcallosal transfer of visual information is more sensitive to stimulus eccentricity than intensity. However, intensity did affect IHTT in another acallosal patient (A. D. Milner et al., 1985). In this patient, a visual signal might have been transferred via the anterior commissure (for a discussion, see Jeeves, 1990).

Summary

Vocal RT and occipital VEP estimates of IHTT are affected by stimulus parameters, suggesting that they index the transfer of some kind of sensory information. Simple RT and central VEP estimates are unaffected by such manipulations, implying that they index transfer of some kind of nonsensory information. The difference between sensory and nonsensory estimates of IHTT suggest that the former are mediated by smaller fibers, giving rise to longer IHTTs. An added layer of complexity comes from recent findings that IHTT may be faster in one direction than the other.

Is There an Asymmetry in IHTT?

Although it generally has been assumed that IHTT is identical from LH to RH and from RH to LH, a recent meta-analysis by Marzi et al. (1991) suggests that IHTT is asymmetrical, as had been discussed by others (e.g., Braun & Daigneault, 1994; Davidson et al., 1990; Saron & Davidson, 1989b). Marzi et al. analyzed 16 simple RT studies of IHTT in right-handers and found overall RT advantages for the LVF and for the right hand. There was no difference in RT between the two uncrossed stimulus–response hand conditions. However, for crossed conditions there was a consistent RT advantage for the LVF–right-hand condition as compared with the RVF–left-hand combination, implying that transfer from the right to left hemisphere is faster than transfer in the opposite direction. The lack of a visual hemifield or hand advantage in the uncrossed condition suggested to Marzi et al. that the effect was not attributable simply to a performance difference between the visual hemifields, the two hands, or both. They did concede, however, that the LVF advantage may be compensated for by the right-hand advantage.

These directional advantages were found in 13 of the 16 studies in the meta-analysis and implied to Marzi et al. that transfer of simple information is faster from the RH to the LH than in the opposite direction (but see Braun & Daigneault, 1994, for an alternative view based on data from a single new experiment). The asymmetry also was found in Saron and Davidson's (1989b) VEP data; IHTT estimates that were based on P100 latencies were longer for RVF than LVF stimuli. A recent meta-analysis of the evoked potential data strongly supports the conclusion that transfer is faster from right-to-left hemisphere than in the opposite direction (Brown, Larson, & Jeeves, 1994).

These directional asymmetries may be evident only in the visual modality when a lateralized motor response is required. Their restriction to visuomotor information processing is suggested by the observation that they are absent when the imperative stimuli are presented in the auditory modality (e.g., Moscovitch & Smith, 1979). That the response output must be lateralized is suggested by findings that no visual hemifield advantage is apparent when a nonlateralized response is required (e.g., blowing; Sergent & Myers, 1985). Moreover, the presence of these directional effects may vary with handedness; left-handers do not show these asymmetries, exhibiting instead inconsistent hand and visual hemifield advantages.

The basis of the asymmetry in IHTT found in right-handers is unclear. It could reflect an asymmetry in the relay of visual, motor, or visuomotor information. Saron and Davidson (1989b) suggested that directional effects may arise from a left-right asymmetry of the density of callosal fibers, based partly on findings of within-hemisphere regional differences in these densities in macaques (e.g., Van Essen, Newsome, & Bixby, 1982). It may be relevant that in a study on split-brain patients, Cronin-Golomb (1986) found that subcortical transfer was more accurate from the RH to the LH than in the other direction, suggesting that an asymmetrical transfer of information may generalize to subcortical transfers.

General Summary

Measurement of IHTT is influenced by many variables, but at least simple RT and EP estimates depend on the integrity of the CC. The magnitude of IHTT decreases with myelination of the CC. In addition, there is evidence that IHTT may differ as a function of hand posture. Many data (e.g., Marzi et al., 1991) suggest that different measures of IHTT may index different kinds of transfer that may occur in different parts of the CC. Finally, recent data suggest that the transfer of visual information may be faster from the RH to the LH than in the opposite direction. That abnormally fast right-to-left interhemispheric transfer correlates with reduced reading skills in dyslexics suggests that variations in IHTT may have important behavioral consequences.

What Does the CC *Do* for a Living?

Although the aforementioned behavioral, electrophysiological, and anatomical methods provide information that permit inferences to be drawn regarding the speed of information transfer, they provide little information on the nature of interhemispheric interaction. It should be noted, however, that variations in the speed of information transfer may be responsible for variations in the quality of information transfer. Thus, excessively fast or slow information transfer may interfere with ongoing processing. The remaining sections focus on the nature of interhemispheric interaction.

The forebrain commissures have been implicated in the integration of a variety of information between the hemispheres. These various roles will be discussed hierarchically, from interhemispheric interaction for simple processes such as binding together stimulus attributes, to those involved in more complex, higher level processes, such as the dynamic allocation of attentional resources.

Role of the CC in Binding Together Stimulus Attributes

Although primary visual callosal fibers were thought to be mainly involved in representation of the visual midline and midline stereopsis in the cat (Berlucchi, 1972), recent work by Engel, König, Kreiter, and Singer (1991) in cats suggests that these neurons also may play a role in "binding stimulus features across the midline of the visual field" (p. 1177). Previously, Gray and Singer (1989) discovered neurons in cat primary visual cortex that show oscillatory firing patterns at frequencies of 40–60 Hz. These patterns showed synchronization across orientation columns in primary visual cortex and were sensitive to stimulus features including contour, orientation, and coherence of motion (see, e.g., Engel, König, Gray, & Singer, 1990; Gray, König, Engel, & Singer, 1989). These authors suggested that this synchronization plays a role in the binding of different features of an object, contributing to scene segmentation and figure–ground segregation.

Engel et al. (1991) investigated whether synchronization of these oscillatory patterns would occur between neurons in opposite hemispheres. They found that it did and that it resembled the oscillations between neurons in the same hemisphere. Between-hemisphere synchronization was disrupted by callosal section, showing that it was mediated by corticocortical, rather than subcortical, connections. Engel et al. recorded from cells whose receptive fields were close to the vertical meridian. Given the putative role of the synchronization of these neurons in *feature binding,* and the necessity of callosal integrity for cross-hemispheric synchronization, Engel et al. suggested that callosally mediated synchronization is involved in feature binding across the vertical midline. This work is controversial because it was conducted in anesthetized animals (see Crick & Koch, 1990, for a discussion) and because the studied frequency band is often contaminated by myogenic intrusions. It awaits replication in the awake, behaving animal with careful controls for muscle activity. However, these results are of interest, for they may generalize to other areas in which the sensory midline is represented.

We now turn to a consideration of information transfer in acallosal and split-brain patients. These studies suggest that some kinds of information can be transferred subcortically but also suggest that the nature of this information may differ qualitatively from information transferred cortically.

The Nature of Information Transfer in the Absence of the CC

Callosal Agenic Patients

Agenic patients do not show disconnection syndromes to nearly the same extent as split-brain patients. This is because they have had a lifetime to develop both behavioral and anatomical compensations (see Jeeves, 1990, for a discussion). However, deficits resulting from callosal agenesis are apparent in some situations (e.g., Jeeves, 1990; Lassonde, 1986). For instance, although acallosal patients can do many easy tactile and visual cross-hemisphere matching tasks, they are slower than healthy subjects (e.g., Lassonde, Sauerwein, McCabe, Laurencelle, & Geoffroy, 1988). This slowing is no doubt related to the longer IHTTs seen in these patients. The lack of accuracy differences in acallosal patients versus healthy subjects may relate to task difficulty. In many cases, control subjects perform at ceiling levels (e.g., Lassonde et al., 1988), making it difficult to detect group differences.

Acallosal patients represent a heterogeneous group who often have low IQs, as well as other neurological anomalies. The generalizability of these patients is therefore contingent on converging evidence from other sources.

Split-Brain Patients

Most of the earlier work with split-brain patients focused on what information could not be transferred. However, recent work, discussed shortly, has shown that limited information can be transferred without the CC.

Although these patients typically have low–normal IQs, the early series of patients tested by Sperry and associates had relatively little extracallosal structural brain damage (see J. J. Myers, 1984, for a discussion). The anterior commissure was sectioned in these earlier patients, which is important because visual information can be transferred via that commissure (Pandya & Seltzer, 1986). These patients have been tested for many years after their surgeries, allowing them to develop sophisticated compensatory strategies. They are adept at using internal or external cues to inform the unstimulated hemisphere. The use of these cues is known as *cross-cuing* (Gazzaniga & Hillyard, 1971). The studies discussed attempted to control for these strategies.

An important determinant of interhemispheric interaction in split-brain patients may be the age at surgery. Thus, Lassonde, Sauerwein, Chicoine, and Geoffroy (1991) found that patients who had undergone callosotomy in childhood were at first inferior but then improved to the level of their healthy peers on the intermanual conditions of tactile matching of objects and shapes, stereognosis, and touch localization, whereas patients operated on during adolescence showed the typical deficits. Lassonde et al. (1991) attributed these results to greater developmental plasticity in ipsilateral and subcortical pathways in younger patients. Both younger and older patients were slower than healthy subjects (Lassonde et al., 1988), again suggesting limits to compensation. Although this is an important issue, the patients in the studies described all underwent surgery in adulthood or adolescence.

Studies of partial callosotomy patients show that visual information is transferred via the splenium, whereas tactile and auditory information is transferred more anteriorly (e.g., Bentin, Sahar, & Moscovitch, 1984).

Few studies have investigated the functions of the anterior CC. Sidtis, Volpe, Holtzman, Wilson, and Gazzaniga (1981) studied patient J.W., who underwent a staged section of the CC. First, the posterior CC was sectioned. When tested in this initial period, J.W. was unable to name words presented in the LVF and could not make same–different judgments when stimuli were presented simultaneously to both visual hemifields. However, on questioning by the experimenter, J.W. made a wide range of associations to objects presented to the LVF, suggesting to the authors that his performance was governed by LH access (via the anterior CC) to a semantic association network in his RH. Thus, Sidtis et al. (1981) concluded that the anterior CC "plays a role in the interaction between cognitive rather than sensory systems in each hemisphere" (p. 345). Several weeks after his initial surgery, the rest of J.W.'s CC was sectioned, and he lost the ability to exchange semantic information, implying that transfer of semantic information was mediated by the anterior CC, as suggested by Sidtis et al.

