The Two Halves of the Brain

Information Processing in the Cerebral Hemispheres

edited by Kenneth Hugdahl and René Westerhausen

Introduction and Overview

Kenneth Hugdahl and René Westerhausen

Aims and Objectives

In this general introduction we outline a theoretical umbrella perspective on the 21 chapters in the book, to emphasize novel theories, methods, and applications of research devoted to hemispheric asymmetry and laterality. Despite all the research devoted to hemispheric asymmetry and laterality over the last decades, this is an area in which big questions remain with respect to understanding the neural under-pinnings of cognition, and the questions being addressed in this field are ones that come up for almost any cognitive science researcher. Moreover, it is not possible to advance a theoretical understanding of brain–behavior relations without taking asymmetry and laterality into account. Similarly, issues related to asymmetry and laterality penetrate most theories and models of neuropsychology and neurocognitive aspects of the major neurological and psychiatric diseases and disorders. However, despite the large amount of empirical data accumulated over the last decades (see Davidson & Hugdahl, 1995; Hugdahl & Davidson, 2003), theoretical understanding of the behavioral significance and the neural basis of laterality remains limited. Thus, the questions of "why," "how," and "what" are as valid today as they were 30 years ago (e.g., Bradshaw & Nettleton, 1981; Bryden, 1982; Harnad et al., 1977; Porac & Coren, 1981).

Our objective when compiling the current volume has therefore been not only to update the reader on the latest data and empirical results but also to provide a coher-ent theoretical perspective whenever possible to put the different chapters and con-tributions into perspective. The field of hemispheric asymmetry has more or less exploded in recent years with ever new data and applications, but there has not been a corresponding explosion of theoretical advances. In this introduction, we comment on the different contributions from a theoretical perspective, moving from molecular, genetic, and evolutionary to cognitive and clinical factors in the understanding of one of the most fascinating phenomena in neuroscience, neuropsychology, psychiatry and neurology, and cognitive sciences.

Functional Segregation and Integration in an Asymmetrical Brain

The issue of functional segregation and integration in the brain has a long history in neuroscience, with the observations of Broca and Wernicke as classic examples for the localization of language areas in the left hemisphere. However, it was not until the development of the hemodynamic neuroimaging techniques that the concept of functional segregation also gained acceptance in mainstream cognitive psychology and cognitive neuroscience (Friston, 2005). Before this development, it was not uncommon to find statements like "Where is memory localized in the brain?—Everywhere and nowhere" in standard textbooks in psychology and neuroscience. Such statements have almost totally disappeared from the literature following the introduction of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) as well as modern analysis techniques—for example, source localization, to supplement magnetic- and electroencephalographical (EEG) methods, such as magnetoencephalography (MEG) and EEG/ERPs. Frith (1997) provides several arguments as to why segregation, rather than integration, is the guiding principle behind the functional organization of the brain, taking arguments from evolution, economy, and the complexity of the design of the brain.

In his review of EEG/MEG measures of hemispheric asymmetry, Alfredo Brancucci (chapter 8) shows how EEG was the first "objective" measure to be used to infer asymmetry of neuronal firing in the two hemispheres by comparing EEG responses obtained from the left and right side of the scalp. The later development of newer recording techniques, for example, the use of MEG, opened up opportunities for more fine-grained analyses of direct neuronal correlates of behavioral asymmetries seen in response to auditory and visual tasks. A general conclusion to be drawn from all electrophysiology studies of hemispheric asymmetry, with a variety of recording and analysis measures, is that the two cerebral hemispheres show different patterns of activation when provoked by specific stimuli or tasks.

A Historical Perspective

Looked at from a more narrow perspective, the study of hemispheric asymmetry and brain laterality has had a long tradition in the neurosciences, and in psychology, biology, and medicine (see Davidson & Hugdahl, 1995, for an overview). The fact that the vertebrate nervous system is divided into two halves has attracted the attention and has sparked the speculation of numerous generations of scientists, actually further back than typically recognized (see Harrington, 1995). In her treatment of the history of research on hemispheric asymmetry, Harrington (1995) argues that many of the fundamental assumptions regarding the "unquestioned truths" about differences between the cerebral hemispheres have their roots in 19th-century theories of what

was called localization theory, which in modern terminology would translate to brain "structure–function relationships."

