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The Role of the Corpus Callosum in Interhemispheric Transfer of Information: Excitation or Inhibition?

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The corpus callosum is the major neural pathway that connects homologous cortical areas of the two cerebral hemispheres. The nature of how that interhemispheric connection is manifested is the topic of this review; specifically, does the corpus callosum serve to communicate an inhibitory or excitatory influence on the contralateral hemisphere? Several studies take the position that the corpus callosum provides the pathway through which a hemisphere or cortical area can inhibit the other hemisphere or homologous cortical area in order to facilitate optimal functional capacity. Other studies suggest that the corpus callosum integrates information across cerebral hemispheres and thus serves an excitatory function in interhemispheric communication. This review examines these two contrasting theories of interhemispheric communication. Studies of callosotomies, callosal agenesis, language disorders, theories of lateralization and hemispheric asymmetry, and comparative research are critically considered. The available research, no matter how limited, primarily supports the notion that the corpus callosum serves a predominantly excitatory function. There is evidence, however, to support both theories and the possibility remains that the corpus callosum can serve both an inhibitory and excitatory influence on the contralateral hemisphere.

KEY WORDS: corpus callosum; interhemispheric communication; excitation; inhibition.

INTRODUCTION

The corpus callosum is the largest neural pathway that connects the two cerebral hemispheres in mammals. Consisting of between 200 and 800 million axon fibers (Banich, 1995a), the primary function of the corpus callosum is to provide a connection between homologous cortical areas. Exactly how that connection is functionally manifested is the topic of this review. Although most researchers believe that the corpus callosum plays an important role in the development of hemispheric asymmetry, the question remains as to whether the corpus callosum exerts an inhibitory or excitatory influence on interhemispheric communication. A number of studies suggest that the corpus callosum provides the pathway through which each hemisphere can inhibit the other in order for one function to predominate. Other studies suggest that the corpus callosum serves an excitatory function and integrates information from both cerebral hemispheres. This review examines what we know about the function of the corpus callosum through studies of callosotomies, callosal agenesis, language disorders, theories of lateralization and hemispheric asymmetry, and related comparative research.

The nature and function of the corpus callosum has long been of interest. Not only is it an evident structure that visibly connects the two hemispheres, but also alterations in this structure are frequently noted in psychiatric and developmental disorders. For example, abnormalities in the size of the corpus callosum have been found in patients diagnosed with schizophrenia, autism (Egaas et al., 1995), mental retardation (Schaefer and Bodensteiner, 1999), Down's syndrome (Wang et al., 1992), Attention Deficit Hyperactivity Disorder (Lyoo et al., 1996), developmental dyslexia (Duara et al., 1991; Hynd et al., 1995), and developmental language disorders (Preis et al., 2000). It is possible that abnormalities in cortical areas, found in all these disorders, might be related to abnormalities in the

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size of the corpus callosum. In fact, deviant asymmetry of cortical areas, possibly related to callosal abnormalities, has been found in developmental dyslexia (Geschwind and Galaburda, 1985; Hynd et al., 1995) and specific language impairment (Shafer et al., 2000). The wide range of disorders in which callosal abnormalities are found underscores the importance of understanding the basic nature of the development and function of the corpus callosum.

THE CORPUS CALLOSUM

Callosal fibers are first found in human embryos at 10–11 weeks of gestation, and by 12–13 weeks a rudimentary callosal plate can be seen (Gilles et al., 1983). The corpus callosum first enlarges caudally then develops rostrally. Myelination occurs relatively slowly over the lifespan, with the process completing in puberty (Hellige, 1993). Myelination progresses caudally to rostrally, much as the corpus callosum develops, from the splenium to the genu and rostrum (Hynd et al., 1995).

It is recognized that the corpus callosum provides a connection between homologous cortical areas (Hellige, 1993). Anterior areas of cortex are connected through more anterior pathways; the same holds true for posterior areas, etc. (Banich, 1995a). The most anterior portion of the callosum is the genu, which connects the prefrontal cortices on either hemisphere. The middle portions of the corpus callosum, connect motor and somatosensory regions. The caudal part of the body of the corpus callosum connects cortex from the temperoparietal-occipital junction, as do portions of the splenium, the most posterior section of the corpus callosum. The splenium also connects dorsal parietal and occipital regions (Banich, 1995a; Hellige, 1993) (Fig. 1).

There are two types of fibers in the corpus callosum. Large diameter fibers mediate sensory-motor coordination whereas small diameter fibers connect association areas. The small diameter fibers are more numerous and individual differences in callosal size have been shown to be a reflection of the small diametered type. It is these small diametered fibers that are thought to be important in maintaining the balance between excitation and inhibition in the cerebral hemispheres (Yazgan et al., 1995).

Many have assumed that the corpus callosum functions as a unitary body; this assumption, however, is not necessarily valid. Banich (1995a) suggests that "different types of information are sent over different sections of the corpus callosum" (p. 431) and concludes that the callosum is not a unitary body, but rather a collection of pathways with the ability to act independently. Distinct areas exist which vary depending on the cortical destination and the degree of myelination of the fibers. If "function follows form, then there are a variety of callosal functions" (Chiarello, 1995, p. 177) and a variety of ways in which interhemispheric communication can take place. These ideas are interesting and challenge the concept that the corpus callosum serves the sole function of "uniting" the cerebral hemispheres. Research exploring these concepts, however, is frought with challenges.

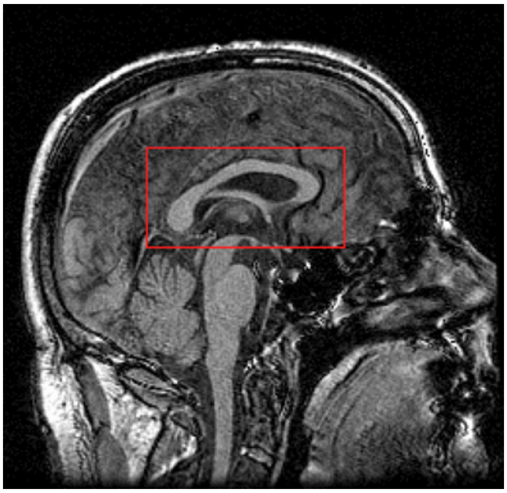

Fig. 1. A mid-sagittal slice of the brain. The area containing the corpus callosum, the large white C-shaped structure, is outlined.

Considerations Regarding Research on the Corpus Callosum

Examining the function of the corpus callosum requires consideration of some assumptions and methodological problems, as pointed out by Banich (1995a). It has been assumed in much of the literature that the size of the callosum correlates positively with the number of nerve fibers. Unfortunately, this is not necessarily true. A lack of correlation between callosal size and the number of fibers has been found in rats and rhesus monkeys and results for humans are ambiguous (Banich, 1995a). Thus, one cannot assume that a larger callosum necessarily indicates a greater number of nerve fibers. This finding greatly complicates drawing conclusions about how callosal size correlates to function. Does a larger callosum mean more interhemispheric connections, as is typically assumed? This assumption is not supported by research at this time. Most of the articles reviewed for this work, however, assume callosal size to be directly related to the number of interhemispheric connections. This is a limit of the literature in this field and therefore of this review of the literature. If possible, future research into the corpus callosum needs to utilize a more direct measure of connectivity other than callosal size, such as a measure of the number of nerve fibers.

