

Cerebral Asymmetry and Dominance in Man

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ABSTRACT

The two human cerebral hemispheres are not mirror images of each other. They show anatomical and functional differences that are termed as cerebral asymmetries. The most striking differences in right-handed people are Broca's motor areas of speech in the left inferior frontal gyrus and Wernicke's area for language comprehension and speech production in the left posterior temporal and inferior parietal lobules. These examples have led to the overall concept of dominant left and subordinate right cerebral hemispheres. Other structural asymmetries are revealed in the perisylvian area, surface area around the central fissure, cortical thickness, cerebral rotation, the volume of the lateral ventricle, lateral geniculate body, posterior cerebral and circle of Willis arteries, deep medullary veins, and type of nervous system of individuals. Functional cerebral asymmetries are also reported regarding verbal and linguistic functions, mathematical skills, analytical thinking, functions of corticobulbar, corticospinal and corticobasal pathways, functional organization of the prefrontal cortex (PFC), orbitofrontal cortex (OFC) and ventromedial temporal cortex (fusiform gyrus, FG), as well as amyloid- β deposition and metabolism. Cerebral asymmetries are thought to play an essential role in the pathogenesis of clinical disorders as aphasia, unilateral left brain lesion, adiadochokinesia, autism spectrum disorder (ASD), corticobasal syndrome, Parkinson's disease (PD), Alzheimer's disease, and adolescents with idiopathic scoliosis (AIS). Age and sex related asymmetries have been sometimes postulated. Genetic, environmental and callosal factors are mentioned to underlie the etiology of cerebral asymmetries. Comparatively, functional, and neuroanatomical asymmetries do exist in nonhuman primates.

Keywords: Cerebral asymmetry, morphological, functional, comparative.

INTRODUCTION

The two cerebral hemispheres in man are not morphologically and functionally identical. Based on the magnitude and number of cerebral asymmetries, Dax et al. in 1830 were the first to suggest that some brain functions might be lateralized.

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This suggestion had been confirmed by Broca in 1861 who described a case of expressive aphasia as a result of infarction in the left inferior frontal gyrus of the

cerebral hemisphere. Such an area had been known as Broca's area or motor areas for speech. Later, Wernicke's area as a language comprehensive area was described in the left posterior temporal and inferior parietal regions of the cerebrum. The association of language impairment in case of left hemispheric lesions had led to the assumption of dominance of the left cerebral hemisphere.^[1]

MORPHOLOGICAL AND STRUCTURAL ASYMMETRIES

By comparing the lengths, weights and other parameters of the two cerebral hemispheres, indefinite macroscopic asymmetries were detected. In a horizontal section of the cerebral hemisphere, the

planum temporale appears to be bounded anteriorly by the Heschl's gyrus, laterally by the Sylvian (lateral) fissure and posteriorly by the end of the posterior ramus of the same fissure. It had been reported that the planum temporale was observed to be larger on the left than the right cerebral hemisphere in 65% of examined brains and on the right than the left hemisphere in 11% with no obvious differences in 24% of brains. As a result of enlarged planum temporale, the Sylvian fissure appeared longer and more horizontal on the left hemisphere. These morphological asymmetries were blamed for the functional asymmetry regarding language representation.^[2]

Other morphological asymmetries of the cerebral hemispheres have been reported as: frequent anticlockwise rotation of the cerebrum with wider left occipital pole and wider right frontal one,^[3] restricted incidence of large pyramidal neurons in Brodmann's area 44 and Broca's area 44 only on the left hemisphere,^[4] larger cortical surface area surrounding the central fissure of Rolando on the left side^[5] and detection significantly more neurons in left entorhinal cortex than in the right one.^[6]

A positive relation was detected between the different transverse diameters of the left- and right-hand thumbnails and MRI asymmetry of the volume of the lateral cerebral ventricles in children with developmental delays. It was concluded that the asymmetry of thumbnails could be used as a marker for asymmetry of the lateral ventricles and child developmental delays.^[7]

Interhemispheric structural asymmetries were compared with the lateralization of activity for gesture in the supramarginal gyrus and language production in Broca's area. The more pronounced leftward structural asymmetries were accompanied by greater left-hemisphere dominance for both functions. Conversely, bilateral or rightward functional shift of gesture and language was accompanied by an attenuated leftward asymmetry of the insula.^[8]