Further support for this inference can be found in a study by Pozzilli et al. (1991). They tested 18 female patients with multiple sclerosis who had MRI-documented demyelinating lesions to the CC. The patients had smaller anterior and posterior callosal areas than did control subjects and had smaller callosal area compared with brain size than did control subjects. In these patients, verbal fluency correlated positively with anterior callosal area. This correlation was significantly higher than the correlation between verbal fluency and posterior callosal area. This finding is particularly interesting because verbal fluency is selectively affected by damage to the left frontal lobe (see, e.g., B. Milner, 1964), which is connected to the right frontal lobe by the anterior CC. The mechanism for this finding is unclear. A larger CC may facilitate information flow from right to left frontal areas allowing greater neurocognitive resources to be brought to the task. Alternatively, a larger callosum may inhibit disruptive input from the RH. A possible complication in the interpretation of these results is that the patients may have demyelination in left frontal regions that would underlie the observed effect. Pozzilli et al. noted that their patients showed no cortical abnormalities on MRI but presented no data.

The work of Sidtis et al. (1981) and Pozzilli et al. (1991) suggests an important role for the anterior CC in the transmission of semantic information between hemispheres and relatively little contribution by the posterior CC. This transmission process may be more complicated, as is suggested in the work of Hines, Chiu, McAdams, Bentler, and Lipcamon (1992). They performed a Principal Components Analysis on callosal area and measures of verbal fluency and found that verbal fluency was positively related to the component representing absolute posterior callosal area (primarily the splenium) in 28 healthy women. The correlation with the component representing anterior callosal area (including genu, "midregion" [body], and isthmus) was nonsignificant, and it was significantly lower than the correlation with posterior callosal area. The basis of these results is unclear, given the neuropsychological properties of verbal fluency and the topographic organization of the CC. They also found that the posterior callosal component correlated negatively with language lateralization. Given the unusual results obtained for verbal fluency, it seems best to suspend judgment on the Hines et al. findings until they are replicated. Together, however, these studies emphasize the point that the topography of callosal connections may have consequences for information transfer. Certain kinds of information can transfer in patients in whom all forebrain commissures have been sectioned. These are discussed next.

Trevarthen and Sperry (1973) showed that information about movement of objects in the LVF could be reported by split-brain patients. Patients could also integrate information about large, moving stimuli across the vertical midline. Trevarthen and Sperry argued that in this task information was processed not by the classical geniculostriate pathway but by the tectopulvinar pathway, a low-resolution visual system involved in movement perception. Similarly, Ramachandran, Cronin-Golomb, and Myers (1986) found that split-brain patients can report apparent motion across the midline.

Johnson (1984a, 1984b) found that split-brain patients could cross-compare and name bilaterally presented numbers, digits, colors, schematic faces, and patterns provided they came from limited sets. J. J. Myers and Sperry (1985) obtained similar results. They presented tactile or visual stimuli using the method of lateral limits (J. J. Myers & Sperry, 1982), a method that permits prolonged viewing of lateralized stimuli. Their results were comparable for both modalities. Patient N.G. could name numbers, digits, and line drawings presented to the LVF if she was given extensive preexposure to a set of two to three items. Similarly, patient L.B. could identify LVF stimuli only if they came from limited sets (digits 0–9, letters A–Z). J. J. Myers and Sperry (1985) speculated that L.B. did some mental rehearsal of digits or letters until the correct answer "popped out," on the basis of observations by Gazzaniga and Hillyard (1971) that he had used this strategy in other contexts. Importantly, J. J. Myers and Sperry (1985) ruled out RH mediation of language because (a) subjects could generate rhymes to the LVF stimuli (which only the LH can do; Levy & Trevarthen, 1977) and (b) when subjects were presented with LVF stimuli and were given the choice array in the RVF, they could identify the stimulus by pointing with the right hand.

Cronin-Golomb (1986) showed that split-brain patients could transfer simple and abstract conceptual information. The method of lateral limits was used in this study. Subjects were to decide which of three choice items presented to one visual hemifield matched a sample presented in the other hemifield. One condition required transfer of simple concepts (e.g., fish and ducks are aquatic animals), and the other required transfer of more complex concepts (e.g., guitars and palettes are both exemplars of art). Subjects were above chance on both tasks, and performance was similar to a condition in which both the sample and the choices were presented in the same hemifield.

Cronin-Golomb (1986) showed that what was transferred was not simply the name of, or a visual representation of, the stimulus. She concluded the former because the task used nonverbal stimuli and a nonverbal (pointing) response. When the left hand made the response, it was controlled primarily by the mute RH. Subjects were unable to name LVF stimuli. Thus, the task could not be mediated by verbal strategies under those conditions. She reached the latter conclusion because subjects sometimes chose nonidentical, but conceptually related, choice stimuli even when the identical stimulus was present in the choice array (experimental condition). This implies that subjects made use of conceptual similarity in making their decision, as they presumably would have always chosen the identical stimulus in the experimental condition if the transfer of a visual image of the stimulus was involved. When the alternatives were unrelated to the sample, they almost always chose the identical stimulus. Cronin-Golomb suggested that some semantic representation of the LVF stimulus is transferred, rather than an orthographic image of the stimulus itself.

A series of studies by Sergent (1987, 1990, 1991) further suggests that more complex information can be transferred in split-brain patients than had previously been thought. She found that they could make a variety of judgments about bilaterally presented information. For instance, they could determine whether two bilaterally presented digits summed to greater than 10, whether bilaterally presented arrows were aligned, whether bilaterally presented arrows pointed to each other, whether letter strings that straddled the midline formed a word (Sergent, 1987), which of two bilaterally presented digits was higher, and whether bilaterally presented digits were the same (Sergent, 1990).

Sergent (1991) also had split-brain patients make various visuospatial judgments regarding the position of a dot within a circle to either unilateral or bilateral (and redundant) stimuli. They completed four different choice RT tasks. She found that RTs to bilateral trials typically were equal to that of the superior visual hemifield and that accuracy for bilateral trials was higher than for either unilateral field, suggesting that some sort of information from the less skilled hemisphere aided but did not speed performance. In a second experiment, Sergent found that split-brain patients could decide whether bilaterally presented spatial stimuli shared similar orientation or size (Sergent, 1991). In this task, subjects could not determine whether the stimuli were identical on the two dimensions. Sergent (1991) found that performance under some conditions was better when the stimuli in the two visual hemifields were in the same rather than different positions. She suggested that although metric information was preserved in the representations on which the bihemispheric comparison was made, subjects were not explicitly aware of that information.

Recently, Corballis and Trudel (1993) suggested that Sergent's (1987) results for her more cognitively demanding tasks such as lexical decision, number summation, and line alignment might have been attributable to an underestimation of performance in the absence of the commissures. Sergent (1987) assumed that interhemispheric interaction would be required for subjects to perform at more than 50% accuracy on bilateral trials. However, Corballis and Trudel argued that if split-brain patients adopted a strategy such as positing that a number greater than 4 in the RVF would likely sum, in combination with unknown LVF information, to greater than 10, performance would be at about 80% without any interaction between hemispheres. If binary information was available from the RH (e.g., high or low number), performance would rise to about 95%. Corballis and Trudel had split-brain patients do a lexical decision task using a larger stimulus set than Sergent (1987) had used and found that their patients performed at chance. Only 1 of their 2 split-brain patients performed above chance on a line alignment task. Thus, in contrast to Sergent's (1987) claim that split-brain patients can integrate high-level information across the midline, Corballis and Trudel concluded that subcortical mechanisms can subserve perceptual integration of lower level, but not higher level, information. Similarly, Cronin-Golomb (1986) suggested that subcortical mechanisms are insufficient to transfer information for which one hemisphere is specialized such as higher order visuospatial or linguistic material.

Sergent's (1991) findings for spatial information contrast with her earlier finding that split-brain subjects could not provide information about the visual characteristics of, or the identity of, emotional or familiar faces presented in the LVF (Sergent, 1990). These findings suggest that subcortical commissures may be limited capacity channels that support the transfer of certain kinds of information. The nature of this transfer is discussed in the next section.

The Nature of Subcortical Information Transfer

In all of these studies, it seems that some sort of nonconscious information is transferred subcortically. This is not meant to imply that all information transferred via the CC is conscious. The information that is transferred subcortically may be nondeclarative in nature (see Squire, 1991). J. J. Myers and Sperry (1985) suggested that interhemispheric transfer in the split-brain patient is "largely connotative, contextual or orientational in nature and may not resemble typical commissural communications" (p. 258). It appears that lower level comparative information about size or orientation can be transferred in split-brain patients. It remains to be seen whether this kind of information transfers subcortically in healthy subjects. However, transfer of higher level information (e.g., identification of LVF stimuli from large sets, lexical decision across the midline) seems to depend on an intact CC. An example of the high degree to which the hemispheres can be unified without the CC comes from a study by Sperry, Zaidel, and Zaidel (1979).

Sperry et al. (1979) demonstrated that the RH of split-brain patients appeared to be self-conscious and socially aware. They presented 2 subjects (N.G. and L.B.) with stimuli having personal relevance (pictures of their children, spouses, famous historical figures, and of the subjects) randomly among neutral stimuli. Subjects viewed these stimuli unilaterally for as long as they chose using a z-lens, a contact lens that projects an image such that it is restricted to one visual hemifield at a time (Zaidel, 1975). Although patients could not name LVF stimuli, they made appropriate, and occasionally witty, reactions to them. For example, L.B. was asked to give a thumbs-up or thumbs-down appraisal of LVF stimuli. When he was presented with a picture of himself, he gave a thumbs-down sign, "but unlike other 'thumbs-down' signals, this one was accompanied by a wide, sheepish and (to all appearances) a self-conscious grin." (p. 163). On questioning, patients occasionally could identify LVF stimuli. Subjects seemed to have a sense of what they saw and, using the questions as clues, could identify the stimuli.

Summary

Despite the limitations on information transfer in split-brain patients, certain kinds of material can be transferred without the forebrain commissures. Split-brain patients can identify numbers and letters projected to the mute RH and can integrate conceptual and low-level visuospatial information across the midline. However, the CC appears to be necessary for the transfer of higher level information (e.g., between-hemifield line alignment and lexical decision), and complex pattern information (e.g., visual characteristics of, or identify of, facial stimuli presented to the LVF). Identity information also seems to be transferred only when it comes from sets of limited size. In addition, although between-field comparisons of stimuli could be made along one visuospatial dimension at a time in split-brain patients, such comparisons could not be made across two dimensions at a time.

These latter findings show that there are limits to how much and what type of information can be transferred subcortically. A general issue that should be kept in mind is that the studies discussed previously were conducted long after the patient's surgery, allowing for the development of compensatory strategies. The data are, however, important, in that they suggest that significant information can be transferred without the CC, presumably via subcortical commissures. These studies underscore the heterogeneity of interhemispheric interaction from cortical to subcortical levels. The apparent necessity of callosal involvement in stimulus identification and cross-integration of complex information suggests that the CC may be involved in transfers of higher level (more complex) information. This implies that in healthy subjects the CC is brought into play in more complex tasks, a point that is discussed in the next section.