It is not possible to discuss the history and theory of hemispheric asymmetry without mentioning the speculations of Franz Joseph Gall, who perhaps more than Paul Broca and Carl Wernicke personifies the idea that the brain is divided into functionally segregated regions with their own cognitive and emotional processing specializations. Gall's ideas with respect to localization theory were not supported by later empirical research, and his views are today mostly forgotten, except in historical overviews. However, as correctly pointed out by Harrington (1995), it was Gall who changed the at that time religiously influenced view that all mental capacities were hierarchically organized with the less "divine" mental faculties like sexual and animal-like behaviors at the bottom and more divine faculty like language and prayers at the top. He also changed the view that the human mind was a holy unity by claiming that it could be broken down into "brain-based building blocks."

Imaging the Asymmetry of the Mind

The notion of localization and specialization of the mind and that different mental capacities could be anatomically localized in the brain along a left–right gradient received new interest with the introduction of functional imaging in the beginning of 1980 (see Friston, 2003). That the functioning of the mind could be visualized on a template brain anatomy image was a revolution in itself but that it also would show differential effects on brain metabolism across the hemispheres depending on the nature of the cognitive task further attested that the human mind was not a holy unity that could not be broken down into its subcomponents. The introduction of functional neuroimaging techniques also ended the view held by many neuroscientists of what could be called the "equipotentiality" and "mass action" principles, originally introduced by Karl Lashley in the 1940s and 1950s (Lashley, 1950). The equipotentiality principle stated that all cortical areas can substitute for each other as far as higher cognitive functions are concerned, as in, for example, learning. The principle of mass action similarly stated that the reduction in performance for a given cognitive function, for example, the ability to learn, is proportional to the amount of brain tissue destroyed, and the more complex the cognitive task, the more disruptive brain lesions would be.

Thus, while the behavioristic view of the functioning of the mind and the brain was a nonlocalized and nonspecialized view, the view of Gall and later brain imagers was a localized and specialized view, in particular, one in which the two cerebral hemispheres had different functions (see also Huettel et al., 2004). However, modern views of specialization of the hemispheres are focused not only on finding specific areas or regions within or between the hemispheres that may show functional

specificity but also on understanding the functional relationships, or connectivity, between different areas and regions in a network perspective. In this regard, the terms functional versus effective connectivity have been used (e.g., Frackowiack et al., 2004). Functional connectivity means the statistical correlation between two areas in the brain with regard to observed signal strength to a common cognitive task, while effective connectivity means how a certain brain region may have a causal influence on another region, or regions, which will require knowledge of possible alternatives, set by knowledge of functional brain anatomy.

An extension of the notion of connectivity is the identification of a resting state, or the default-mode cortical activation network in the absence of explicit external (or internal) stimuli (Raichle et al., 2001; Raichle & Snyder, 2007). An fMRI default-mode network analysis is applied to the study of hemispheric asymmetries in the chapter by Nathan Swanson, Tom Eichele, Godfrey Pearlson, and Vince Calhoun (chapter 20). The analysis of asymmetry of default-mode activation (also during activation) is a novel application of fMRI data for the study of hemispheric asymmetry that could have important theoretical as well as clinical consequences. Theoretically, it could mean that the hemispheres differ in their "idling" state, which could have consequences for increases or decreases in activation in a "running" state when the brain is required to process certain stimuli or instructions. Clinically, it could help us understand how hemispheric asymmetries differ between different clinical states and diagnostic categories, as well as why patients in a specific diagnostic category may shift hemispheric asymmetry pattern across time.