It is also important to keep in mind that although the corpus callosum is the primary axonal pathway connecting the two cerebral hemispheres, subcortical commissures also exist. The anterior commissure connects the hemispheres at the lateral striatal ridge, the region of the amygdala, at 8–10 weeks' gestation (Gilles et al., 1983). At 10–11 weeks, a clear-cut hippocampal commissure is found. Studies of patients with commissurectomies have demonstrated that the integration of some aspects of spatial attention and emotional information can occur without cerebral commissures (Sperry et al., 1979), and it is presumed this transfer of information occurs with the subcortical commissures. Both of these structures develop before the corpus callosum, and likely exist as an interhemispheric pathway in both so-called "split-brain" and callosal agenesis patients. The existence of additional commissures in the brain is an important confound in these studies and an important aspect to consider when examining the role of the corpus callosum in interhemispheric transfer of information. Although the corpus callosum may mediate these commissures when intact, it is important to the validity of future studies to research the possible roles of subcortical commissures (Hellige, 1993).

Asymmetry

Research into the possible functionality of the corpus callosum is grounded in research on lateralization of function. The theories of callosal function outlined in this review are based on the idea that the two cerebral hemispheres are not identical either at an anatomic or functional level. The role of the corpus callosum in asymmetrical processing of information and possibly the development of anatomic asymmetries is the subject of this work. A brief discussion of what anatomic asymmetries exist is therefore warranted.

Anatomic Asymmetry

Asymmetry has been found in fossil skulls of early hominids (Corballis, 1983). LeMay (1984) found that a Neanderthal fossil skull showed asymmetry of the Sylvian fissure comparable to modern-day humans (Galaburda, 1995). The fossil skulls of Australopithecines, Homo habilis and Homo erectus have all shown asymmetry in the perisylvian cortex. In addition, right-handedness has been postulated in the early hominids based on evidence that their prey were killed by blows to their left side as if by right-handed attackers and that their tools were more worn on the right side (LeMay, 1984).

There is little doubt that anatomic asymmetries of the brain occur in modern humans and other animals (Galaburda, 1995). Although a great deal of individual variation occurs, certain asymmetries are consistently found in most human brains. These asymmetries are found at a gross morphological level and at a cellular level. For example, the right frontal lobe is typically larger than the left, whereas the left temporal lobe is typically larger than the right (Hellige, 1993). The right hemisphere has a greater level of myelination compared to the left hemisphere (Buono, 1997). It is in the relative sizes of certain brain structures, however, particularly those related to language, that most morphological asymmetries occur. These areas include the planum temporale, Sylvian fissure, and inferior frontal cortex, which contains Broca's area.

Broca's area is demonstrably bigger in the left hemisphere, although a great deal of individual variability exists (Galaburda, 1995). The Sylvian fissure, which borders this inferior frontal area, is more sharply curved upwards and longer in the left hemisphere (Hellige, 1993; LeMay, 1984). This allows for the larger temporal lobe in the left hemisphere. The bulk of language and lateralization research, however, has been focused on the planum temporale. In a seminal study, Geschwind and Levitsky (1968) reported their findings on the asymmetry of the planum temporale, an area that contains auditory association cortices and is thought to be very important in language. Of 100 postmortem brains, 65% of the sample showed a longer left planum temporale, 11% showed a longer right planum temporale, and the remaining 24% were symmetrical. These results were highly significant, replicated by numerous subsequent studies (Hynd et al., 1990; Larsen et al., 1990), and have led to much speculation and research on the role of this structure in language lateralization (Galaburda, 1995).

These anatomic asymmetries are relatively consistent across individuals and might provide the structural basis for the numerous functional differences in the hemispheres. It is important to remember, however, that the two hemispheres are much more the same than they are different. As Galaburda stated, "there appears to be no structure or chemical constituent that is present in one hemisphere and not the other" (Galaburda, 1995, p. 52).

Functional Asymmetry

Asymmetry at a structural level is expressed in asymmetries in function. Neurobiological asymmetries found in the language areas of the brain have been related to lateralization of language function in imaging studies (Larsen et al., 1990; Shaywitz et al., 1995), demonstrating that a connection between anatomic and functional asymmetries exist. Furthermore, Hughlings Jackson's notion that the left hemisphere is specialized for linguistic functions and the right hemisphere for processing perceptual information has been validated by split-brain studies and is now generally accepted by the scientific community (Hellige, 1993; Lassonde, 1986).

One of the most widely researched of these functional asymmetries is handedness. Humans are overwhelmingly right-handed, and there is little question that this preference is genetically determined (Lezak, 1995). Between 95.5 and 99.67% of right-handers have left hemisphere language representation (Lezak, 1995), and a much higher percentage of left-handed people display language dominance in the right hemisphere than right-handed people. In addition, despite considerable confusion in the literature due to methodological issues, it is reasonable to conclude that there is a slightly higher incidence of nonright handedness in disabled readers than the overall population (Beaton, 1985).

These two observations led to the theory that reading disabilities are in part due to incomplete cerebral dominance. If this is the case, the corpus callosum might play a role in the development of such incomplete dominance because hemispheric asymmetry develops in part as a result of interhemispheric connections (Hellige, 1993). The possible role of the corpus callosum on the development of both lateralization of function and possible anatomical correlates will be examined shortly.

Another example of functional asymmetry has been shown by the specialization of each hemisphere for certain auditory stimuli, as has been shown in studies using the dichotic listening task. In dichotic listening, competing auditory stimuli are presented to both ears simultaneously. When asked to repeat what they have heard, subjects with left-hemisphere language lateralization are more accurate in reporting verbal information presented to the right ear (Bryden, 1988). This right-ear advantage has been taken as evidence for the specialization of language to the left hemisphere. A left-ear advantage has been shown to exist for nonverbal sounds, such as music, suggesting that these sounds are more efficiently processed by the right hemisphere (Bryden, 1988).

Although it is widely recognized that anatomic and functional asymmetries exist, the question remains as to whether or not the corpus callosum contributes its own influence on the lateralization of function.

THE POSSIBLE FUNCTIONS OF THE CORPUS CALLOSUM

Historical Perspectives

Despite the fact that the corpus callosum is the largest fiber tract in the brain, its possible functions were not widely studied until recently (Chiarello, 1995). Uncertainty has surrounded the function of the corpus callosum since the nineteenth century, when psychiatrists and neurologists were debating the double-brain hypothesis, the notion that the two sides of the brain function independently. Supporters of this position believed that a unified consciousness was achieved through callosal connections. The case studies of that time, however, did not support this conclusion; patients afflicted by callosal lesions did not show any "split" in personality or consciousness (Chiarello, 1995). Researchers continued to question, however: if unified consciousness is not achieved via the largest bundle of fibers connecting the separate cerebral hemispheres, how is it achieved?