Advantages to Interhemispheric Interaction

Many researchers have investigated the nature of interhemispheric interaction in healthy subjects. In general, they have focused on examining whether and when there is an advantage of inter- over intrahemispheric processing. Most studies have asked subjects to make within- versus between-hemisphere comparisons of stimuli. However, many early studies suffered from methodological flaws that call their findings into question. These studies confounded variables such as reading habits, processing load, and stimulus location with distinctions of inter- versus intrahemispheric processing (see Banich & Belger, 1990, for a discussion). Recent studies, especially by Banich's and Liederman's groups, have addressed these problems.

Banich and Belger (1990) showed that when confounding variables are controlled, consistent within- or between-field advantages are found depending on task demands. In one experiment, subjects were presented with three digits and a central fixation letter. Two digits were above fixation, one in either visual hemifield. The other digit was below fixation in either hemifield. Subjects were to respond with a buttonpress if the bottom digit matched either of the top two digits, which never matched. Half of the matches were with the top digit in the same hemifield, and half were with the top digit in the opposite hemifield. They found a within-field RT advantage on this task. Subjects also showed a within-field advantage on a task in which they were asked whether a bottom letter matched either of the top two letters, suggesting that Banich and Belger's results generalized to at least one other class of stimuli (i.e., letters).

In another experiment, the same arrangement was used, but the type of decision was varied. Subjects were asked whether a lowercase bottom letter was the same letter as one of the top two uppercase letters. On this task, RTs were significantly longer than for the first task, and there was a between-field advantage. Between-field advantages also were found on tasks in which subjects determined whether (a) the sum of two of three digits was greater than 10 and (b) a given digit was less than the other two. These tasks were more difficult than the digit-matching task, and both produced between-field advantages. Recently, Belger and Banich (1992) found that increasing the number of stimuli on their physical identity task from three to five also led to between-field advantages. Adding additional inputs did not increase further the between-field advantage on the name identity task. Sereno and Kosslyn (1991) also showed an increased benefit to interhemispheric processing as task difficulty increased.

This benefit is not ubiquitous, however. Belger (1993; Belger & Banich, 1994) found that on a rhyming task (which only the LH can do in the majority of right-handers), there was no between-hemisphere advantage, despite high task difficulty. These data suggested to Belger that between-hemisphere advantages are only obtained on difficult tasks for which a dispersal of processing load is possible. However, in most cases, both hemispheres have some competence for a task.

Liederman's group (Liederman, Merola, & Martinez, 1985; Merola & Liederman, 1985, 1990) took a somewhat different perspective, stressing the benefit to dividing conflicting tasks between hemispheres. Liederman et al. presented subjects with two words to either the same (unilateral) or opposite (bilateral) visual hemifields. The words belonged to one of four semantic categories. Subjects were to decide whether the categories of the two words matched. Liederman et al. found that the bilateral condition was as fast as the faster of the two individual unilateral conditions (RVF) and faster than their average but that this pattern only occurred early in a trial sequence. The accuracy of bilateral trials was higher than the average of the unilateral conditions throughout the task, but it was only higher than the better unilateral condition at the beginning of the experiment. For both accuracy and RT, performance on unilateral, but not bilateral, trials improved with practice. Increases in unilateral performance across blocks might have occurred because the task became easier over blocks. Bilateral trials might have been at their ceiling, meaning that this learning effect for unilateral trials would eliminate the bilateral advantage.

Merola and Liederman (1990) systematically examined the issue of task difficulty. In their basic task, subjects were presented with a set of four letters, half of which were upright. They referred to the identification of upright versus inverted letters as conflicting tasks. On unilateral trials, all four letters were in one visual hemifield; on bilateral trials, each hemifield contained a vertically arranged pair of letters. Furthermore, on half the trials, pairs of letters were either both upright or both inverted (separated condition), whereas on the other half, one member of each pair was inverted (unseparated condition). The unseparated trials were included as a control to determine whether there would be a between-hemisphere advantage to division of the absolute number of inputs when the stimuli were presented so that each hemisphere had to do conflicting tasks (i.e., inverted and upright letter identification).

In a first experiment, there was an accuracy advantage for bilateral over unilateral trials. This effect held, however, only for the separated condition. This suggests that it was important that the two hemispheres performed conflicting tasks separately. Bilateral, but not unilateral, trials were more accurate under the separated than unseparated condition.

Merola and Liederman (1990) made their task easier by reducing the processing load (only two letters were used in this condition). There could be no unseparated condition in this easier condition. Thus, in a direct comparison of the two- and four-letter conditions, only the separated condition was evaluated. In the two-letter condition, there was a nonsignificant trend for bilateral trials to be more accurate than unilateral trials. However, for the four-letter condition there was a significant bilateral advantage, revealing that the benefit to interhemispheric processing increased under more demanding conditions. When task difficulty was increased by adding a visual mask 40 ms after stimulus offset, there was a significant bilateral advantage under both two- and four-letter conditions. Clearly, the benefit of interhemispheric processing increased with increasing task difficulty, as Banich and Belger (1990) had found.

Norman, Jeeves, Milne, and Ludwig (1992) tested subjects on a task in which they had to indicate whether two arrays of dots had the same or different spatial arrangement. Task complexity was manipulated by varying the number of dots in the array. They found that the size of the bilateral RT advantage increased only for "same" responses and that it increased only relative to RVF trials. Bilateral trials for "same" responses were faster than unilateral LVF trials, but the size of this RT advantage did not increase with task difficulty. For accuracy measures, bilateral performance increased relative to both unilateral RVF and LVF trials, although, again, this pattern held only for "same" responses. This finding seems to contradict those discussed earlier, in that the bilateral advantage increased with task difficulty only for "same" trials. However, the "different" condition is conceptually more difficult, requiring an exhaustive search of the arrays to detect a difference. The Norman et al. data suggest a speed–accuracy tradeoff, as "different" trials were slower, but more accurate, than "same" trials. Thus, it is difficult to evaluate differences between "same" and "different" conditions because of the speed–accuracy tradeoff. In summary, however, the data suggest that interhemispheric processing is more beneficial at higher levels of task difficulty. This benefit may increase in childhood in parallel with development of the CC.

Developmental Issues

Merola and Liederman (1985) used the same task as used by Merola and Liederman (1990) and found that an accuracy advantage for the bilateral condition was not apparent in 10-year-olds but was present in 12- and 14-year-olds. Merola and Liederman (1985) suggested that "as the brain develops, processing that is occurring in one hemisphere may be better *shielded* [italics added] from processing occurring in the other hemisphere" (p. 1193). They interpreted this finding as evidence that the benefit to dividing conflicting processing between hemispheres followed a developmental time course similar to that of the CC. Liederman, Merola, and Hoffman (1986) followed a subset of these subjects and found that almost all of the 10-year-olds showed a bilateral advantage 2 years later and that almost all subjects who had shown a bilateral advantage retained it 2 years later. These studies suggest that the bilateral advantage develops in parallel with the CC.

Interhemispheric Inhibition and Excitation

J. M. Clarke, Lufkin, and Zaidel (1993) proposed that an interhemispheric inhibitory mechanism operates particularly on tasks exclusively specialized to one hemisphere (e.g., dichotic listening). On these tasks, a larger callosum would inhibit processing in the specialized hemisphere due to transmission of disruptive processing by the nonspecialized hemisphere. Thus, their group predicts that better performance in the specialized hemisphere on such tasks should be correlated with smaller callosal areas.

In an MRI study, J. M. Clarke et al. (in press; see also J. M. Clarke & Zaidel, 1993) examined relations among areal measures of the CC and performance on a verbal dichotic listening task in 60 healthy subjects. They found a right ear advantage for the identification of nonsense syllables that was stronger for right-handers than left-handers. Performance on this task is thought to be dependent entirely on the LH, as split-brain patients show an almost complete suppression of left-ear performance (B. Milner, Taylor, & Sperry, 1968; Sparks & Geschwind, 1968).

In right-handers, right-ear performance was negatively correlated with total CC area and with the area of the anterior third of the CC. Similar correlations were obtained for overall performance. However, there was a sex difference in the pattern of correlations, such that men (left-handers and right-handers combined) showed significant negative correlations between right-ear performance and all CC regions except the posterior midbody, whereas women showed no significant correlations. These data were not reported by sex *and* handedness, so it is unclear whether the correlations with anterior regions held for right-handers of both sexes. It would be parsimonious, then, to discuss only predictions about correlations of right-ear performance with total CC area, with the caveat that there may be Sex × Handedness differences.

J. M. Clarke et al. (1993) suggested that these data are consistent with their inhibitory model. The basis for this inference is that right-ear items do not require callosal relay in a dichotic listening task. Thus, they argued, the negative correlations for the right-ear must be due to RH inhibition. This interpretation implies that split-brain patients should have better right-ear performance than control subjects, which they found. However, J. M. Clarke et al. (Table 3) also reported that correlations between callosal area and left-ear performance were in the same direction as those for right-ear performance, with no significant difference between them. Moreover, ear asymmetry scores were uncorrelated with callosal measures. This raises a question about their interpretation of the data, particularly the degree to which callosal differences are related to overall performance across ears, versus right-ear performance specifically. Nonetheless, the results are interesting.

It seems unlikely, a priori, that the RH would inhibit the specialized LH on a dichotic listening task. However, as noted earlier, J. M. Clarke et al. (1993) found enhanced right-ear performance in split-brain patients, consistent with their argument of callosal inhibition by the RH in healthy subjects. A larger CC may permit the transmission of disruptive control signals leading to reductions in LH performance.

An alternative interpretation, however, is that with larger CCs, excitatory signals that are sent from the RH appear to be inhibitory because they disrupt ongoing LH processing, in the same way that certain groups of dyslexics show abnormally fast, and presumably disruptive, transmission of information from the RH to the LH (Davidson et al., 1990). This idea could be tested by obtaining IHTT information from the same subjects in whom MRI measures and dichotic listening data have been obtained and is an example of how IHTT may have implications for more complex interhemispheric interaction.