Cortical Structural Asymmetries and White Matter Tracts

Recent years have also brought us new methods to look at structural asymmetries between the two hemispheres, namely, cytoarchitectonic mapping (Amunts & Zilles, 2001) and diffusion-tensor imaging (DTI; see Jones, 2008; LeBihan, 2003) that have significantly widened our perspective on the brain's asymmetry. Based on cytoarchitectonic analysis of postmortem brains, it was shown that macroanatomical landmarks often do not allow for an exact localization of functional modules of the cerebral cortex and that there is a substantial interindividual variability in the exact location of these modules. This observation not only led to the development of cytoarchitectonic maps that support a probabilistic localization of functional cortex modules (see Eickhoff et al., 2005) but also advanced the understanding of asymmetries in the cerebral cortex.

Structural brain imaging results are summarized by Katrin Amunts in chapter 6, in which she reviews the available evidence about brain structural asymmetries. In her comprehensive review, she comes to the conclusion that structural asymmetries are to be found in many, perhaps all, other brain regions (e.g., visual cortex, parietal

cortex, hippocampus); that such previously thought to be static differences are subject to dynamic modulation through environmental influences; and that the degree of asymmetry differs with respect to brain region, handedness, gender, and disease.
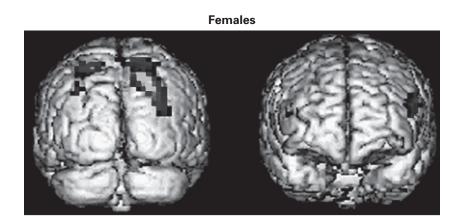
Marco Catani, Stephanie Forkel, and Michel Thiebaut de Schotten (chapter 7) advance a hodological view on hemispheric asymmetry, that not only the functional modules of the brain networks but also the anatomical connections between the spatially distributed modules are of importance. Studies regarding brain hodology were until recently limited to studies on the effect of lesions or postmortem dissection of the brain white matter. However, with the introduction of DTI into neuroimaging about 10 years ago and its "boom" during the last 5 years, it is now possible to non-invasively examine white matter brain connections. DTI allows researchers to calculate indices representing white matter tissue characteristics (e.g., anisotropy) that are supposed to reflect factors like axon myelination and fiber density (Beaulieu, 2002). Moreover, it allows researchers to track white matter fiber bundles throughout the brain and thus to assess the connections between distant cerebral cortex areas. Marco Catani and colleagues demonstrate that DTI fiber tracking can be used to reveal hemispheric asymmetries in structural connections and gain information that goes beyond the knowledge derived from the more traditional approaches.

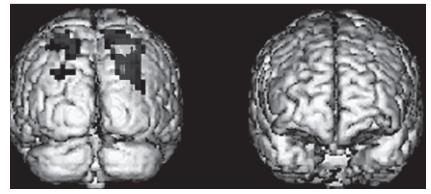**Effects of Asymmetry on Inter- and Intraindividual Differences**

Figure I.1 (plate 1) shows an example of superior activation in the right posterior parietal lobule when healthy subjects solve a three-dimensional mental rotation task (Hugdahl, Thomsen, & Ersland, 2006), attesting to the specificity of functional segregation in the brain. Interestingly, the lower panel of Figure I.1 shows that while female subjects in addition activated speech production brain regions overlapping with Broca's area, no such activation was seen in the male subjects. Thus, fMRI also highlights sex differences in hemispheric asymmetry that had been observed in psychological experiments over a long period of time. Thus, it seems that males and females utilize different processing strategies when approaching the same task, with females using a verbal, or language-guided, approach, and males using a spatial, or perceptually guided, approach.

The results seen in figure I.1 may lend themselves also to a discussion of the origin of hemispheric asymmetry in an evolutionary perspective. Perhaps the different brain activations in males and females seen in figure I.1 are modern variants of a functional division of labor made necessary from the need to socialize the next generation of offspring into a language-guided culture versus the need to orient in three-dimensional space to localize prey and to find the way back home to feed the members of the culture.