The discoveries of Dax and Broca concerning left hemisphere dominance for language caused other researchers to theorize that the left hemisphere was dominant for all functions. Hughlings Jackson referred to the left hemisphere as the "dominant" and "leading" one and the right hemisphere as "nondominant" and "minor" (Corballis, 1983). At this point in history, the degree and role of interhemispheric communication in cerebral dominance was largely unexplored.

The twentieth century saw the emergence of another theory of cerebral lateralization. Based on his finding from clinical studies that the left hemisphere is essential for voluntary motor movements on both sides of the body, Hugo Liepmann postulated that the corpus callosum served as the conduit through which the left hemisphere exerts control over the right hemisphere. Left brain domination had been theorized before, but Liepmann expanded the theory to include this new view of function of the corpus callosum. This view was not held by all researchers of the time, however. In fact, it was jokingly suggested a few decades later that the sole function of the corpus callosum was structural, namely to prevent the hemispheres from sagging (Lashley, 1929, as reported in Beaton, 1985).

The latter half of the twentieth century saw a reemergence of brain laterality research, driven in part by animal research and the practice of callosotomy (Harrington, 1995). In the 1950s and 1960s, Myers and Sperry demonstrated the crucial role of the corpus callosum in the transfer of information between hemispheres through animal studies (Myers and Sperry, 1953; Myers, 1960; Sperry, 1958; Sperry et al., 1956). Later, many epileptic patients

	Theory of Excitation	**Theory of Inhibition**
Corpus Callosum Size as Laterality Increases	Decrease	Increase

Fig. 2. Expected changes to corpus callosum size as the hemispheres becomes more lateralized according to the theories of inhibition and excitation.

were treated with callosotomy, or the severing of the corpus callosum. This procedure was done to prevent intractable seizures from spreading to the other hemisphere in the hopes that it would lessen the severity of the seizures. These "split-brain" patients have been extensively studied by Sperry and other researchers to determine the role of the corpus callosum in various cognitive tasks (for reviews of this literature see Gazzaniga, 2000; Sperry, 1974). Work with split-brain and intact monkeys also contributed to the notion that the corpus callosum is integral for interhemispheric transfer (Hellige, 1993).

Current Thought on Callosal Function

There is little question that the corpus callosum permits interhemispheric transfer of information, but the nature of how this occurs is under dispute. In the 1990s, the two contrasting theories of interhemispheric interaction were debated in the literature. Some believed the corpus callosum serves an excitatory function, integrating information across hemispheres; others postulated that the corpus callosum serves as an inhibitory pathway.

In discussing this issue, it is important to keep in mind the difference between inhibition at a neural level versus a functional level. Excitation at a neural level simply means that an increase in the firing rate of a neuron causes the neuron on which it synapses to increase in firing as well. Inhibition, conversely, occurs when an increase in the firing rate of one neuron causes the neuron that it synapses upon to decrease firing. These differences are primarily due to neurotransmitter and receptor differences. Inhibitory neural connections are much more common in the brain than excitatory connections due to the fact that GABA, the most common neurotransmitter in the brain, is almost exclusively inhibitory (Smock, 1999). Both inhibitory and excitatory messages have been demonstrated to travel through the corpus callosum (Lassonde, 1986).

Excitation versus inhibition is more difficult to ascertain at a functional level, but Hellige (1993) defines it with respect to the corpus callosum as "whether processing that involves specific regions of one hemisphere tends to activate or suppress processing in similar regions of the other hemisphere" (p. 173). It is important to understand that although connections between inhibition and excitation at the neural and functional level may exist, they are not mandatory. For example, a connection may excite a group of neurons that inhibit another region, causing an overall effect of inhibition. Thus, our interpretations between inhibition and excitation from the neural to the functional level must be cautious (Hellige, 1993). Unless otherwise specified, in this work we will be discussing inhibition and excitation at the functional level (Fig. 2).

The validity of these two theories is best explored by examining callosal size compared to functional and anatomic laterality. In the case of the theory of inhibition, if a larger corpus callosum can be expected to transfer more inhibition and functional laterality is accomplished by inhibiting the contralateral hemisphere, the size of the corpus callosum would be expected to increase as asymmetry increases (Yazgan et al., 1995). If the theory of excitation is correct, the size of the corpus callosum would be expected to decrease as laterality increased.

Theories of Inhibition

The theory that the corpus callosum inhibits activity between hemispheres has been postulated by a variety of researchers, including Cook (1984), and Kinsbourne (1975), in many different forms. All of these theories state that the corpus callosum aids in the development of hemispheric asymmetry by providing a pathway through which one hemisphere can inhibit the other to dominate a given function (Hellige, 1993; Lassonde, 1986) (Tables 1 and 2).

Cook outlined the homotopic inhibition theory in 1984. This theory postulates that the corpus callosum connects homologous areas of the cerebral hemispheres in an inhibitory manner, and those areas connect to neighboring areas in the cortex in a mutually inhibitory fashion

Table 1. Evidence Supporting the Theory of Inhibition

Study	Subjects	Method	Results
Banich and Belder (1990)	Normal human adults	Lexical-decision tasks	Each hemisphere processed the information independently
Clarke et al. (1993)	Normal human adults	Dichotic listening tasks, Magnetic Resonance Imaging	1. CC size unrelated to laterality 2. CC size negatively correlated with ear accuracy
Denenberg et al. (1986)	Rats	Severing of the corpus callosum	Resulted in an increase in muricide, showing the inhibition is mediated through the CC.
Dennis (1976)	Two congenitally acollosal patients, ages 14 and 21 years	Tactile discrimination and intermanual transfer tasks	Inhibitory action of the CC is essential during ontogeny.
Hynd et al. (1995)	Children with dyslexia and matched control subjects	Magnetic Resonance Imaging scans were obtained and correlated with diagnostic group	1. The genu of the CC was smaller in dyslexic children 2. Genu and splenium size were significantly correlated with reading achievement

(Cook, 1984). Hellige (1993) summarizes Cook's theory by stating:

> Adjacent areas within a hemisphere are connected in a mutually inhibitory manner, in something of a center-surround fashion. As a result, when a small cortical area in one hemisphere is inhibited (e.g., by callosal fibers activated by the homologous area in the opposite hemisphere), the immediately surrounding area becomes more active. Thus, the corpus callosum tends to produce mirror-image patterns of activation and inhibition in the two hemispheres. (p.174)

This view is contrasted with other more standard theories of commissural transfer of information, which suppose that activity in one hemisphere will be duplicated in the homologous area of the other hemisphere. In Cook's theory, however, activity in one hemisphere will reduce activity in the homologous area in the other hemisphere (Chiarello, 1995; Cook, 1984). Lateralization of function ensues from this inhibition, and Cook also theorizes that hemispheric asymmetry develops via callosal inhibition (Chiarello, 1995; Cook, 1984), which leads the two hemispheres to become dominant for complementary functions.

