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Review

A brain of two halves: Insights into interhemispheric organization provided by near-infrared spectroscopy

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ABSTRACT

The discovery of functional lateralization and localization of the brain marked the beginning of a new era in neuroscience. While the past 150 years of research have provided a great deal of knowledge of hemispheric differences and functional relationships, the precise organization of functional laterality remains a topic of intense debate. Here I will shed light on the functional organization of the two hemispheres by reviewing some of the most recent functional near-infrared spectroscopy (NIRS) studies that have reported hemispheric differences in activation patterns. Most NIRS studies using visual stimuli, which revealed functional differentiation between the hemispheres, have reported unilateral activation, i.e., significant levels of activation in only one hemisphere. Auditory stimuli, including speech sounds, elicited bilateral activation, while the limited number of studies on young infants revealed primarily unilateral activation. The stimulus modality and the age of the participants therefore determine whether the resulting cortical activation is unilateral or bilateral. By combining a review of the existing literature with NIRS results regarding homologous connectivity across hemispheres, I hypothesized that the origin of functional lateralization changes from the independence of each hemispheric region, to mutual inhibition between homologous regions during development. Future studies applying multi-modal measurements along with NIRS and spatiotemporal analyses will further deepen our understanding of the interhemispheric organization of brain function.

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Introduction

The human cerebrum consists of two hemispheres: the left and right hemispheres. In adults, the two hemispheres are not mirror images, but show numerous macroscopic anatomical asymmetries (Toga and Thompson, 2003). The right frontal lobe protrudes anteriorly, and is wider than the left frontal lobe, with the occipital lobe showing the opposite trend. As a result, the volumes of the frontal and occipital regions differ between the hemispheres; the right frontal lobe is larger than the left, and the left occipital lobe is larger than the right. Other anatomical asymmetries include the gentler curve of the left Sylvian fissure (Hochberg and Le May, 1975; Sowell et al., 2002), and the wider area of the left planum

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temporale (Geschwind and Levitsky, 1968; Good et al., 2002). Besides such morphological differences, the left and the right hemispheres show marked functional differences, i.e., brain functions are lateralized.

The functional difference between the two hemispheres was first reported in the domain of language functions, where it was demonstrated that the left hemisphere is dominant in language processing (Damasio and Geschwind, 1984). Our understanding of hemispheric differences and interhemispheric communication was considerably deepened through a series of studies on split-brain patients (for a review, see Gazzaniga, 2000). In addition to the surgical disconnection of the cerebral hemispheres, clinical studies on agenesis of the corpus callosum (AgCC) have improved our understanding of hemispheric interactions (Friederici et al., 2007; Paul et al., 2007). The development of functional neuroimaging methods, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), further facilitated the characterization of the laterality of multiple brain functions. Thus, the different roles of the two hemispheres, and their cooperative function, have long been a fundamental topic in cognitive neuroscience.

In this review, I will focus on the functional organization of the two hemispheres by examining some of the recent functional near-infrared spectroscopy (NIRS) studies that have reported hemispheric differences in neural activation patterns. Because NIRS methodology makes it feasible to record brain activation in infants, many of these studies have compared activation in the left and right hemispheres of infants, and differences between infants and adults. Thus, my main discussion will concentrate on developmental aspects of cerebral laterality. I will combine this review of the literature with our NIRS results on homologous connectivity across the hemispheres, to develop a hypothesis regarding the functional development of the interhemispheric organization of the brain. The importance of NIRS measurements in cognitive neuroscience is demonstrated through the consideration of cerebral specialization and interaction. There have been a number of excellent reviews on the use of NIRS in cognitive neuroscience (Aslin, 2012; Dieler et al., 2012; Gervain et al., 2011; Lloyd-Fox et al., 2010; Minagawa-Kawai et al., 2008; Obrig et al., 2010; Quaresima et al., 2012; Rossi et al., 2012), most of which focused on stimulus-driven activation of the cortex. The present review attempts to merge our knowledge of brain structure with spontaneous and functional activation data obtained by NIRS studies, in order to examine the background neural systems underlying cognitive functions.