The important issue of sex differences in hemispheric asymmetry is further reviewed and discussed in the chapter by Iris Sommer (chapter 10), who provides an updated

Females

Males

Figure I.1 (plate 1)
Functional magnetic resonance imaging/blood-oxygen-level-dependent activations in males and females to a three-dimensional mental rotation task. Note the profound right-over-left parietal asymmetry in both males and females and the unique female left asymmetry in the frontal cortex.

review and meta-analysis of existing research on sex differences, coupled with a thorough discussion of a possible underlying mechanism in a more bilateral brain in females. Such an underlying mechanism would explain why there are more boys than girls with language-related disorders such as dyslexia and specific language impairment. It would also explain why more males than females are affected by psychiatric dysfunctions and disorders like autism, attention-deficit/hyperactivity disorder (ADHD), and schizophrenia. A problem, as pointed out by Sommer, is that although such a hypothesis is theoretically reasonable, it has been difficult to provide empirical evidence supporting it.

Sex differences in hemispheric asymmetry can be seen as a variant of individual differences, which is further elaborated on by Markus Hausmann and Ulrike Bayer (chapter 9) in their chapter on the effect of sex hormones on hemispheric asymmetry and interhemispheric integration. Thus, the authors address a factor influencing brain asymmetry previously neglected or treated as error variance to be ignored. By systematically investigating the effects of sex hormones on brain function and hemispheric asymmetry, Hausmann and Bayer show that sex hormones are important modulators of performance asymmetries and that this reveals an intraindividual variation (the different phases in the menstrual cycle) in addition to interindividual variation (males vs. females). Thus by focusing on the change in performance on tasks involving the differential engagement of the right and left hemisphere, Hausmann and Bayer show how new theoretical advances are made in the understanding of what previously was labeled errors not of interest for asymmetry research.

The chapter by Maria Casagrande (chapter 11) further pushes our understanding of state-dependent asymmetries by showing how hemispheric asymmetry patterns and interactions vary with sleep and different sleep stages. Casagrande's research extends the notion of hemispheric asymmetry to altered states of consciousness as in sleep states.

Genes and Evolution—Are Humans Unique?

One the most important developments in asymmetry research was the discovery in 2005 by Tao Sun (see also chapter 1 in the current volume) of a possible link to a specific gene (LMO4) which is differentially expressed on the right and left side of the brain in the perisylvian region. This region of the brain overlaps both Wernicke's functional area for speech sound perception and the planum temporale structural area in the brain.

This raises again the issue of the uniqueness of human asymmetry and asymmetry for language as the dominant principle of organization of the two cerebral hemispheres. Such a view is supported by Crow (1997; see also chapter 21, this volume). However, the findings by Gannon et al. (1998) that chimpanzees have a larger left than right planum temporale call into question a human uniqueness for language asymmetry. Thus, on the one hand, it can be argued that the neuronal underpinning for language and speech processing is not uniquely human. This then raises the question of what evolutionary pressure would have caused primates not to develop language. It has been speculated that an upright body position (see Lieberman, 2006) was necessary for the development of language, because of the need for a critical length of the vocal tract for production of the sounds necessary for speech. Primates have the head tilted forward compared to humans, with a corresponding shortening of the vocal tract, probably a consequence of the need for using both arms and legs when

walking and climbing. An alternative explanation may be that planum temporale asymmetry developed for some other (unknown) purpose in both species and that it later took on a speech-related function in humans but not in the great apes.

Since efficient speech perception presupposes the existence of an equally effective speech production module (it would not make sense to have a perception module if no one was speaking), the absence of a structural asymmetry for Broca's area (but see chapter 6 by Amunts, this volume) could speak to the independent nature of speech perception and planum temporale asymmetry. Sun makes the important observation in chapter 1 that

> even though genetic models of human handedness have been proposed, the "genes" that may control preferential hand use in humans have not been identified. Taking advantage of large-throughput screening approaches, we are beginning to uncover the differential gene expression in human left and right hemispheres. These candidate genes can serve as references in revealing the molecular mechanisms of brain asymmetry and handedness in humans and animal models.