Kinsbourne (1975) proposed a slightly different theory for the purpose of the inhibitory function of the corpus callosum. In this view, activation in one

Table 2. Evidence Against the Theory of Inhibition

Study	Subjects	Method	Results
Chiarello et al. (1995)	Normal human adults: 192 college students	Prime-target stimulus onset asynchronies were used to obtain equivalent priming of subordinate meanings over visual fields	Initial right hemisphere activation of subordinate word meanings is not due to homotopic callosal inhibition
Olk and Hartje (2001)	Normal human adults: 20 female and 20 male college students	Lexical decision task with unilateral and bilateral stimulation and response with the right or left hand	Response time to visual stimulation in adults inconsistent with inhibition of callosal information
Watson et al. (1984)	Two stump-tailed mazaques	Ablation of the frontal arcuate gyrus alone or several months after CC transection	1. Neglect was significantly worse in subjects with a CC transection 2. The authors concluded that the cerebral hemispheres may be mutually excitatory or compensatory

hemisphere tends to cause a decrease in the activation of the other hemisphere, and this asymmetry of activation is mediated by the corpus callosum. The two hemispheres are in a constant mutually inhibitory relationship with each other. Also included in this theory is the notion that the corpus callosum serves as an "inhibitory barrier" between the hemispheres to prevent maladaptive cross talk between the hemispheres for which a given function is dominant (Kinsbourne, 1975, 1982; Kinsbourne and Hiscock, 1977).

Kinsbourne's ideas relate to another theory of interhemispheric processing - that of metacontrol. In metacontrol, information presented to both hemispheres is taken control of by one dominant hemisphere (Banich, 1995a). In language, for example, the dominant left hemisphere would exert an inhibitory influence on the nondominant right hemisphere so that the dominant hemisphere would control the processing. Metacontrol was theorized from studies of patients who had undergone callosotomies based on the observation that one hemisphere dominated responding, regardless of whether or not it was the hemisphere specialized for the task (Banich, 1995a).

Evidence Supporting the Theory of Inhibition

There is some evidence to support the theory of an inhibitory function of the corpus callosum. It is sometimes the case that the hemisphere that receives a stimulus carries out all the processes necessary to respond to it even with an intact callosum. In a series of lexical-decision tasks where the stimulus was presented to either but not both hemispheres, each hemisphere processed the information independently, including the final decision if the stimulus was a word or a nonword (Hellige, 1993). Banich and Belder's (1990) experiment demonstrated that the hemispheres divide processing for complex tasks, either by working in parallel or performing two distinct actions simultaneously. Thus, it is possible that the corpus callosum is inhibiting connections between the two hemispheres to allow for more efficient intrahemispheric processing.

Further evidence to support the theories of inhibition comes from dichotic listening research. As has been noted, in the dichotic listening paradigm, two contradictory pieces of information are presented simultaneously into each ear. The ears send projections to both the ipsilateral and contralateral hemispheres, though the connections to the contralateral hemispheres are stronger and faster than connections to the ipsilateral pathways (Bryden, 1988). Thus, subjects with a right-ear advantage for verbal information processing have this advantage because the information sent to the left-hemisphere language centers overpowers the information sent to the right-hemisphere via less efficient and less powerful projections. But why do these subjects not become confused by the contradictory input? The corpus callosum might play a role in inhibiting the interhemispheric processing occurring during dichotic listening. In this particular case, the corpus callosum might block information from the right auditory cortex to the left auditory cortex so that instead of working together, those two cortical areas do not communicate contradictory information to one another.

Despite these studies, evidence directly supporting either Cook's or Kinsbourne's theories has been scarce. Chiarello et al. (1995) did not find evidence to support an inhibitory role of the corpus callosum in a study specifically designed to test Cook's homotopic inhibition theory. In this study, 192 right-handed college students were presented with verbal stimuli in a prime-target fashion using onset asynchronies. Equivalent priming of subordinate meanings over visual fields was obtained. The authors suggest that this data rules out Cook's homotopic inhibition as the mechanism by which initial activation of subordinate meanings occurs and challenges the theory in general (Chiarello et al., 1995). While this is the only study designed specifically to test Cook's theory, the physiological evidence substantiating the inhibitory action of the corpus callosum is also scarce (Lassonde, 1986). It must be considered, however, that these theories are relatively new and few paradigms have been carried out with the idea of explicitly testing them (Chiarello et al., 1995).

Theories of Excitation

Many other researchers focus on the corpus callosum's excitatory role in interhemispheric processing (Galaburda, 1984; Galaburda et al., 1990a, 1990b; Lassonde, 1986), which was suggested by Sperry in 1962 and developed by Berlucchi in 1981 and 1983 (Cook, 1984). The belief is that the corpus callosum enforces integration of cerebral processing between the two hemispheres (Galaburda and Geschwind, 1984; Lassonde, 1986; Lezak, 1995) and activates the unstimulated hemisphere (Yazgan et al., 1995). Support for the excitation hypothesis includes the effectiveness of callosotomy in treating intractable epilepsy, evidence that corpus callosum size is increased in individuals capable of completing demanding tasks, evidence that corpus callosum size in individuals with greater behavioral laterality is reduced, and evidence that corpus callosum size in developmental dyslexia is reduced.

Although initially a supporter of the theory of callosal inhibition, in recent years Kinsbourne has contributed to the body of evidence that supports the theory of callosal excitation in that he and his colleagues have found evidence that the corpus callosum plays an excitatory role during certain cognitive tasks (Yazgan et al., 1995). In this study, 11 adult, right-handed subjects (nine men and two women) participated in neuropsychological testing and a structural MRI scan. Performance on measures of behavioral laterality (dichotic listening, line bisection, and turning bias tests) was significantly negatively correlated with corpus callosum size. Specifically, behavioral laterality increased as the corpus callosum became smaller. The authors suggest that the relationship between callosal size and outcomes on tests of laterality "suggest that the corpus callosum plays an excitatory role when subjects perform these tasks" (Yazgan et al., 1995, p. 769). This evidence supports the theory of functional excitation, as one would expect laterality to be inversely correlated with corpus callosum size.

Other supporters of the excitation hypothesis, Galaburda and Geschwind (1984), postulated that more symmetric brains have stronger interhemispheric connections, suggesting that the development of asymmetry is related to a lack of excitatory connections between the hemispheres. This would suggest that greater asymmetry would be associated with a smaller corpus callosum, as has been suggested by other researchers (Hopkins and Rilling, 2000; Preis et al., 2000). If this theory is correct, the size of the corpus callosum should be smaller in individuals with greater functional asymmetry, which is associated with greater language ability. This has been shown to be true in primates and cetaceans as will be discussed later in this review. However, at this point it is appropriate to focus on reading disabilities as a way to explore this theory of callosal excitation.