J. M. Clarke et al. (1993) and others (e.g., Cook, 1984; Denenberg, 1984) have stressed the role of the CC in inhibiting information flow between the hemispheres. For instance, Cook (1984, 1986) developed an elaborate and complex model of homotopic interhemispheric inhibition that, at its present state of development, does not have a substantial body of empirical support. However, the facilitative functions of the CC have been recognized as well (see, e.g., Levy, 1985). Evidence of this role comes from findings that (a) split-brain subjects have problems distributing attention bilaterally (see *Selective Attention*); (b) the CC is necessary for many kinds of information transfer; (c) regional cerebral metabolism is highly and positively correlated between homologous brain sites in humans (e.g., Horwitz, Duara, & Rapoport, 1984); (d) interhemispheric EEG coherence (a measure of the covariance of activity for given EEG frequencies) is reduced during sleep in infant acallosal patients compared with healthy infants (Kuks, Vos, & O'Brien, 1987); and (e) commissurotomy prevents the spread of epileptic seizures. Clearly, the heterogeneity of callosal connections allows for both inhibitory and excitatory influences.

Interhemispheric excitation and inhibition might best be viewed from spatial and temporal perspectives. The spatial and temporal relations between behavior and callosal anatomy are only beginning to be understood. Studies examining relations between regional callosal anatomy and behavior have been conducted by a few investigators described previously (e.g., J. M. Clarke et al., 1993; Hines et al., 1992). These data do not address the question of the temporal aspects of interhemispheric interaction; inhibitory and excitatory influences may vary over milliseconds. Thus, although providing useful structural information, studies that examine relations between CC anatomy and task performance are limited in that excitatory and inhibitory effects that occur over short time periods are not reflected in the measures. Behavioral and EP methods can be used to examine these temporal relations.

Summary

Studies on healthy subjects suggest that the benefit to interhemispheric processing increases with task difficulty. The CC also may be involved in interhemispheric inhibition under some circumstances. However, the basis of this inhibition is unclear, because it is found only as correlations between performance and callosal size. The negative correlations mean that a bigger CC does not invariably predict better performance. Additional research is needed that examines the conjoint influence of callosal size and callosal speed on measures of task performance.

Role of the CC in High-Level Attentional Functions

Attention

Selective attention. Levy et al. (1972) presented split-brain patients with lateralized stimuli for brief durations. These *chimeric figures* consisted of the left half of one stimulus joined at the vertical midline with the right half of another stimulus. In this way, each half of the chimeric figure was projected to a different visual hemifield. Patients noticed no abnormality in the stimulus, whereas healthy subjects did. The patients seemed to effect a visual completion of the object in the attended hemifield. Performance varied with task demands, as patients typically named only the word that corresponded to the RVF half-stimulus and pointed, with either hand, only to the alternative that matched the LVF half-stimulus. These results suggested to Levy et al. that split-brain patients could not allocate attention normally when stimuli were presented in both visual hemifields. There was a completion of the stimulus in the field contralateral to the hemisphere controlling processing, with a suppression of information in the unattended hemifield. The material in the unattended field could, however, be brought to consciousness on trials in which the ongoing response mode (e.g., pointing) was interrupted, with the request to respond in the opposite mode (e.g., naming). Similarly, split-brain patients show almost complete suppression of left-ear performance in verbal dichotic listening tasks. These data suggest a larger than normal asymmetry of attention in split-brain patients.

Sustained attention. Split-brain patients also show deficits in vigilance. Dimond (1976) found that whereas patients with partial commissurotomy (anterior two thirds of the CC and anterior commissure cut) could maintain nearly perfect visual monitoring for up to 30 min, complete split-brain patients showed defective performance 10 min into the vigil and showed gaps of awareness during the task. Ellenberg and Sperry (1979) also showed that although split-brain patients were not impaired on monotonous sorting tasks, they were markedly impaired on a tactile vigilance task compared with healthy subjects. These results suggest that the CC plays a crucial role in the maintenance of normal sustained attention (see the discussion in Levy, 1985).[5]

This role of the CC in attention has been supported in a recent study (Rueckert, Sorensen, & Levy, 1994) of healthy children aged 6–10 years. Rueckert et al. constructed an index of tachistoscopic interhemispheric facilitation (TIF) from a task in which subjects had to decide whether two arrows differed. The arrows were presented either in the same or opposite hemifields. The TIF consisted of the advantage for between- over within-hemisphere RTs relative to within-hemisphere RTs. Subjects were divided into high and low TIF groups by median

---

[5] Split-brain patients may have an advantage for certain aspects of attention. Luck, Hillyard, Mangun, and Gazzaniga (1989) found that split-brain patients were superior to healthy subjects on the bilateral condition of a visual search task.

split. They also tested these children on a vigilance task that required them to sustain their attention in the presence of little external stimulation. This was achieved by presenting stimuli at interstimulus intervals (ISIs) varying from 2 to 10 s and requiring a response to each. No response-irrelevant stimuli were presented, thereby limiting the amount of external stimulation, especially at longer ISIs. RTs were faster for subjects with high than with low TIF scores only at longer ISIs, suggesting to the authors that in healthy subjects the CC is involved in the same kind of attentional functions as are impaired in split-brain patients.

Divided attention. Other data also suggest selective attention deficits in split-brain patients. For instance, Kreuter, Kinsbourne, and Trevarthen (1972) found that split-brain patients showed marked deficits, compared with healthy subjects, on concurrent verbal and tapping tasks. Wale and Geffen (1989) also found that split-brain patients showed attentional deficits. They presented dichotic word pairs in which one word was spoken by a male and the other by a female. In the focused condition, subjects made a unimanual response to targets in one voice, whereas in the divided attention condition, they responded to targets in either voice. Patients performed worse than control subjects under both conditions, and responded more often to distractor and unattended items, suggesting that both divided and focused attention were disrupted in this sample.

In summary, the findings we have discussed suggest deficits in selective, sustained, and divided and focused attention among split-brain patients. Data from children suggest that as interhemispheric interaction improves, so does sustained attention, consistent with the split-brain data. It may be that in healthy brains, attentional resources are shared between the hemispheres, whereas this does not happen in split-brain patients.[6] Commissurotomy may reduce the resources available for a given task, leading to decrements in performance, especially on tasks that demand attention (e.g., Levy, 1985).

Neural bases of attentional effects. Deficits in attention in split-brain patients may arise from a failure to maintain bilateral cerebral arousal. This implies that the CC may play a key role in maintaining a positive feedback loop between the hemispheres that sustains bilateral arousal (Levy, 1985; Trevarthen, 1974). Arousal in this context is being used in the sense that Pribram and McGuiness (1975) proposed: a readiness to incorporate sensory information. The role of the CC in the maintenance of bilateral arousal may be one reason interhemispheric interaction is more beneficial on complex tasks (as hypothesized by Levy, 1985) and why split-brain patients cannot transfer certain kinds of higher level information.[7] This may be so for two reasons: (a) The overall level of arousal may be higher with an intact CC, thereby permitting more resources for task performance, and (b) the presence of the CC allows for processing to be distributed between differently specialized hemispheres. Individual differences in the degree of interhemispheric connectivity may serve to increment or decrement the overall level of arousal and may permit better sharing of processing resources between hemispheres.

Support for this idea comes from Watson, Valenstein, Day, and Heilman's (1984) finding that unilateral neglect in monkeys with lesions restricted to one hemisphere worsened following callosal section, suggesting that the CC mediates mutually facilitative or compensatory interactions between hemispheres, which benefits attentional function. Bremer's (1958) data also support this notion. He tested anesthetized cats and showed that when a sensitizing volley of callosal impulses arrived at a sensory area, that area was more responsive to subsequent ipsilateral thalamo–cortical input. This facilitation of arousal may be especially important as task difficulty increases, possibly explaining the increasing benefit to bihemispheric processing in healthy subjects as tasks become more difficult.

Tucker and Williamson (1984) proposed that arousal processes are mediated by the RH, and other data (see Levy et al., 1990, for a discussion) suggest that this kind of attentional control is mediated by right parietal regions. This region has been implicated in metacontrol processes, which are involved in the dynamic allocation of attention in response to task demands.

Metacontrol and the CC

As was noted earlier, the Levy et al. (1972) data support the idea of metacontrol by showing that the less skilled hemisphere can dominate processing. Levy et al. tested split-brain patients on a task in which left–right composite, three-element stimuli consisting of squares and Xs were presented. As noted previously, patients did not see these stimuli as peculiar. When subjects were to point to the pattern that matched what they saw, which each hemisphere can do, they consistently chose the LVF pattern. However, subjects were more accurate when they made verbal responses (with the LH) than when they made pointing responses. Thus, the RH dominated performance despite its lower capacity on the task (Levy, 1974). Levy (1985) concluded that the

> depletion of higher control that occurs with division of the corpus callosum not only reduces perceptual awareness for one half of space but often does so in a maladaptive fashion, so that the more capable hemisphere is not employed in cognitive processing. (p. 24)

Split-brain patients also show dissociations between the hemisphere controlling performance and the strategy of match-

---

[6] Although Holtzman and Gazzaniga (1982) claimed to have obtained evidence that attentional resources can be pooled in split-brain patients on the basis of visual dual-task performance in patient V.P., J. J. Myers (1984) noted that this patient had left hemisphere damage at around age 2 years, as well as an intact anterior commissure. Brain damage at that age generally causes reorganization of cerebral function. Thus, V.P. might have had both an atypical brain organization and the ability to transfer visual information cortically via the anterior commissure. This result awaits replication.

[7] As noted earlier, Pribram and McGuiness (1975) also proposed an *activation* system that is involved in motor readiness. Some of the attentional deficits observed in split-brain patients may be due to disruption of the activation system. The relation of activation processes to performance in healthy subjects could be tested by examining the effects of motor readiness on the benefit to interhemispheric interaction. Whether manipulations that influence arousal systems are separable from those that involve activation systems remains to be tested.

ing, again suggesting that the less skilled hemisphere can dominate performance. Levy and Trevarthen (1976) asked split-brain patients to match lateralized stimuli to pictures in free vision on the basis of either appearance or function. Thus, if a picture of a cake was presented, under appearance instructions the subject would match it to a picture of a hat, whereas under functional instructions, the subject would match it to a knife and fork. On each trial, a left–right chimeric stimulus was presented tachistoscopically, and subjects were to make matches under either functional, appearance, or ambiguous instructions. In general, function instructions elicited functional matches to the RVF stimulus. Appearance instructions typically elicited appearance matches to the LVF stimulus. Under ambiguous instructions, subjects made appearance matches to LVF stimuli and function matches to RVF stimuli. However, there were significant dissociations between the controlling hemisphere and the strategy of matching in 3 of 4 patients. One patient responded to the RVF stimulus on trials with functional instructions and to the LVF stimulus on trials with appearance instructions, but he almost always matched on the basis of appearance, regardless of condition (i.e., functional, appearance, or ambiguous instructions). This subject aroused the task-appropriate hemisphere,[8] but failed to make functional matches when instructed to do so. Another patient switched strategies appropriately but tended to perform matches with the LH (i.e., always matched to the RVF stimulus); thus, he used the less skilled hemisphere for appearance matches. In summary, these studies suggest that metacontrol is a process whose disruption can be observed following section of the forebrain commissures, such that patients often use the less skilled hemisphere to perform a task. As we shall see, the metacontrol system may function through the selective allocation of attentional resources depending on task demands.