Thus, recent advancements in genetic and molecular techniques such as microarray methods for observation of gene expression in brain tissue increase the probability that we will be in a position to identify the genes responsible for hemispheric asymmetry. It seems that the available empirical evidence would suggest that the left and right hemispheres in humans show differences in gene expression and that this can be seen early in fetal development. What is, however, still not resolved is how such differential gene expression is related to structural and functional asymmetries as seen in speech perception, visuospatial coordination, or handedness to take a few examples.

In his chapter on the evolutionary origin of hemispheric asymmetry, Michael Corballis (chapter 3) asks the question of whether there is "a middle ground" between the opposing views held by proponents of a unique humanness for hemispheric asymmetry (e.g., Crow, 1997) and, for example, Rogers (2004) making the argument that asymmetry seen in the chicken brain has similar functional consequences as asymmetry seen in the human brain. Corballis starts by stating that no one would deny that there "are some asymmetries that are distinctively human," but he then considers the issue from the opposite direction, beginning with two functions that are generally considered unique to our species. These functions are manual dexterity and language. Both are represented asymmetrically in the human brain, and he examines the possible evolutionary and genetic sources of these asymmetries, invoking concepts like genetics of handedness, mirror neurons, and manual gestures as possible sources for language asymmetry in humans.

In chapter 2, Patrick Gannon approaches the topic from still another angle. He looks at the evolutionary origin of language and any signs of asymmetry in language areas, such as the leftward asymmetry seen in the planum temporale in the posterior

temporal lobe, citing evidence from paleontology that Wernicke's area may have been represented in the brains of our prehistoric ancestors. It is, however, not entirely clear whether other anatomical landmarks of asymmetry for language, such as the different slopes of the sylvian fissure on the left and right side of the brain, are also found in the primate brain. This may be dependent on the measuring method used and should be carefully considered whenever comparisons between species are made. As also pointed out by Gannon in his chapter, statistical correlations and statistical significance are not the same as inference of functionality and theoretical significance. Gannon moreover points out the importance of having blinded procedures when investigating anatomical differences in human and nonhuman brains, something which is difficult in postmortem studies. The issue of human uniqueness for hemispheric asymmetry is a difficult question to answer since in order to disqualify a unique human perspective, observed asymmetries in other species should be possible to interpret in a similar frame of reference as is relevant in the human case. An emerging view is, however, that the homologues of human brain areas for language also existed in ancestors of ours who are far more distant from us than the primates, which may mean two things: Either these species had the necessary brain preparations for developing language, or the so-called language areas in the brain are independent of actual language use, at least when it comes to nonhuman species.

Asymmetry as an Evolutionary Advantage?

As mentioned above, an unanswered question in research on hemispheric asymmetry is what evolutionary advantage would have been gained through a division of labor between the two cerebral hemispheres. Several theories have been suggested over the years, most pointing to the advantage of not having a competition for processing between two identical messages (Hugdahl, 2000; Cook, 1986). This implies that there would be an advantage to having a single information-processing system which facilitates communication at high speed and to avoiding having identical forms of cortical representations. The simultaneous activation of homologous areas in each hemisphere would run the risk of attenuating and blurring information, thus slowing down sensory processing and subsequent motor output.

A variant of this is to say that evolution of higher cognitive functions pushed for a division of labor between the hemispheres, forcing the development of the two hemispheres as a result of a demand for processing speed and efficiency (Ringo et al., 1994). This would have been accompanied by an increase in neural capacity, since specializing one hemisphere for a particular function leaves the other hemisphere free to perform other functions. Thus, lateralization may have been a way to increase brain capacity to carry out simultaneous, parallel processing without the mutual inhibition

and information loss that may have been the case in a situation where information would have been duplicated. An extension of this argument is that it would also have been advantageous to avoid shuffling information across long distances, which would mean the loss of processing speed. It would therefore be preferable that information be processed in a single hemisphere with the involvement of spatially restricted neural networks as discussed above.