Developmental Dyslexia, Functional Asymmetry, and Corpus Callosum Size

The corpus callosum certainly plays an important role in language in the intact brain, as language is an extremely lateralized behavior, especially in males (Shaywitz et al., 1995). The degree to which the language areas of the brain are asymmetric distinguishes dyslexic from nondyslexic brains (Galaburda, 1995). Galaburda has theorized that developmental dyslexia is due to a larger right planum temporale, and evidence for this anatomical difference in dyslexics and normal readers is substantial (Geschwind and Galaburda, 1985; Galaburda, 1995). Galaburda suggests that the larger right planum temporale is interfering in the normal dominance of the left planum temporale for language processing. The right planum temporale is thought to be larger due to insufficient pruning, and Galaburda and colleagues (1990) also suggest that increased callosal connections might also be due to insufficient pruning. The interference of the right planum temporale on the left planum temporale's dominance for language may manifest itself through the corpus callosum.

If Cook's theory of homotopic inhibition is correct, a larger right planum temporale would not interfere with the phonological processing in the left planum temporale since the corpus callosum would be inhibiting simultaneous activation of both regions. Support for Cook's theory would be found if individuals with developmental dyslexia have a smaller callosum compared to normals, whereas a larger callosum when compared to normals would be expected to support the Galaburda and Geschwind hypothesis.

While there has been conflicting evidence regarding the size of the corpus callosum in developmental dyslexia (Duara et al., 1991; Hynd et al., 1995, Preis et al., 2000), most studies have found abnormalities in size. These abnormalities are thought to be directly related to reduced cortical asymmetry. Hynd and colleagues (1995) found that areas of the callosum were smaller in dyslexics, supporting Cook's homotopic inhibition theory. Other researchers (Larsen et al., 1992), however, have found larger corpus callosum in developmental dyslexia, supporting the theory of callosal excitation. Preis and colleagues (2000) point out that the current results in studies examining this issue are split evenly. Considering the fact that research has found both larger and smaller corpus callosi in individuals with dyslexia, it is possible that the corpus callosum is not a relevant variable to reading ability. Thus, despite the link of language and laterality, research on language and language disorders leaves us no closer to a conclusion about the functionality of the corpus.

A great many methodological issues remain to be resolved in this line of research, including criteria for inclusion in the clinical and control groups, the method of measuring the corpus callosum and other relevant brain structures, and variability within the imaging technology that make results difficult to compare.

Evidence Supporting the Theory of Excitation

Integration between the two cerebral hemispheres, as posited by the theory of excitation, may increase the amount of cortex that can be devoted to a particular task, which would assist with the processing of demanding tasks (Yazgan et al., 1995). In fact, according to Yazgan et al. (1995), there is some evidence that measures of intelligence correlate positively with the size of the splenium, which supports the idea that the corpus callosum may assist in the processing of difficult tasks.

Most neuropsychologists conceptualize the corpus callosum as a structure that integrates information from the two cerebral hemispheres through excitation. This is a large part of the reason that callosotomies are performed on patients with intractable epilepsy—the corpus callosum is viewed as a conduit by which seizures in one hemisphere propagate to the other hemisphere. Thus, the effectiveness of callosotomies in treating epilepsy supports the theory that callosal connections are excitatory. Although callosotomies are most often effective in disrupting the spread of seizures from one hemisphere to the other hemisphere, it has also been recognized that seizure inhibition between hemispheres is disrupted by the callosotomy as well (Roberts, 1999). This effect is not as profound an effect as the improvement that occurs after callosotomy (Roberts, 1999), but its existence lends support to the theory that the corpus callosum also provides functional inhibition between the cerebral hemispheres.

Split-Brain Studies. Sergent noted that one surprising fact about split-brain patients is that, only a few years after surgery, they seldom display confusion, hesitation, or disassociation in their daily lives (Sergent, 1983). This is quite remarkable considering the two halves of their cerebral cortexes are functioning almost entirely independently. Despite their seemingly normal functioning, however, there are some clear signs of "disconnection syndrome." For example, these patients are unable to compare sensory information presented to the different hemispheres (Lassonde, 1986). They are unable to name objects felt with the left hand, sounds heard with the right ear, and odors perceived by only the right nostril (Crandall, 1985). In addition, Banich (1995a) determined from her research on split-brain patients that the corpus callosum is the critical channel for transferring information needed to identify an item and determine its precise position in space. Consequently, the disabilities split-brain patients exhibit provide evidence that the corpus callosum is necessary to communicate information to the contralateral hemisphere. As information is being shared, not suppressed, studies of split-brain patients support the theory of excitation.

Limitations of Research on Split-Brain Patients. There are some potential confounds that limit our ability to draw clear conclusions from the split-brain studies. First, all these patients had intractable epilepsy of a magnitude so severe that it required invasive surgery. The epilepsy could have caused or been caused by neurological abnormalities that could impact the results of split-brain studies. A second and related issue is that most of these patients were on high levels of antiepileptic medications prior to or even after the callosotomy. These drugs could have caused alterations in functioning as well, confounding the results of the studies. Thus, our ability to conclude information from studies of patients who have undergone commissurectomies is compromised by these and other confounds.

Agenesis of the Corpus Callosum. Patients with congenital callosal agenesis typically exhibit specific linguistic and visuospatial deficits and tend to be slower on perceptual and language tasks (Chiarello, 1995; Lezak, 1995). These findings are consistent with the deficits found in patients who had undergone callosotomies. As with split-brain patients, the deficits are remarkably mild considering the importance of interhemispheric communication. Normally these patients are identified only when a comorbid condition requires structural imaging (Lezak, 1995).

Theories of callosal inhibition posit that functional asymmetries occur in part due to one hemisphere inhibiting the activation of the other hemisphere for certain tasks, such as language. This model for the development of cerebral lateralization implies that in the absence of a corpus callosum during development, normally lateralized functions would develop in both hemispheres (Lassonde, 1986). Research refutes this idea, however. There has been no evidence to suggest that lateralized functions are bilaterally represented in callosal agenesis, and there is evidence that hemispheric specialization continues to develop (Lassonde, 1986). Some researchers have concluded that cerebral lateralization does not develop, but is essentially ordained from birth (Hellige, 1993).

Limitations of Research on Patients with Callosal Agenesis. Potential problems exist in interpreting the results of the literature on callosal agenesis as well. Acallosal patients often have other anomalies of brain morphology, ongoing or static disease processes, and, often, low intelligence (Hynd and Willis, 1988). Also, the brain has developed without this structure, and the other commissures might have developed additional or stronger connections. Acallosal patients are generally more functional than split-brain patients because their brains were able to make use of neural plasticity to compensate (Lassonde, 1986), although deficits in processing speed exist. In one study, Lassonde found that acallosal subjects were able to make interhemispheric comparisons as well as a control group, but at a much slower rate (1986).

Comparative Studies

Much can be learned about the function of the corpus callosum in the development of lateralization by comparing corpus callosum size in species with different levels of hemispheric asymmetry and individuals with varying levels of functional lateralization.