Hemispheric differences in brain structure

The recent accumulation of structural evidence from MRI studies has begun to clarify how the brain develops throughout infancy and childhood (Almli et al., 2007; Evans, 2006). One MRI study reported that the left hemisphere of neonates in the first few weeks after birth was larger than the right hemisphere, and that the fronto-occipital asymmetry commonly observed in adults was not present (Gilmore et al., 2007). This study also demonstrated that the gray matter of the occipital and parietal regions grew significantly faster than that of the prefrontal region. In contrast, during the first 2 years after birth, the frontal lobes grew more rapidly than the temporal lobes, and that the right frontal and temporal lobes showed a greater increase in volume than the left frontal and temporal lobes (Matsuzawa et al., 2001). Recently, Tanaka et al. (2012) reported the developmental trajectories of the frontal and temporal lobes from 1 month to 25 years old. The volumetric changes were non-linear in all regions, and gray matter volume reached its peak at an earlier age in the frontal lobe than in other regions. Moreover, the left frontal and temporal lobes continued to increase in volume for a longer period of time than the same regions in the right hemisphere. These studies suggest that development of the cerebral cortex is not straightforward, and that the speed of maturation in the frontal region is selectively accelerated after the neonatal period. The cerebral blood flow pattern at rest also showed hemispheric differences in infancy and early childhood. Although no hemispheric difference could be detected before 1 year of age, there was a right hemispheric dominance between 1 and 3 years of age, and asymmetrical shifts to the left hemisphere after 3 years of age (Chiron et al., 1997). This study suggests that both structural asymmetry and functional asymmetry occur prior to 3 years of age.

Hemispheric differences in brain function

Behavioral studies have suggested that the left and right hemispheres of infants younger than 1 year work differentially (Bertoncini et al., 1989; Holowka and Petitto, 2002). High-density recordings of event-related potentials (ERPs) have also demonstrated the asymmetrical distribution of evoked potentials over the scalp while the subject is hearing phonological or syllabic stimuli (Dehaene-Lambertz, 1997; Dehaene-Lambertz and Dehaene, 1994). More recently, speech perception and face processing have been examined using neuroimaging methods such as fMRI and PET, and the neural activation patterns evoked by speech and face stimuli were reported to be consistent between infants and adults (Dehaene-Lambertz et al., 2002; Tzourio-Mazoyer et al., 2002).

Recent NIRS studies and reviews have compared the laterality characteristics of infants with those of adults. One interesting topic is the relative sensitivity of the left and right hemispheres to the temporal structure of sounds (Minagawa-Kawai et al., 2011a; Telkemeyer et al., 2009, 2011). The sensitivity of the two hemispheres in adults has been extensively debated, and several possible mechanisms have been proposed to explain the relationship to language processing (McGettigan and Scott, 2012; Poeppel et al., 2008; Tervaniemi and Hugdahl, 2003; Zatorre and Gandour, 2008; Zatorre et al., 2002). Telkemeyer et al. (2009, 2011) showed that neural responses to slow acoustic modulations are lateralized in the right hemisphere of neonates, 3-month-old infants, and 6-month-old infants. This trend of right hemisphere lateralization is consistent with the findings of a previous fMRI study in adults (Boemio et al., 2005). However, Minagawa-Kawai et al. (2011a) reported bilateral activation if neonates, in response to both rapidly and slowly modulated sounds. The authors of the previous study state that “our results line up with the previous newborn study, where the evidence for lateralization was scarce (one-tailed *t-test* on 1 channel selected among 6, $0.03 < p_{uncorr} < 0.05$; Telkemeyer et al., 2009)” (p. 9), and they hypothesized that functional asymmetries might develop during early infancy. Although the conclusions of the two studies are not consistent, both are important not only in the context of understanding the acoustic and speech-sound processing of infants, but also in the context of examining the relationship between the two cerebral hemispheres. If the left and right temporal regions develop to utilize different mechanisms, or perhaps different time scales of acoustic processing during early development, the question remains of how these functionally differentiated regions interact with each other. The formation of the brain structure, which connects these homologous regions, namely the corpus callosum, plays a key role in these interactions.

The role of the corpus callosum in functional differentiation

The left and right hemispheres of the human brain are connected by three major commissural fibers: the anterior commissure, the hippocampal (or posterior) commissure, and the corpus callosum, the last of which is the largest (composed of more than 200 million fibers), and exists only in placental mammals. The corpus callosum has a topographical distribution of fiber connections, and can be divided into morphologically distinct subregions, which correspond to the cortical regions that the fibers connect. The fiber size and