Auditory and Visual Asymmetries

Apart from the question of the existence of language-like asymmetry structures in the brain of nonhuman species and the evolutionary origin of language and handedness, a range of other asymmetries have been observed in nonhuman species; perhaps the best known examples are auditory asymmetries in songbirds and visual asymmetries in pigeons as covered in the chapters by Isabell George (chapter 4) and Onur Güntürkün and Martina Manns (chapter 5), respectively. An important issue in all cross-species comparisons is whether there is an early common origin of lateralization and hemispheric asymmetry. An aspect of this is that population-based asymmetry biases (favoring one direction over the other) are the result of a social constraint (Ghirlanda & Vallortigara 2004) emphasizing that unidirectional biases will favor social communication among members of the same species.

For example, gestures to communicate in baboons elicit a right-hand bias (Meguerditchian & Vauclair 2009). Animal models of hemispheric asymmetry may more easily allow for an understanding of the underlying neuronal circuitry and will more easily allow such experimentation. As argued by George, "songbirds … form a unique model because they allow experimental investigation of the interplay of neurobiological substrate and the behavior that characterizes them, that is, song, which is a learned behavior whose critical function is to communicate with other birds." In this respect, the study of song behavior in songbirds provides a particularly important model for the understanding of the underlying mechanisms of hemispheric asymmetry across species when it comes to communications, whether this is phonetic language as in humans or song as in birds. Recent advances in research on songbirds may therefore cast new light on the eternal issue of language lateralization in both humans and nonhumans.

Güntürkun and Manns (chapter 5) show in their chapter that genetic models alone cannot explain the development of hemispheric asymmetry since environmental factors act as important modulator of biologically inherent laterality effects. In this respect, hemispheric asymmetry is a form of brain plasticity (cf. Steinmetz et al., 1995). Güntürkün and Manns demonstrate that pigeons show distinct asymmetry for various visual tasks where the left and right hemispheres differ in the capacity for detailed, fine-grained analysis of the visual environment for stimulus discrimination, memory,

and other aspects of visual processing and that these behavioral asymmetries can be related to the development of the visual system at the neuronal level. These findings then raise the question of whether a common underlying principle for the existence of a lateralized brain is to optimize adaption to the ecological niche each species occupies. That chickens show visual asymmetries for grain picking, when occluding one eye may be as ecologically important as the use asymmetry of a phoneme based language in humans. Seen in this perspective, the controversy of whether functional asymmetry is a unique human trait could be resolved into saying that it depends on the specific function studied and the position of a certain behavior–function in a response–function hierarchy for a particular species. Thus, a common underlying cause for lateralization may be the need for processing efficiency and the need to avoid task duplication, which occupies processing resources and delays speed of processing.

In the chapter by Joseph Hellige, Bruno Laeng, and Chikashi Michimata (chapter 13), visual asymmetries are further discussed, from a human perspective, focusing on the underlying spatial properties that give rise to object perception and how these features are lateralized in the human brain. Specifically, left- and right-hemisphere specialization for processing categorical versus coordinate spatial relations, respectively, are the focus of Hellige's and colleagues' discussion, following the original suggestions by Kosslyn (1987) of a lateralization gradient regarding categorical versus coordinate classification of object perception. This is followed by a discussion of hemispheric asymmetry in processing high versus low ranges of visual spatial frequency and how this relates to the processing of categorical versus coordinate spatial relations. Through the understanding of such features as categorical versus coordinate relations, and high and low spatial frequencies, new theoretical advances have been made in the understanding of asymmetries of object recognition and asymmetries in the processing of spatial relations.