Gender Differences. Gender differences in the size of the corpus callosum have consistently been reported in the human literature (Oka et al., 1999) with females having larger callosi relative to the size of their cortex. It has been theorized that the larger corpus callosum permits more interhemispheric communication with regards to language. Furthermore, language functions are more likely to be lateralized in males and more likely to be represented in both hemispheres in females. Functional MRI studies, in fact, have shown unilateral activation in males and more bilateral activation in females during phonological processing tasks (Shaywitz et al., 1995).

Asymmetry in Primates. The types of asymmetries that are found in humans have also been found in some nonhuman primates, although to a lesser degree. Sylvian fissure morphology has been found to be asymmetric in the orangutan, baboon, and chimpanzee (Galaburda, 1984). A preference for the right hand has also been found in nonhuman primates (Corballis, 1983).

Hopkins and Rilling (2000) examined magnetic resonance images of the brains of 45 primates including Old and New World monkeys, lesser apes, greater apes and humans. The ratios of corpus callosum size to both brain volume and neuroanatomical asymmetry were determined for all species. Results showed both ratios were significantly lower in humans than nonhuman primates, and that brain asymmetry significantly predicted both. Thus, the brains of nonhuman primates have larger callosi compared to brain volume and less neuroanatomical asymmetry when compared to humans. This comparative study shows that as laterality increases across primates, corpus callosum size decreases, supporting the excitation hypothesis.

The authors concluded that "leftward brain asymmetries may have evolved as a consequence of reduced interhemispheric connectivity." The authors posit that as the brain grew larger in primate evolution, it became more efficient to process information in smaller networks and long-distance interhemispheric axonal projections going through the corpus callosum were pruned. Functions became confined to single hemispheres, and laterality emerged. This possible explanation for the evolution of laterality and its relation to callosal size also supports the theory of excitation.

Asymmetry in Dolphins. It is known that in dolphins and other cetaceans, sleep alternates between the two cerebral hemispheres. At any one time in the sleep cycle, one hemisphere shows the electroencephalographic signs of wakefulness and one shows the signs of sleep (Rattenborg et al., 2000). This phenomenon implies a tremendous amount of independence between the hemispheres. If the corpus callosum produced an inhibitory effect on the hemispheres, one would expect that the callosi of dolphins would be much larger than in that of animals who experience sleep simultaneously in both hemispheres. The opposite is true, however; the corpus callosum of dolphins is smaller (Marino, personal communication, 1996). This is further evidence to support the Galaburda and Geschwind hypothesis that the corpus callosum carries an overall excitatory and unifying effect on the cerebral hemispheres.

EXCITATION OR INHIBITION?

Both theories of callosal function have support in the literature. The theory of inhibition is supported by evidence that the hemispheres divide processing for complex tasks, which would likely be mediated by an inhibiting corpus callosum, and dichotic listening research. Support for the excitation hypothesis includes evidence that corpus callosum size is increased in individuals capable of completing demanding tasks, the effectiveness of callosotomy in treating intractable epilepsy, decreased corpus callosum size in individuals with greater behavioral laterality, and corpus callosum size in developmental dyslexia. Comparative research, including the degree of laterality present in nonhuman primates and dolphins, also supports the theory of excitation. In consideration of the significant methodological issues, studies of split-brain patients and agenesis of the corpus callosum do not greatly contribute to our knowledge regarding the theories of excitation and inhibition at this time (Table 3).

The corpus callosum is not a single body (Chiarello, 1995), but a complex bundle of fibers with distinct components that act separately. Banich's work (1995a), in particular, suggests that the corpus callosum cannot be thought of as simply a passive conduit of information transfer. Rather, it is an active body that aids in collaboration between hemispheres for certain computationally demanding tasks.

It is likely that there is not just one method of interhemispheric interaction, but several varieties that occur depending on the processing demands of the task (Hellige, 1993) and the anatomic asymmetry that reflects the dominance of the hemisphere for the task. Thus, the corpus callosum may be inhibitory at times and excitatory at other times, depending on the task. In some instances, it might be more efficient for the hemispheres to operate independently and in some instances interhemispheric communication might be necessary to complete the task. Banich suggests that "interhemispheric processing is used more when tasks are computationally demanding and require multiple steps in processing" (Banich, 1995a, p. 438) because it enhances the capacity of the brain to process

Table 3. Evidence Supporting the Theory of Excitation

Study	Subjects	Method	Results
Zaidel (1995)	Adults who have undergone commissurectomies and control subjects	Local and global visual recognition tasks presented to each visual field	The CC is the critical channel for transferring sensory information in split-brain adults.
Dorion et al. (2000)	35 adult humans	MRI	A decrease in CC size with increasing hemispheric asymmetry in adult males but not females.
Duara et al. (1991)	Adults with dyslexia and matched control subjects	MRI	Larger CC in developmental dyslexia in children.
Hopkins and Rilling (2000)	45 primates	MRI	As laterality increases across primate species, CC size decreases.
Rattenborg et al. (2000);	Dolphins	Dolphin brains are extremely lateralized and independent as has been shown by their capacity for unihemispheric sleep.	Dolphin CCs are smaller than brain volume would predict.
Yazgan et al. (1995)	Adult humans	MRI; dichotic word listening, line bisection, and turning bias tests	Performance on measures of behavioral laterality was significantly negatively correlated with CC size

complex tasks. Therefore, a likely possibility is that the degree to which the brain's cerebral hemispheres process information independently or together is a "relative phenomenon rather than an absolute one" (Lezak, 1995). Another point to consider is to what extent the benefits of the transfer of information are offset by the potential decrease in efficiency caused by collaboration between the hemispheres (Hellige, 1993). This cost to benefit ratio may play a part in when the corpus callosum inhibits interhemispheric communication and when it serves an excitatory function.

Furthermore, connections in the brain are extraordinarily complex. Almost all callosal fibers are excitatory at a neurochemical level, but the functional effect of those connections depends on other factors (Yazgan et al., 1995). Although an individual callosal connection can produce either a facilitatory or inhibitory effect, functional inhibition or excitation can occur depending on the neurotransmitters, receptors, and interneurons involved. Excitation can function to produce inhibition, and "the effects on behavior would not appear simply as inhibition or excitation, but as changes in *patterns* of processing" (Pribram, 1986).

In sum, although there is more evidence to support the notion that the corpus callosum plays an excitatory function in interhemispheric communication rather than an inhibitory function, there is some evidence that inhibition occurs. It would be premature to abandon homotopic inhibition as a mechanism of callosal functions (Chiarello, 1995) and it seems likely that it plays a role in the development of lateralization of function and hemispheric asymmetry. Given the anatomical heterogeneity of the corpus callosum, the most likely conclusion based on current evidence is that both inhibition and excitation occur through callosal channels. Thus, the corpus callosum is likely both inhibitory and excitatory in its function. Functional inhibition or excitation may occur at different times depending on the task or may even occur simultaneously.