A considerable body of data (e.g., Heilman & Van den Abell, 1979; Posner, Walker, Friedrich, & Rafal, 1984) suggests that the right parietal lobe may serve as a neural substrate for a metacontrol system. This evidence demonstrates a critical role for the right parietal lobe in distributing attentional resources bilaterally in response to sensory input to either visual hemifield.

From these data, Levy et al. (1990) predicted that presenting a stimulus to the LVF (i.e., initially to the RH) should improve performance on the next trial of a verbal task regardless of stimulus laterality. This prediction was confirmed in three separate experiments in which subjects were to identify lateralized nonsense syllables. Levy et al. termed this pattern of results the *prefield effect.*

This effect varies with task demands, suggesting to Luh (1990) that it is not simply an alerting response. Luh (1990) found that when subjects were given either bilateral redundant or central syllables, in addition to LVF and RVF syllables, LVF trials improved only the performance of subsequent trials to the RVF. However, because these findings have not yet been replicated, some caution is warranted.

These data provide tentative support for the notion that some sort of metacontrol mechanism has a neural substrate in right posterior regions. It can then be asked how this system exerts its effects over task-relevant regions. Levy and Trevarthen (1976) suggested that it functions by recruiting ipsilateral arousal via facilitative corticofugal inputs into the ascending reticular activating system (Morruzzi & Magoun, 1949). They also suggested that the CC increases the degree to which attentional resources are shared between hemispheres. Task-relevant regions of the RH can be recruited via association fibers, whereas task-relevant regions of the LH could be recruited via the CC. No prediction is made here regarding the locus within the CC of interhemispheric transfer of attentional resources. However, given the pattern of convergence between, and similarity of, heterotopic and associational connections (discussed in Kennedy et al., 1991), heterotopic fibers may play a key role. A general problem with this model is the lack of an adequate account of how the right posterior region "knows" where to direct arousal. A more parsimonious account may rely only on the interaction between the alerting function of stimuli delivered initially to the RH and the pattern of asymmetrical activation induced by the task.

The findings discussed earlier imply that insults to the integrity of the CC should impair metacontrol, especially for tasks that are specialized to the LH. This is consistent with the impairments of metacontrol observed in split-brain patients. It also would be interesting to examine metacontrol processes in populations in which interhemispheric interaction may be abnormal (e.g., certain populations of dyslexics).

Another prediction is that selective damage to association fibers in the RH should selectively impair metacontrol as it affects that hemisphere. Thus, lesions to RH fiber tracts that originate in the parietal lobe may impair metacontrol within the RH. Also, reductions in the correlations of positron emission tomography and EEG activity between right parietal and other regions may be accompanied by decreases in metacontrol. These hypotheses could be examined using the Levy et al. (1990) paradigm.

There are other important metacontrol hypotheses. For instance, Hellige and colleagues (e.g., Hellige, 1987, 1993; Hellige, Jonsson, & Michimata, 1988; Hellige, Taylor, & Eng, 1989) emphasized the finding in split-brain patients that one or the other hemisphere dominates performance on lateralized tasks. Hellige's group indexed metacontrol by comparing performance on centrally presented visual field (CVF) or bilaterally redundant visual field (BVF) trials to performance of the two unilateral visual hemifields. If one hemisphere is exerting control, the logic goes, performance on BVF or CVF trials should resemble performance by that hemisphere. Hellige and colleagues found this pattern on a variety of tasks.[9]

---

[8] The phrase *task-appropriate hemisphere* is not meant to indicate an absolute difference in skill. Thus, both hemispheres can do matching by appearance and function, but the left hemisphere is superior for function matches and the right hemisphere is superior for appearance matches.

[9] Luh and Levy (1994) advocated performing multiple correlational analyses, in addition to the analyses on means used by Hellige's group, to determine the basis of performance on bilaterally redundant visual field (BVF) or centrally presented visual field (CVF) trials. Luh and Levy found that both unilateral fields contributed significantly to BVF and CVF performance on the same task used by Hellige, Taylor, and Eng (1989). Banich and Karol (1992) noted additional difficulties in the interpretation of BVF trials.

A general issue that must be addressed is that the relation between arousal and performance can be nonlinear (e.g., Stennett, 1957). Thus, the initial arousal level of a particular hemispheric region must be known before determining whether further increases in arousal would be beneficial or detrimental to performance. Variability of findings in this area could be due to differences in regional arousal that are attributable to the hemispheres, tasks, and individuals studied. Therefore, another significant research direction would involve studies in which several levels of arousal are varied in the same subjects. It would be particularly important to complement behavioral indexes of arousal with physiological ones.

Summary

Split-brain patients show deficits in selective, sustained, divided, and focused attention. These deficits may be due to a reduction in between-hemisphere facilitation such that commissurotomy disrupts a positive feedback loop that maintains bilateral cerebral arousal. It may be that as task difficulty increases, these attentional resources are called on to a greater degree. Metacontrol processes, which are most observable in split-brain patients, may play an important role in distributing arousal to task-relevant regions in healthy subjects. This could explain the benefits to interhemispheric interaction in healthy subjects as task complexity is increased, as well as the failure in split-brain patients to transfer certain kinds of high-level information.

Conclusions

The CC plays the dominant role in interhemispheric interaction. It is the largest bundle of fibers in the brain and appears late in both evolution and development, suggesting that it subserves high-level integrative functions. Recent anatomical evidence has highlighted the significance of heterotopic callosal axons, whereas it was once assumed that only homotopic fibers were present. Individual differences in CC anatomy suggest further avenues of research because the functional significance of these effects is unknown.

Measures of interhemispheric transfer time provide insight into the temporal dynamics of callosal function. There may be temporal limits on aspects of interhemispheric interaction that involve the CC, and IHTTs that fall outside of this range may interfere with cortical processing. Research is critically needed that combines structural information about the CC from magnetic resonance imaging, temporal information on interhemispheric transfer from behavioral and/or EP measures of IHTT, and performance indexes for tasks that require interhemispheric interaction, all obtained on the same subjects. To our knowledge, no study has combined data from all of these sources, although the methods are now readily available.

The studies on IHTT that were reviewed also underscore the notion that transfer time may not be a unidimensional measure and that different measures of IHTT may be mediated by different regions of the CC and therefore may proceed at different rates. These findings imply that different types of information may be transferred at different speeds, with the same input often leading to several transfers prior to response execution. Thus, the topographic and cytological variation in the CC may have important implications for IHTT.

Subcortical commissures can transfer some aspects of information (e.g., comparative information), but the CC is required for transfers of certain kinds of higher level information (e.g., LVF stimulus identity, between-hemisphere lexical decision). Thus, bihemispheric processing may be especially beneficial under difficult task conditions that demand attentional resources in greater degree (as hypothesized by Levy, 1985). This also is suggested by studies in healthy subjects showing that bihemispheric processing becomes more beneficial with increasing task demands and by studies in split-brain patients showing that attentional allocation is compromised with callosal section. Information transfer takes longer without the CC, suggesting that subcortical pathways are less efficient than cortical ones. This efficiency may be at a premium when task complexity reaches a certain level.

Thus, researchers have evidence that the timing of interhemispheric processes is highly intricate and that there may be a particular advantage to callosal involvement in more complex tasks. Unfortunately, although relations between CC anatomy and behavioral indexes of interhemispheric interaction have been examined, the temporal aspects of this interaction have been largely ignored. Studies suggesting that the CC has primarily inhibitory influences could especially benefit from a temporal analysis of interhemispheric interaction. These could be examined with behavioral and EP studies.

All of the evidence suggests that the CC plays a significant role in high-level attentional and cognitive functions. The most important issues that need to be addressed in future research include (a) an understanding of the functional significance of individual differences in callosal anatomy, (b) a temporal analysis of interhemispheric interactions, (c) a further delineation of the conditions under which interhemispheric interaction affects cognitive processing, and (d) additional investigation into the role of the CC in attentional systems. Research in the past 30 years has provided investigators with a start on these questions. We expect that research during the next 30 years will provide even more information on these issues, especially because the anatomy is now better understood and methods exist for precisely assessing both the structure and function of the CC in the intact person.

References

Aboitiz, F., Scheibel, A. B., Fisher, R. S., & Zaidel, E. (1992a). Fiber composition of the human corpus callosum. *Brain Research, 598,* 143–153.

Aboitiz, F., Scheibel, A. B., Fisher, R. S., & Zaidel, E. (1992b). Individual differences in brain asymmetries and fiber composition in the human corpus callosum. *Brain Research, 598,* 154–161.

Aboitiz, F., Scheibel, A. B., & Zaidel, E. (1992). Morphometry of the Sylvian fissure and the corpus callosum, with emphasis on sex differences. *Brain, 115,* 1521–1541.

Akelaitis, A. J. (1941). Studies on the corpus callosum: II. The higher visual functions in each homonymous field following complete section of the corpus callosum. *Archives of Neurology and Psychiatry, 45,* 788–796.

Amadeo, M., Roemer, R. A., & Shagass, C. (1977). Can callosal speed of transmission be inferred from verbal reaction times? *Biological Psychiatry, 12,* 289–297.

Annett, M. (1967). The binomial distribution of right, mixed, and left handedness. *Quarterly Journal of Experimental Psychology, 19,* 327–333.

Banich, M. T., & Belger, A. (1990). Interhemispheric interaction: How do the hemispheres divide and conquer a task. *Cortex, 26,* 77–94.

Banich, M. T., Goering, S., Stolar, N., & Belger, A. (1990). Interhemispheric processing in left- and right-handers. *International Journal of Neuroscience, 54,* 197–208.

Banich, M. T., & Karol, D. L. (1992). The sum of the parts does not equal the whole: Evidence from bihemispheric processing. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 763–784.

Bashore, T. R. (1981). Vocal and manual reaction time estimates of interhemispheric interaction time. *Psychological Bulletin, 89,* 352–368.

Belger, A. (1993). *Influences of hemispheric specialization and interaction on task performance.* Unpublished doctoral dissertation, University of Illinois at Urbana-Champaign.

Belger, A., & Banich, M. T. (1992). Interhemispheric interaction affected by computational complexity. *Neuropsychologia, 30,* 923–929.

Belger, A., & Banich, M. T. (1994, February). *Task demands limit interhemispheric facilitation.* Paper presented at the 22nd Annual Meeting of the International Neuropsychological Society, Cincinnati, OH.