Patricia Cowell takes a different approach in chapter 12 and looks at linguistic and cultural factors that impact laterality of speech perception. It is interesting to note in this regard that such "basic" lateralized processes as language and verbal behavior are also influenced by modulatory factors, which Cowell discusses at length. She states that

two important themes emerge from the research of the past 10 years. First, the degree and direction of lateralization in speech perception involve a rich interplay between biological and experiential influences; this has taken scientific inquiry beyond the search for "main effects" and more deeply into the study of multifactorial interactions. Second, the nature of the stimuli that evoke lateralized neural and behavioral responses in speech perception is more complex than originally believed; thus, lateralized speech processing appears to involve a range of functions from the processing of acoustic input to the processing of integrated input such as words and phrases.

Top-Down Modulation of Bottom-Up Asymmetries

A classic view of hemispheric asymmetry is a bottom-up, or stimulus-driven, view of the functional bias of the cerebral hemispheres, supported by structural asymmetries in the brain that would facilitate the processing of a certain class of stimuli, or cognitive functions rather than other classes. This is, however, a static view, leaving little room for environmental influences, that is not in accordance with research on the plasticity and dynamic change across development of cognitive capacities. For example, if speech perception were completely decided by the processing characteristics of the left hemisphere, and in left perisylvian region, the understanding of another person speaking to me would be impossible if there are more than two sources of input at the same time, as in the well-known "cocktail party phenomenon" wherein several people speak at the same time.

Humans, and perhaps also other species, solve this situation quite easily by directing attention to a single source of input, mentally "filtering out" other sound sources occurring simultaneously (see also Westerhausen and Hugdahl, chapter 16). This is a cognitive, top-down modulation of the complex speech signal input that is necessary in order to gain intelligibility of speech perception. Dichotic listening studies—which can be said to mimic the cocktail party phenomenon in that they entail presenting two simultaneous sources of speech sound input, one in the left ear and one in the right ear—have shown that preliterate children have problems in using attention to shift from a bottom-up, stimulus-driven, right-ear report in the dichotic listening situation to a left-ear report (Hugdahl & Andersson, 1987; Hugdahl et al., 2001). Thus, these studies show that the ability to use top-down cognitive strategies to modulate a stimulus-driven laterality effect is dependent on the cognitive maturation of the brain.

Heikki Hämäläinen and Fiia Takio (chapter 14) take a top-down modulation of a stimulus-driven laterality effect by showing how auditory and visual asymmetry are integrated and that there is a default right-sided bias for spatial perceptual and attentional capacity. This phenomenon is seen in its severest form as hemispatial neglect and/or extinction after right parieto–temporo–frontal disorders/lesions. Hämäläinen and Takio argue that this bias is multimodal including auditory and visual space and that it is present in childhood and in old age. They propose that the early developing asymmetricity in cognitive ability is balanced by later developing executive functions and cognitive control functions. The asymmetricity again becomes evident in old age with the decline of executive functions.

Stefan Pollmann (chapter 15) addresses top-down modulation of the right-ear advantage in dichotic listening by asking the question of whether it is primarily the auditory input or an attentional signal which is exchanged via the corpus callosum

and whether the right-ear advantage in reality is caused by attentional modulation and the transfer of information across the corpus callosum.

Still another aspect of cognitive functioning is asymmetry of memory, as described and discussed by Grégoria Kalpouzos and Lars Nyberg (chapter 17), who take their starting point in the notion of episodic memory (Tulving, 1972), which is the memory of past personal experiences and events, not necessarily shared by others. The use of fMRI and other neuroimaging techniques for the study of lateralization of episodic memory has implicated the medial temporal lobe and suggests that the left and right side are stimulus specific, such that the right medial temporal lobe, and the hippocampus, is activated for items containing visuospatial features while the left medial temporal lobe is recruited for verbalizable items, and that this seems to be related to both encoding and retrieval. However, not only does lateralization of memory follow a verbal/visuospatial gradient but asymmetry of episodic memory is also contingent on novelty versus familiarity and on depth of processing, that is, semantically versus perceptually encoded materials.