Future studies are important in order to elucidate under what conditions inhibition and excitation occur, if both excitation and inhibition can occur at the same time, and what role anatomical and functional asymmetries contribute to each type of interhemispheric communication. The role of the corpus callosum in the development of functional asymmetry and further comparisons of callosal size between highly lateralized species and less lateralized species should also be researched further. Furthermore, future research should utilize a more direct measure of connectivity other than callosal size, such as a measure of the number of nerve fibers.

Most researchers who conduct research on laterality do so under the assumption that the corpus callosum works as a whole to unite the cerebral hemispheres and are not aware of the possibility that the corpus callosum may inhibit communication between hemispheres. In fact, as has been illustrated in this review of the literature, this structure is composed of distinct components that act independently and may produce contralateral inhibition under some conditions. As long as there exists the possibility that the assumptions underlying research are incorrect, the research is compromised. Thus, more researchers need to be aware that the corpus callosum can be a conduit for both excitation and inhibition between the cerebral hemispheres.

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REFERENCES

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

Banich, M. T. (1995a). Interhemispheric processing: Theoretical considerations and empirical approaches. In Davidson, R. J., and Hugdahl, K. (eds.), *Brain Asymmetry*, MIT Press, Cambridge, MA. pp. 427–450.

Banich, M. T. (1995b). Interhemispheric interaction: Mechanisms of unified processing. In Kitterle, F. L. (ed.), *Hemispheric Communication: Mechanisms and Models*, Erlbaum, Hillsdale, NJ. pp. 271–300.

Beaton, A. (1985). *Left Side, Right Side: A Review of Laterality Research,* London, England: Batsford Academic and Educational.

Beaton, A. (1997). The relation of planum temporale asymmetry and morphology of the corpus callosum to handedness, gender and dyslexia: A review of the evidence. *Brain Language* **60**: 255–322.

Bryden, M. P. (1988). An overview of the dichotic listening procedure and its relation to cerebral organization. In Hugdahl, K. (ed.), *Handbook of Dichotic Listening: Theory, Methods, and Research*. Chichester, Great Britain: Wiley.

Buono, L. A. (1997). Evidence for nonverbal learning disability in children with brain tumors. (Doctoral dissertation). *Abstr. Int.: Sect. B: Sci. Eng.* **57**(8-B): 5318.

Chiarello, C. (1995). Does the corpus callosum play a role in the activation and suppression of ambiguous word meanings? In Kitterle, F. L. (ed.), *Hemispheric Communication: Mechanisms and Models*, Erlbaum, Hillsdale, NJ. pp. 271–300.

Chiarello, C., Maxfield, L., and Kahan, T. (1995). Initial right hemisphere activation of subordinate word meanings is not due to homotopic callosal inhibition. *Psychonom. Bull. Rev.* **2**(3): 375–380.

Clarke, J. M., Lufkin, R. B., and Zaidel, E. (1993). Corpus Callosum morphometry and dichotic listening performance: Individual differences in functional interhemispheric interaction. *Neurops.* **31**(6): 547–557.

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

Cook, N. D. (1999). Simulating consciousness in a bilateral neural network: "Nuclear" and "fringe" awareness. *Consciousness Cogn.: Int. J.* **8**(1): 62–93.

Corballis, M. C. (1983). *Human Laterality.* New York: Academic Press.

Crandall, P. H. (1985). Clinical phenomenology following hemispherectomy and the syndromes of hemispheric disconnection. In Benson, D. F., and Zaidel, E. (eds.), *The Dual Brain: Hemispheric Specialization in Humans*, Guilford Press, New York. pp. 277–288.

Denenberg, V. H., Gall, J. S., Berrebi, A., and Yutzey, D. A. (1986). Callosal mediation of cortical inhibition in the lateralized rat brain. *Brain Res.* **397**(2): 327–332.

Dennis, M. (1976). Impaired sensory and motor differentiation with corpus callosum agenesis: A lack of callosal inhibition during ontogeny? *Neuropsychol.* **14**(4): 455–469.

Dorion, A. A., Chantome, M., Hasboun, D., Zouaoui, A., Marsault, C., Capron, C., et al. (2000). Hemispheric asymmetry and corpus callosum morphometry: A magnetic resonance imaging study. *Neurosci. Res.* **36**: 9–13.

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

Egaas, B., Courchesne, E., and Saitoh, O. (1995). Reduced size of the corpus callosum in autism. *Arch. Neurol.* **52**(8): 794–801.

Galaburda, A. M. (1984). Anatomical asymmetries. In Galaburda, A. M., and Geschwind, N. (eds.), *Cerebral Dominance*, Harvard Press, Cambridge, MA. pp. 11–25.

Galaburda, A. M. (1995). Anatomic basis of cerebral dominance. In Davidson, R. J., and Hugdahl, K. (eds.), *Brain Asymmetry*, MIT Press,Cambridge, MA. pp. 51–74.

Galaburda, A. M., Rosen, G. D., and Sherman, G. F. (1990a). Individual variability in cortical organization: Its relationship to brain laterality and implications to function. *Neuropsy.* **28**(6): 529–546.

Galaburda, A. M., Sherman, G. F., Rosen, G. D., Aboitiz, F., and Geschwind, N. (1990b). Developmental dyslexia: Four consecutive patients with cortical abnormalities. *Annals of Neurology* **18**: 222–233.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain* **123**: 1293–1326.

Geschwind, N., and Galaburda, A. M. (1985). Cerebral lateralization: Biological mechanisms, associations, and pathology. *Arch. Neurol.* **42**: 428–459.

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

Gilles, F. H., Leviton, A., and Dooling, E. C. (1983). *The Developing Human Brain: Growth and Epidemiologic Neuropathology*, Great Road, Littleton, MA: John Wright & Sons.

Harrington, A. (1995). Unfinished business: models of laterality in the nineteenth century. In Davidson, R. J., and Hugdahl, K. (eds.), *Brain Asymmetry*, MIT Press, Cambridge, MA. pp. 3–27.

Hellige, J. B. (1993). *Hemispheric Asymmetry: What's Right and What's Left,* Harvard University Press, Cambridge, MA.

Hopkins, W. D., and Rilling, J. K. (2000). A comparative MRI study of the relationship between neuroanatomical asymmetry and interhemispheric connectivity in primates: Implication for the evolution of functional asymmetries. *Behav. Neurosci.* **114**(4): 739–748.

Hynd, G. W., and Willis, W. G. (1988). *Pediatric Neuropsychology*, New York: Grune & Stratton.

Hynd, G. W., Hall, J., Novey, E. S., Eliopulos, D., Black, K., Gonzalez, J. J., Edmonds, J. E., Riccio, C., & Cohen, M. (1995). Dyslexia and corpus callosum morphology. *Arch. Neurol.* **52**: 32–38.

Hynd, G. W., Semrud-Clikeman, M., Lorys, A. R., Novey, E. S., and Eliopulos, D. (1990). Brain morphology in developmental dyslexia and attention-deficit disorder/hyperactivity. *Arch. Neurol.* **47**: 919–926.