Benson, D. F., & Zaidel, E. (Eds.). (1985). *The dual brain: Hemispheric specialization in humans.* New York: Guilford Press.

Bentin, S., Sahar, A., & Moscovitch, M. (1984). Intermanual information transfer in patients with lesions in the trunk of the corpus callosum. *Neuropsychologia, 22,* 601–611.

Berlucchi, G. (1972). Anatomical and physiological aspects of visual functions of corpus callosum. *Brain Research, 37,* 371–392.

Berlucchi, G., Crea, F., Di Stefano, M., & Tassinari, G. (1977). Influence of spatial stimulus–response compatibility on reaction time of ipsilateral and contralateral hand to lateralized light stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 3,* 505–517.

Berlucchi, G., Heron, W., Hyman, R., Rizzolatti, G., & Umiltà, C. (1971). Simple reaction times of ipsilateral and contralateral hand to lateralized visual stimuli. *Brain, 94,* 419–430.

Berlucchi, G., Tassinari, G., & Antonini, A. (1986). The organization of the callosal connections according to Sperry's principle of supplemental complementarity. In F. Leporé, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 171–188). New York: Alan R. Liss.

Braun, C. M. J. (1992). Estimation of interhemispheric dynamics from simple unimanual reaction time to extrafoveal stimuli. *Neuropsychology Review, 3,* 321–364.

Braun, C. M. J., & Daigneault, S. (1994). Effects of a right hemifield advantage on crossed-uncrossed differentials in simple reaction time: Toward a new model of interhemispheric relay. *Acta Psychologica, 85,* 91–98.

Bremer, F. (1958). Physiology of the corpus callosum. In H. C. Solomon, S. Cobb, & W. Penfield (Eds.), *The brain and human behavior* (pp. 424–448). Baltimore: Williams & Wilkins.

Brizzolara, D., Casalini, C., Cioni, G., & Ferretti, G. (1992, July). *Callosal agenesis and intellectual development: A variation within the norm?* Paper presented at a satellite workshop on the corpus callosum and interhemispheric transfer, XXV International Congress of Psychology, Priorij Corsendonk, Belgium.

Brown, W. S., Larson, E. B., & Jeeves, M. A. (1994). Directional asymmetries in interhemispheric transmission time: Evidence from visual evoked potentials. *Neuropsychologia, 32,* 439–448.

Brysbaert, M. (1992, July). *Behavioral estimates of interhemispheric transfer time: What are we measuring?* Paper presented at a workshop on the corpus callosum and interhemispheric transfer, Priorij Corsendonk, Belgium. Satellite Workshop of the XXV International Congress of Psychology.

Burton, A., Pepperell, S., & Stredwick, J. (1991). Interhemispheric transfer in males and females. *Cortex, 27,* 425–429.

Byne, W., Bleier, R., & Houston, L. (1988). Variations in human corpus callosum do not predict gender: A study using magnetic resonance imaging. *Behavioral Neuroscience, 102,* 222–227.

Clarke, J. M., Lufkin, R. B., & Zaidel, E. (1993). Corpus callosum morphometry and dichotic listening performance: Individual differences in functional interhemispheric inhibition? *Neuropsychologia, 31,* 547–557.

Clarke, J. M., & Zaidel, E. (1989). Simple reaction times to lateralized light flashes: Varieties of interhemispheric communication routes. *Brain, 112,* 849–870.

Clarke, J. M., & Zaidel, E. (in press). Anatomical-behavioral relationships: Corpus callosum morphometry and hemispheric specialization. *Behavioural Brain Research.*

Clarke, S., & Miklossy, J. (1990). Occipital cortex in man: Organization of callosal connections, related myelo- and cytoarchitecture, and putative boundaries of functional visual areas. *Journal of Comparative Neurology, 298,* 188–214.

Cook, N. D. (1984). Homotopic callosal inhibition. *Brain and Language, 23,* 116–125.

Cook, N. D. (1986). *The brain code.* New York: Methuen.

Corballis, M. C., & Trudel, C. I. (1993). Role the forebrain commissures in interhemispheric integration. *Neuropsychology, 7,* 306–324.

Cowell, P. E., Allen, L. S., Zalatimo, N. S., & Denenberg, V. H. (1992). A developmental study of sex and age interactions in the human corpus callosum. *Developmental Brain Research, 66,* 187–192.

Crick, F., & Koch, C. (1990). Some reflections on visual awareness. *Cold Spring Harbor Symposia on Quantitative Biology, 55,* 953–962.

Cronin-Golomb, A. (1986). Subcortical transfer of cognitive information in subjects with complete forebrain commissurotomy. *Cortex, 22,* 499–519.

Curtis, H. J. (1940). Intercortical connections of corpus callosum as indicated by evoked potentials. *Journal of Neurophysiology, 3,* 407–413.

Davidson, R. J. (1984). Affect, cognition, and hemispheric specialization. In C. E. Izard, J. Kagan, & R. Zajonc (Eds.), *Emotions, cognition and behavior* (pp. 320–365). Cambridge, England: Cambridge University Press.

Davidson, R. J., Chapman, J. P., Chapman, L. P., & Henriques, J. B. (1990). Asymmetrical brain electrical activity discriminates between psychometrically-matched verbal and spatial cognitive tasks. *Psychophysiology, 27,* 528–543.

Davidson, R. J., Leslie, S. C., & Saron, C. (1990). Reaction time measures of interhemispheric transfer time in reading disabled and normal children. *Neuropsychologia, 28,* 471–485.

Davidson, R. J., & Saron, C. D. (1992). Evoked potential measures of interhemispheric transfer time in reading disabled and normal boys. *Developmental Neuropsychology, 8,* 261–277.

Davidson, R. J., Schaffer, C. E., & Saron, C. (1985). Effects of lateralized presentations of faces on self-reports of emotion and EEG asymmetry in depressed and non-depressed subjects. *Psychophysiology, 22,* 353–364.

Degos, J. D., Gray, F., Louarn, F., Ansquer, J. C., Poirier, J., & Barbizet, J. (1987). Posterior callosal infarction: Clinicopathological correlations. *Brain, 110,* 1155–1171.

De Lacoste-Utamsing, C., & Holloway, R. L. (1982). Sexual dimorphism in the human corpus callosum. *Science, 216,* 1431–1432.

Demeter, S., Ringo, J. L., & Doty, R. W. (1988). Morphometric analysis of the human corpus callosum and anterior commissure. *Human Neurobiology, 6,* 219–226.

Denenberg, V. H. (1984). Behavioral asymmetry. In N. Geschwind & A. M. Galaburda (Eds.), *Cerebral dominance: The biological foundations* (pp. 114–133). Cambridge, MA: Harvard University Press.

Denenberg, V. H., Kertesz, A., & Cowell, P. E. (1991). A factor analysis of the human's corpus callosum. *Brain Research, 548,* 126–132.

Dimond, S. J. (1976). Depletion of attentional capacity after total commissurotomy in man. *Brain, 99,* 347–356.

Duara, R., Kushch, A., Gross-Glenn, K., Barker, W. W., Jallad, B., Pascal, S., Loewenstein, D. A., Sheldon, J., Rabin, M., Levin, M., & Lubs, H. (1991). Neuroanatomic differences between dyslexic and normal readers on magnetic resonance imaging scans. *Neurology, 48,* 410–416.

Dufresne, A., Lapierre, D., Chouinard, M.-J., Daigneault, S., & Braun, C. M. J. (1993). Are human callosi bigger and faster in men than women? Behavioral evidence. *Journal of Clinical and Experimental Neuropsychology, 15,* 34 [Abstract].

Dunkerley, G. B. (1975). *A basic atlas of the human nervous system.* Philadelphia: F. A. Davis.

Ellenberg, L., & Sperry, R. W. (1979). Capacity for holding sustained attention following commissurotomy. *Cortex, 15,* 421–438.

Engel, A. K., König, P., Gray, C. M., & Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: Inter-columnar interaction as determined by cross-correlation analysis. *European Journal of Neuroscience, 2,* 588–606.

Engel, A. K., König, P., Kreiter, A. K., & Singer, W. (1991). Interhemispheric synchronization of oscillatory neuronal responses in cat visual cortex. *Science, 252,* 1177–1179.

Filbey, R. A., & Gazzaniga, M. S. (1969). Splitting the normal brain with reaction time. *Psychonomic Science, 17,* 335–336.

Gazzaniga, M. S., Bogen, J. E., & Sperry, R. W. (1962). Some functional effects of sectioning the cerebral commissures in man. *Proceedings of the National Academy of Science, 48,* 1765–1769.

Gazzaniga, M. S., & Hillyard, S. A. (1971). Language and speech capacity of the right hemisphere. *Neuropsychologia, 9,* 273–280.

Geffen, G. M., Jones, D. L., & Geffen, L. B. (in press). Interhemispheric control of manual motor activity. *Behavioural Brain Research.*

Geschwind, N., & Kaplan, E. (1962). A human deconnection syndrome. *Neurology, 12,* 675–685.

Geschwind, N., & Levitsky, W. (1968). Human brain: Left-right asymmetries in temporal speech region. *Science, 161,* 186–187.

Gray, C. M., König, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature, 338,* 334–337.

Gray, C. M., & Singer, W. (1989). Stimulus-specific neuronal oscillations in orientation columns of the cat visual cortex. *Proceedings of the National Academy of Science, U.S.A., 86,* 1698–1702.

Gur, R. E., Gur, R. C., Sussman, N. M., O'Connor, M. J., & Vey, M. M. (1984). Hemispheric control of the writing hand: The effect of callosotomy in a left-hander. *Neurology, 34,* 904–908.

Habib, M., Gayraud, D., Oliva, A., Regis, J., Salamon, G., & Khalil, R. (1991). Effects of handedness and sex on the morphology of the corpus callosum: A study with brain magnetic resonance imaging. *Brain and Cognition, 16,* 41–61.

Harris, L. J. (1992). Left-handedness. In F. Boller & J. Grafman (Series Eds.) & I. Rapin & S. Segalowitz (Vol. Eds.), *Handbook of neuropsychology: Vol. 6. Child neuropsychology* (pp. 145–208). New York: Elsevier.

Harris, L. J. (in press). The corpus callosum and hemispheric communication: An historical survey of theory and research. In F. Kitterle (Ed.), *Hemispheric communication: Mechanisms and models.* Hillsdale, NJ: Erlbaum.

Hedreen, J. C., & Yin, T. C. T. (1981). Homotopic and heterotopic callosal afferents of caudal inferior parietal lobule in *Macaca mulatta. Journal of Comparative Neurology, 197,* 605–621.