As can be seen in the emergence of the hemispheric encoding/retrieval asymmetry (HERA) model (Tulving et al., 1994), another brain structure that has played a key role in recent theoretical models of lateralization of memory is the prefrontal cortex. Although the HERA model has been challenged, and there are other more recent models, it is still a reasonable model for the theoretical understanding of how asymmetry of episodic memory is organized in the frontal cortex.

Altered Asymmetry—Clinical Perspectives

Any theory or model of clinical disorders related to language and speech processing, as, for example, dyslexia and other language neuropediatric disorders, will be unfinished business without taking hemispheric asymmetry into consideration. This is covered in the chapter by Deborah Moncrieff (chapter 19). Similarly, several neurological disorders clearly have a lateralized component, perhaps the most well-known being visual neglect and the neglect syndrome, covered in the chapter by Victoria Singh-Curry and Masud Husain (chapter 18). Recent developments in both structural and functional neuroimaging of patients with schizophrenia and psychotic disorders have moreover shown a greater degree of brain morphological abnormality, particularly in temporal and frontal areas, than previously thought (Williams, 2008). Of particular interest in this context is the fact that areas in the left temporal lobe, overlapping with the planum temporale and Wernicke's regions, seem to be the most vulnerable brain regions in schizophrenia. Since these areas also involve the regulation of language and speech perception, it is a short step to infer that abnormal lateralization of language in schizophrenia may be a critical factor behind the disorder as suggested in chapter 21 by Tim Crow.

It is also of theoretical interest why the same brain region, the planum temporale area, shows structural abnormalities in both schizophrenia and dyslexia, two disorders that from the outside have very little, if anything, in common from an etiological point of view. The important question about similarities in brain asymmetry in individuals with different diagnostic disorders is further pursued in the chapter by Moncrieff, who states that as more and more data are accumulated with neuroimaging techniques like fMRI and PET, it has become more and more apparent that similarly abnormal brain structure is evident in children diagnosed with different developmental disorders, such as autism, ADHD, and dyslexia. She then goes on to ask whether overlapping findings could potentially be due to errors in diagnostic classification of study subjects or whether they may represent systematic and similar alterations occurring in neural systems across several pediatric disorders. The involvement of the same brain structures and similar asymmetries across diagnostic categories is a critical issue in the understanding of hemispheric asymmetry and may also point in the direction of dimensionality rather than categorization when it comes to psychiatric diagnostics and treatment.

A clinical perspective is also evident when it comes to the specialized function of the right hemisphere. Singh-Curry and Husain (chapter 18) point to the interesting fact that it took a long time after the discoveries of Broca and Wernicke that the left hemisphere was specialized for language and verbal functions for researchers to explore whether the right hemisphere could also have corresponding specializations (although this had already been hinted at by Broca). As stated by Singh-Curry and Husain, it was not until the 20th century that the evidence for a special role of the right hemisphere in visuospatial functions began to develop (e.g., De Renzi, 1982). A series of investigations which started in the 1930s and 1940s demonstrated that while insults to the left hemisphere resulted in difficulties with verbal ability, damage to the right hemisphere consistently led to poor performance on tests involving the manipulation of geometrical figures, completion of missing parts of shapes and patterns, and other tasks incorporating the analysis of form, distance, and spatial relationships. These discoveries subsequently led to the realization that damage to the right hemisphere, in particular right posterior parietal lobe lesions, could lead to clinical symptoms related to visuospatial function, the so-called neglect syndrome (see also Heilman, 1995).

As also stated by Curry-Singh and Husain in their chapter, "such a striking deficit in the visuospatial representation of the external world following right-hemisphere damage has fueled the proposal of a special role of the right hemisphere in visuospatial and, more generally, spatial functions." An important consequence of studies of the neglect syndrome is that they have shed new light on the underlying functional organization of the right hemisphere related to attention, visuospatial function, and spatial working memory. This is a nice example of how a clinical syndrome can con-

tribute to advancing our theoretical understanding of the functional integrity of the cerebral hemispheres.

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