Kinsbourne, M., and Hiscock, M. (1977). Does cerebral dominance develop? In Segalowitz, S. J., and Gruber, F. A. (eds.), *Language development and neurological theory*, Academic Press, New York. pp. 171–191.

Kinsbourne, M. (1975). The mechanism of hemispheric control of the lateral gradient of attention. In Rabbit, P. M., and Dornic, S. (eds.), *Attention and Performance,* Vol. 5, Academic Press, New York.

Kinsbourne, M. (1982). Hemispheric specialization and the growth of human understanding. *Am. Psychol.* **37**: 411–420.

Larsen, J. P., Hoein, T., and Odegaard, H. (1992). Magnetic resonance imaging of the corpus callosum in developmental dyslexia. *Cogn. Neuropsychol.* **9**: 123–134.

Larsen, J. P., Hoien, T., Lundberg, I., and Odegaard, H. (1990). MRI evaluation of the size and symmetry of the planum temporale in adolescents with developmental dyslexia. *Brain Language* **39**: 289–301.

Lassonde, M. (1986). The facilitatory influence of the corpus callosum on intrahemispheric processing. In Lepore, F., Ptito, M., and Jasper, H. H. (eds.), *Two Hemispheres—One Brain: Functions of the Corpus Callosum*, Alan Liss, New York. pp. 385–402.

LeMay, M. (1984). Radiological, development, and fossil asymmetries. In Galaburda, A. M., and Geschwind, N. (eds.), *Cerebral Dominance*, Harvard Press, Cambridge, MA. pp. 26–42.

Lezak, M. D. (1995). *Neuropsychological Assessment*, Oxford University Press New York.

Liederman, J. (1995). A reinterpretation of the split-brain syndrome: Implications for the function of cortico-cortical fibers. In Davidson, R. J., and Hugdahl, K. (eds.), *Brain Asymmetry*, MIT Press, Cambridge, MA. pp. 451–490.

Lyoo, K., Noam, G. G., Lee, C. K., Lee, H. K., Kennedy, B. P., and Renshaw, P. F. (1996). The corpus callosum and lateral ventricles in children with attention-deficit hyperactivity disorder: A brain magnetic resonance imaging study. *Biol. Psychiatr.* **40**: 1060–1063.

Myers, R. E. (1960). Failure of intermanual transfer in corpus callosum-sectioned chimpanzees. *Anatom. Rec.* **136**: 358.

Myers, R. E., and Sperry, R. W. (1953). Interocular transfer of a visual form discrimination habit in cats after section of the corpus callosum and optic chiasm. *Anatom Rec.* **115**: 351–352.

Oka, S., Miyamoto, O., Janjua, N. A., Honjo-Fujiwara, N., Ohkawa, M., Nagao, S., Kondo, H., Minami, T., Toyoshima, T., & Itano, T. (1999). Re-evaluation of sexual dimorphism in human corpus callosum. *Neuro Report* **10**(5): 937–940.

Olk, B., and Hartje, W. (2001). The bilateral effect: Callosal inhibition or intrahemispheric competition? *Brain Cogn.* **45**(3): 317–324.

Preis, S., Steinmetz, H., Knorr, U., and Jancke, L. (2000). Corpus callosum size in children with developmental language disorder. *Cogn. Brain Res.* **10**: 37–44.

Pribram, K. H. (1986). The role of cortico-cortical connections. In Lepore, F., Ptito, M., and Jasper, H. H. (eds.), *Two Hemispheres—One Brain: Functions of the Corpus Callosum*, Alan Liss, New York. pp. 523–540.

Purves, D., Augustine, G., Fitzpatrick, D., Katz, L., LaMantia, A., and McNamara, J. (1997). *Neuroscience,* Sinauer, Sunderland, MA.

Ramachandran, V. S., and Blakeslee, S. (1998). *Phantoms in the Brain: Human Nature and the Architecture of the Mind*, Fourth Estate. London, England.

Rattenborg, N. C., Amlaner, C. J., and Lima, S. L. (2000). Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neurosci. Biobehav. Rev.* **24**(8): 817–842.

Roberts, D. W. (1999). Corpus callosotomy in the treatment of neuronal migration disorders. In Kotagal, P., and Luders, H. O. (eds.), *The Epilepsies: Etiologies and Prevention*, Academic Press, San Diego, CA. pp. 103–112.

Schaefer, G. B., and Bodensteiner, J. B. (1999). Developmental anomalies of the brain in mental retardation. *Int. Rev. Psychiatr.* **11**: 47–55.

Sergent (1983). Unified response to bilateral hemispheric stimulation by a split-brain patient. *Nature* **305**: 800–802.

Shafer, V. L., Schwartz, R. G., Morr, M. L., Kessler, K. L., and Kurtzberg, D. (2000). Deviant neurophysiological asymmetry in children with language impairment. *Cogn. Neurosci. Neuropsychol.* **11**(17): 3715–3718.

Shaywitz, B., Shaywitz, S., Pugh, K., Constable, T., Skudlarksi, P., Fulbright, R., Bronen, R., Fletcher, J., Shankweiler, D., Katz, L., & Gore, J. (1995). Sex differences in the functional organization of the brain for language. *Nature* **373**(6515): 607–609.

Smock, T. K. (1999). *Physiological Psychology: A Neuroscience Approach*, Prentice-Hall Upper Saddle River, NJ.

Sperry, R. W. (1958) Corpus callosum and interhemispheric transfer in the moneky (Macaca mulatta). *Anatom. Rec.* **131**: 297.

Sperry, R. W. (1974) Lateral specialization in the surgically separated hemispheres. In Schmitt, F. D., and Worden, F. G. (eds.), *The Neuroscience: Third Study Program*, MIT Press, Cambridge, MA. pp. 5–19.

Sperry, R. W., Stamm, J. S., and Miner, N. (1956). Relearning tests for interocular transfer following division of the optic chiasma and corpus callosum in cats. *J. Comp. Physiol. Psychol.* **49**: 529–533.

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

Wang, P. P., Doherty, S., Hesselink, J. R., and Bellugi, U. (1992). Callosal morphology concurs with neurobehavioral and neuropathological findings in two neurodevelopmental disorders. *Arch. Neurol.* **49**: 407–411

Watson, R. T., Valenstein, E., Day, A. L., and Heilman, K. M. (1984). The effect of corpus callosum lesions on unilateral neglect in monkeys. *Neurology* **34**(6): 812–815.

Yazgan, M. Y., Wexler, B. E., Kinsbourne, M., Peterson, B., and Leckman, J. F. (1995). Functional significance of individual variations in callosal area. *Neuropsy.* **33**(6): 769–779.

Zaidel, E. (1995). Interhemispheric transfer in the split brain: Long-term status following complete cerebral commissurectomy. In Davidson, R. J., and Hugdahl, K. (eds.), *Brain Asymmetry*, MIT Press, Cambridge, MA. pp. 491–532.