Heilman, K. M., & Van Den Abell, T. (1979). Right hemispheric dominance for mediating cerebral activation. *Neuropsychologia, 17,* 315–321.

Hellige, J. B. (1987). Interhemispheric interaction: Models, paradigms, and recent findings. In D. Ottoson (Ed.), *Duality and unity of the brain* (pp. 454–466). London: Macmillan.

Hellige, J. B. (1993). Unity of thought and action: Variations of interaction between and left and right cerebral hemispheres. *Current Directions in Psychological Science, 2,* 21–25.

Hellige, J. B., Jonsson, J. E., & Michimata, C. (1988). Processing from LVF, RVF, and BILATERAL presentations: Metacontrol and interhemispheric interaction. *Brain and Cognition, 7,* 39–53.

Hellige, J. B., Taylor, A. K., & Eng, T. L. (1989). Interhemispheric interaction when both hemispheres have access to the same stimulus information. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 711–722.

Hines, M., Chiu, L., McAdams, L. A., Bentler, P. M., & Lipcamon, L. (1992). Cognition and the corpus callosum: Verbal fluency, visuospatial ability, and language lateralization related to midsagittal surface areas of callosal subregions. *Behavioral Neuroscience, 106,* 3–14.

Holtzman, J. D., & Gazzaniga, M. S. (1982). Dual task interactions due exclusively to limits in processing resources. *Science, 218,* 1325–1327.

Hoppe, K. D. (1977). Split brains and psychoanalysis. *Psychoanalytic Quarterly, 46,* 220–244.

Horwitz, B., Duara, R., & Rapoport, S. I. (1984). Intercorrelations of glucose metabolic rates between brain regions: Application to healthy males in a state of reduced sensory input. *Journal of Cerebral Blood Flow and Metabolism, 4,* 484–499.

Huttenlocher, P. R. (1979). Synaptic density in human frontal cortex—Developmental changes and effects of aging. *Brain Research, 163,* 195–205.

Innocenti, G. (1986). General organization of callosal connections in the cerebral cortex. In E. G. Jones & A. Peters (Eds.), *Cerebral cortex: Vol. 5. Sensory-motor areas and aspects of cortical connectivity* (pp. 291–354). New York: Plenum.

Jackson, J. H. (1958). Evolution and dissolution of the nervous system. In J. Taylor (Ed.), *Selected writings of John Hughlings Jackson* (Vol. 2, pp. 45–75). New York: Basic Books. (Original work published 1884).

Jeeves, M. A. (1969). A comparison of interhemispheric transmission times in acallosals and normals. *Psychonomic Science, 16,* 245–246.

Jeeves, M. A. (1990). Agenesis of the corpus callosum. In F. Boller & J. Grafman (Series Eds.) & R. Nebes (Vol. Ed.), *Handbook of neuropsychology:* Vol. 4. *The Commissurotomized Brain* (pp. 99–114). New York: Elsevier.

Johnson, L. E. (1984a). Vocal responses to left visual field stimuli following forebrain commissurotomy. *Neuropsychologia, 22,* 153–166.

Johnson, L. E. (1984b). Bilateral visual cross-integration by human forebrain commissurotomy subjects. *Neuropsychologia, 22,* 167–175.

Kennedy, H., Meisserel, C., & Dehay, C. (1991). Callosal pathways and their compliancy to general rules governing the organization of corticocortical connectivity. In B. Dreher & S. R. Robinson (Eds.), *Neuroanatomy of the visual pathways and their development* (pp. 324–359). Boca Raton, FL: Chemical Rubber Company.

Kertesz, A., Polk, M., Howell, J., & Black, S. E. (1987). Cerebral dominance, sex, and callosal size in MRI. *Neurology, 37,* 1385–1388.

Kinsbourne, M., & Fisher, M. (1971). Latency of uncrossed and crossed reaction in callosal agenesis. *Neuropsychologia, 9,* 471–473.

Kreuter, C., Kinsbourne, M., & Trevarthen, C. (1972). Are deconnected cerebral hemispheres independent channels? A preliminary study of the effect of unilateral loading on bilateral finger tapping. *Neuropsychologia, 10,* 453–461.

Kuks, J. B. M., Vos, J. E., & O'Brien, M. J. (1987). Coherence patterns of the infant sleep EEG in absence of the corpus callosum. *Electroencephalography and Clinical Neurophysiology, 66,* 8–14.

LaMantia, A.-S., & Rakic, P. (1990a). Cytological and quantitative characteristics of four cerebral commissures in the rhesus monkey. *Journal of Comparative Neurology, 291,* 520–537.

LaMantia, A.-S., & Rakic, P. (1990b). Axon overproduction and elimination in the corpus callosum of the developing rhesus monkey. *Journal of Neuroscience, 10,* 2156–2175.

Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffries (Ed.), *Cerebral mechanisms in behavior: The Hixon symposium.* (pp. 112–146). New York: Wiley.

Lassonde, M. (1986). The facilitatory influence of the corpus callosum on intrahemispheric processing. In F. Leporé, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 385–401). New York: Alan R. Liss.

Lassonde, M., Sauerwein, H., McCabe, N., Laurencelle, L., & Geoffroy, G. (1988). Extent and limits of cerebral adjustment to early section or congenital absence of the corpus callosum. *Behavioural Brain Research, 30,* 165–181.

Lassonde, M., Sauerwein, H., Chicoine, A.-J., & Geoffroy, G. (1991). Absence of disconnexion syndrome in callosal agenesis and early callosotomy: Brain reorganization or lack of structural specificity during ontogeny? *Neuropsychologia, 29,* 481–495.

Levy, J. (1974). Psychobiological implications of bilateral asymmetry. In S. J. Dimond & J. G. Beaumont (Eds.), *Hemisphere function of the human brain* (pp. 121–138). New York: Wiley.

Levy, J. (1984). A review, analysis, and some new data on hand-posture distributions in left-handers. *Brain and Cognition, 3,* 105–127.

Levy, J. (1985). Interhemispheric collaboration: Single-mindedness in the asymmetric brain. In C. T. Best (Ed.), *Hemispheric function and collaboration in the child* (pp. 11–31). San Diego, CA: Academic Press.

Levy, J. (1986). Two hemispheres are better than one: Manual regulation in some left-handers. In F. Leporé, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 511–521). New York: Alan R. Liss.

Levy, J., & Reid, M. (1976). Variations in writing posture and cerebral organization. *Science, 194,* 337–339.

Levy, J., & Reid, M. (1978). Variations in cerebral organization as a function of handedness, hand posture in writing, and sex. *Journal of Experimental Psychology: General, 107,* 119–144.

Levy, J., & Trevarthen, C. (1976). Metacontrol of hemispheric function in human split-brain patients. *Journal of Experimental Psychology: Human Perception and Performance, 2,* 299–312.

Levy, J., & Trevarthen, C. (1977). Perceptual, semantic and phonetic aspects of elementary language processes in split-brain patients. *Brain, 100,* 105–118.

Levy, J., Trevarthen, C., & Sperry, R. W. (1972). Perception of bilateral chimeric figures following hemispheric deconnexion. *Brain, 95,* 61–78.

Levy, J., & Wagner, N. (1984). Handwriting posture, visuomotor integration, and lateralized reaction-time parameters. *Human Neurobiology, 3,* 157–161.

Levy, J., Wagner, N., & Luh, K. (1990). The previous visual field: Effects of lateralization and response accuracy on current performance. *Neuropsychologia, 28,* 1239–1249.

Liederman, J., Merola, J. L., & Hoffman, C. (1986). Longitudinal data indicate that hemispheric independence increases during early adolescence. *Developmental Neuropsychology, 2,* 183–201.

Liederman, J., Merola, J., & Martinez, S. (1985). Interhemispheric collaboration in response to simultaneous bilateral input. *Neuropsychologia, 23,* 673–683.

Lines, C. R., Rugg, M. D., & Milner, A. D. (1984). The effect of stimulus intensity on visual evoked potential estimates of interhemispheric transmission time. *Experimental Brain Research, 57,* 89–98.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature, 342,* 543–545.

Luh, K. E. (1990). *Right hemisphere dominance in the metacontrol of cerebral arousal.* Unpublished doctoral dissertation, University of Michigan, Ann Arbor.

Luh, K. E., & Levy, J. (1994). *Interhemispheric cooperation: Left is left and right is right, but sometimes the twain shall meet.* Manuscript submitted for publication.

Machiyama, Y., Watanabe, Y., & Machiyama, R. (1987). Neuroanatomical studies of the corpus callosum in schizophrenia: Evidence of aberrent interhemispheric fibre connections. In R. Takahashi, P. Flor-Henry, & S. Niwa (Eds.), *Cerebral Dynamics: Laterality and psychopathology* (pp. 411–412). New York: Elsevier.

Mangun, G. R., Luck, S. J., Gazzaniga, M. S., & Hillyard, S. A. (1991, November). *Electrophysiological measures of interhemispheric transfer of visual information: Studies in split-brain patients.* Paper presented at the annual meeting of the Society for Neuroscience, New Orleans, LA.

Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia, 29,* 1163–1177.

McCulloch, W. (1949). Mechanisms for the spread of epileptic activation in the brain. *Electroencephalography and Clinical Neurophysiology, 1,* 19–24.

McKeever, W. F., Gill, K. M., & VanDeventer, A. D. (1975). Letter versus dot stimuli as tools for "splitting the normal brain with reaction time." *Quarterly Journal of Experimental Psychology, 27,* 363–373.

McKeever, W. F., & Hoff, A. L. (1979). Evidence of a possible isolation of left hemisphere visual and motor areas in sinistrals employing an inverted handwriting posture. *Neuropsychologia, 17,* 445–455.

Merola, J. L., & Liederman, J. (1985). Developmental changes in hemispheric independence. *Child Development, 56,* 1184–1194.

Merola, J. L., & Liederman, J. (1990). The effect of task difficulty upon the extent to which performance benefits from between-hemisphere division of inputs. *International Journal of Neuroscience, 54,* 35–44.

Milner, A. D., Jeeves, M. A., Silver, P. H., Lines, C. R., & Wilson, J. (1985). Reaction times to lateralized visual stimuli in callosal agenesis: Stimulus and response factors. *Neurophyschologia, 23,* 323–331.

Milner, A. D., & Lines, C. R. (1982). Interhemispheric pathways in the simple reaction time to lateralized light flash. *Neuropsychologia, 20,* 171–179.

Milner, B. (1964). Some effects of frontal lobectomy in man. In J. M. Warren & K. Akert (Eds.), *The frontal granular cortex and behavior* (pp. 313–324). New York: McGraw-Hill.

Milner, B., Taylor, L., & Sperry, R. W. (1968). Lateralized suppression of dichotically presented digits after commissural section in man. *Science, 161,* 184–186.

Morruzzi, G., & Magoun, H. W. (1949). Brain stem reticular formation and activation of the EEG. *Electroencephalography and Clinical Neurophysiology, 1,* 455–473.

Moscovitch, M., & Smith, L. C. (1979). Differences in neural organization between individuals with inverted and noninverted handwriting postures. *Science, 205,* 710–713.

Myers, J. J. (1984). Right hemisphere language: Science or fiction? *American Psychologist, 39,* 315–320.

Myers, J. J., & Sperry, R. W. (1982). A simple technique for lateralizing visual input that allows prolonged viewing. *Behavior Research Methods and Instrumentation, 14,* 305–308.

Myers, J. J., & Sperry, R. W. (1985). Interhemispheric communication after section of the forebrain commissures. *Cortex, 21,* 249–260.

Myers, R. E., & Sperry, R. W. (1953). Interocular transfer of a visual form discrimination habit in cats after section of the optic chiasma and corpus callosum. *Anatomical Record, 115,* 351–352 [Abstract].

Norman, W. D., Jeeves, M. A., Milne, A., & Ludwig, T. (1992). Hemispheric interactions: The bilateral advantage and task difficulty. *Cortex, 28,* 623–642.

Pandya, D. N., & Seltzer, B. (1986). The topography of commissural fibers. In F. Leporé, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 47–73). New York: Alan R. Liss.

Poffenberger, A. T. (1912). Reaction time to retinal stimulation with special reference to the time lost in conduction through nerve centers. *Archives of Psychology, 21,* 1–73.

Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. D. (1984). Effects of parietal lobe injury on covert orienting of attention. *Journal of Neuroscience, 4,* 1863–1874.

Pozzilli, C., Bastianello, S., Padovani, A., Passaflume, D., Millefiorini, E., Bozzao, L., & Fieschi, C. (1991). Anterior corpus callosum atrophy and verbal fluency in multiple sclerosis. *Cortex, 27,* 441–445.

Preilowski, B. (1990). Intermanual transfer, interhemispheric interaction, and handedness in man and monkeys. In C. Trevarthen (Ed.), *Brain circuits and functions of the mind: Essays in honor of Roger W. Sperry* (pp. 168–180). Cambridge, England: Cambridge University Press.

Pribram, K. H., & McGuiness, D. (1975). Arousal, activation, and effort in the control of attention. *Psychological Review, 82,* 116–149.

Rakic, P., & Goldman-Rakic, P. S. (1982). Development and modifiability of the cerebral cortex: Overview. *Neurosciences Research Program Bulletin, 20,* 433–438.

Rakic, P., & Yakovlev, P. I. (1968). Development of the corpus callosum and cavum septi in man. *Journal of Comparative Neurology, 132,* 45–72.

Ramachandran, V. S., Cronin-Golomb, A., & Myers, J. J. (1986). Perception of apparent motion by commissurotomy patients. *Nature, 320,* 358–359.

Reynolds, D. McQ., & Jeeves, M. A. (1974). Further studies of crossed and uncrossed pathway responding in callosal agenesis: Reply to Kinsbourne and Fisher. *Neuropsychologia, 12,* 287–290.

Risse, G. L., Gates, J., Lund, G., Maxwell, R., & Rubens, A. (1989). Interhemispheric transfer in patients with incomplete section of the corpus callosum: Anatomic verification with magnetic resonance imaging. *Archives of Neurology, 46,* 437–443.

Rueckert, L. M., Sorensen, L. G., & Levy, J. (1994). Callosal efficiency is related to sustained attention. *Neuropsychologia, 32,* 159–173.

Rugg, M. D., Lines, C. R., & Milner, A. D. (1984). Visual evoked potentials to lateralized visual stimuli and the measurement of interhemispheric transmission time. *Neuropsychologia, 22,* 215–225.

Rugg, M. D., Milner, A. D., & Lines, C. R. (1985). Visual evoked potentials to lateralised stimuli in two cases of callosal agenesis. *Journal of Neurology, Neurosurgery and Psychiatry, 48,* 367–373.

Salamy, A. (1978). Commissural transmission: Maturational changes in humans. *Science, 200,* 1409–1411.

Saron, C. D., & Davidson, R. J. (1989a). Reliability of evoked potential estimates of interhemispheric transfer time: Further studies. *Psychophysiology, 26,* S53 [Abstract].

Saron, C. D., & Davidson, R. J. (1989b). Visual evoked potential measures of interhemispheric transfer time in humans. *Behavioral Neuroscience, 103,* 1115–1138.

Sereno, A. B., & Kosslyn, S. M. (1991). Discrimination within and between hemifields: A new constraint on theories of attention. *Neuropsychologia, 29,* 659–675.

Sergent, J. (1987). A new look at the human split brain. *Brain, 110,* 1375–1392.

Sergent, J. (1990). Furtive incursions into bicameral minds: Integrative and coordinating role of subcortical structures. *Brain, 113,* 537–568.

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

Sergent, J., & Myers, J. J. (1985). Manual, blowing, and verbal simple reactions to lateralized flashes of light in commissurotomized patients. *Perception and Psychophysics, 37,* 571–578.

Sidtis, J. J., Volpe, B. T., Holtzman, J. D., Wilson, D. H., & Gazzaniga, M. S. (1981). Cognitive interaction after staged callosal section: Evidence for transfer of semantic activation. *Science, 212,* 344–346.

Sparks, R., & Geschwind, N. (1968). Dichotic listening in man after section of neocortical commissures. *Cortex, 4,* 3–16.

Sperry, R. W., Zaidel, E., & Zaidel, D. (1979). Self recognition and social awareness in the deconnected minor hemisphere. *Neuropsychologia, 17,* 153–166.

Squire, L. R. (1991). The medial temporal lobe memory system. *Science, 20,* 1380–1386.

Steinmetz, H., Jäncke, L., Kleinschmidt, A., Schlaug, G., Volkmann, J., & Huang, Y. (1992). Sex but no hand difference in the isthmus of the corpus callosum. *Neurology, 42,* 749–752.

Stennett, R. G. (1957). The relationship of performance level to level of arousal. *Journal of Experimental Psychology, 54,* 54–61.

St. John, R., Shields, C., Krahn, P., & Timney, B. (1987). The reliability of estimates of interhemispheric transmission times derived from unimanual and verbal response latencies. *Human Neurobiology, 6,* 195–202.

Swadlow, H. A., Geschwind, N., & Waxman, S. G. (1979). Commissural transmission in humans. *Science, 204,* 530–531.

Tomasch, J. (1954). Size, distribution, and number of fibres in the human corpus callosum. *Anatomical Record, 119,* 119–135.

Trevarthen, C. (1974). Functional relations of the disconnected hemispheres with the brain stem, and with each other: Monkey and man. In M. Kinsbourne & W. L. Smith (Eds.), *Hemispheric disconnection and cerebral function* (pp. 187–207). Springfield, IL: Charles C Thomas.

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

Tucker, D. M., & Williamson, B. A. (1984). Asymmetric neural control systems in human self-regulation. *Psychological Review, 91,* 185–215.

Van Essen, D. C., Newsome, W. T., & Bixby, J. L. (1982). The pattern of interhemispheric connections and its relationship to extrastriate visual areas in the macaque monkey. *Journal of Neuroscience, 2,* 265–283.

Wale, J., & Geffen, G. (1989). Focused and divided attention in each half of space with disconnected hemispheres. *Cortex, 25,* 33–45.

Watson, R. T., Valenstein, E., Day, A. L., & Heilman, K. M. (1984). The effect of corpus callosum lesions on unilateral neglect in monkeys. *Neurology, 34,* 812–815.

Whitteridge, D. (1965). Area 18 and the vertical meridian of the visual field. In E. G. Ettlinger (Ed.), *Functions of the corpus callosum* (pp. 115–120). Boston: Little, Brown.

Witelson, S. F. (1985). The brain connection: The corpus callosum is larger in left-handers. *Science, 229,* 665–668.

Witelson, S. F. (1989). Hand and sex differences in the isthmus and genu of the human corpus callosum: A postmortem morphological study. *Brain, 112,* 799–835.

Witelson, S. F. (1992). Cognitive neuroanatomy: A new era. *Neurology, 42,* 709–713.

Witelson, S. F., & Goldsmith, C. H. (1991). The relationship of hand preference to anatomy of the corpus callosum in men. *Brain Research, 545,* 175–182.

Witelson, S. F., & Nowakowski, R. S. (1991). Left out axons make men right: A hypothesis for the origin of handedness and functional asymmetry. *Neuropsychologia, 29,* 327–333.

Wood, F. B., Flowers, D. L., & Naylor, C. E. (1991). Cerebral laterality in functional neuroimaging. In F. L. Kitterle (Ed.), *Cerebral laterality: Theory and research* (pp. 103–115). Hillsdale, NJ: Erlbaum.

Yakovlev, P. I., & Lecours, A.-R. (1967). The myelogenetic cycles of regional maturation of the brain. In A. Minkowski (Ed.), *Regional development of the brain in early life* (pp. 3–65). Philadelphia: F. A. Davis.

Zaidel, E. (1975). A technique for presenting lateralized input with prolonged exposure. *Vision Research, 15,* 283–289.

Received January 5, 1993
Revision received January 7, 1994
Accepted January 17, 1994 ■

Low Publication Prices for APA Members and Affiliates

Keeping You Up-to-Date: All APA members (Fellows; Members; Associates, and Student Affiliates) receive–as part of their annual dues–subscriptions to the *American Psychologist* and *APA Monitor.*

High School Teacher and International Affiliates receive subscriptions to the *APA Monitor,* and they can subscribe to the *American Psychologist* at a significantly reduced rate.

In addition, all members and affiliates are eligible for savings of up to 60% (plus a journal credit) on all other APA journals, as well as significant discounts on subscriptions from cooperating societies and publishers (e.g., the American Association for Counseling and Development, Academic Press, and Human Sciences Press).

Essential Resources: APA members and affiliates receive special rates for purchases of APA books, including the *Publication Manual of the APA,* the *Master Lectures,* and *Journals in Psychology: A Resource Listing for Authors.*

Other Benefits of Membership: Membership in APA also provides eligibility for low-cost insurance plans covering life, income protection, office overhead, accident protection, health care, hospital indemnity, professional liability, research/academic professional liability, student/school liability, and student health.

For more information, write to American Psychological Association,
Membership Services, 750 First Street, NE, Washington, DC 20002-4242, USA