The left lateral geniculate nucleus or body (LGN) had been observed to be significantly smaller in volume and different in shape in subjects with dyslexia while no differences were observed in the right LGN. No functional significance of this asymmetry was assumed. Developmental dyslexia is a common learning disability characterized by normal intelligence but with difficulty in reading, writing and spelling skills.^[9]

Morphological asymmetries and variations of the posterior cerebral artery (PCA) in human cadaveric

brains were observed to include aplasia (2.35%), hypoplasia (5.29%), duplication (2.35%), fenestration (1.17%), common trunk shared with the superior cerebellar artery (1.76), direct origin from basilar artery (1.17%) or from internal carotid artery (2.35%), and aneurysm (1.76%). Awareness of these variations is likely to be useful in cerebrovascular procedures.^[10]

A hypothesis has been raised that asymmetry of cerebral arteries sharing in the circle of Willis creates phase difference between the four pressure waves-propagation and reduces downstream cerebral pulsatility.^[11] Using susceptibility weighted imaging (SWI), asymmetric visualization of deep medullary veins (DMV) in patients with acute middle cerebral artery (MCA) stroke, which are difficult to depict under physiological circumstances, is a fast and easy parameter for the prediction of stroke severity.^[12]

Male adolescents with substance use disorder (SUD) versus controls of the same age, sex and IQ, have been reported to show no cortical thickness differences in the region-of-interest (ROI) analyses. Additionally, they have demonstrated significantly less right > left asymmetry in the inferior frontal gyrus (IFG), weaker insular-to whole-cerebrum cortical thickness correlations, and positive association of conduct disorder symptom count with cortical thickness in a superior temporal gyrus cell cluster.^[13]

Dyslexics have shown atypical brain synchronization at both syllabic (slow) and phonemic (fast) rates. In skilled readers, a left hemispheric asymmetry in cortical thickness has been claimed to be functionally related to a stronger left hemispheric lateralization of neural synchronization to the phonemic rate- auditory stimuli. In dyslexics, the same anatomical index is related to a stronger right hemispheric dominance for neural synchronization to syllabic rate- auditory stimuli.^[14]

Schizophrenia is a neuro developmental disorder that is marked by structural abnormalities of the brain and aberrant dermatoglyphics. Directional asymmetry (DA) and bilateral hippocampal volume have been observed to be significantly lower in schizophrenic patients than controls. Significant positive correlation has been also found between DA and palmar ridge count with bilateral anterior hippocampal volume. It is hypothesized that dermatoglyphic markers could be utilized in identifying cerebral structural changes that form the basis for neurodevelopmental pathogenesis in schizophrenia.^[15]

FUNCTIONAL ASYMMETRIES

Cerebral asymmetry is a common feature of human functions. Several studies have proved that the left hemisphere prevails for verbal and linguistic functions, mathematical skills and analytical thinking. Many studies have argued for distinct but complementary contributions from each hemisphere in the control of movements to visual targets.^[16] Moreover, verbal memory is a left hemispheric function while the nonverbal memory is a right one.^[17] Such asymmetries are mentioned to apply primarily to right-handed persons and those with left or mixed handedness show reduced left lateralization rather than a simple reversal of the situation in right handers.^[18] However, it has been clarified that the left primary motor cortex (M1) is more connected with areas involved in the motor system than right M1, and that the right supplementary motor area (SMA) specifically in the posterior part (SMA-proper) is more functional connections than its left counterpart.^[19] Although handedness represents the most striking example of motor asymmetries, other asymmetries as footedness, tonguedness and chewing preferences have attracted several investigator propositions.^[20]

The motor cerebral cortex has been mentioned to present variable asymmetry patterns (left and right dominant, as well as bilateral) for rapid silent syllable repetition (/lalala/./papapa/, known as oral diadochokinesis or DDK) despite the predominantly left hemisphere dominance for language-related activity in Broca's area and the absence of structural asymmetry within the corticobulbar tract. The predominance of dysarthria following left hemisphere infarct is assumed to be probably a consequence of disrupted feedback or input from left hemispheric language and speech planning areas, rather than structural asymmetry of the corticobulbar tract itself.^[21] The degree of hand-preference is not in accordance to the degree of language lateralization because the prevalence of right and bilateral hemispheric language lateralization has been observed to rise with the increasing strength of left-handedness. Thus, the genetic basis of one mechanism defining both hand-preference and language lateralization could not be accepted.^[22]

In autism spectrum disorder (ASD), anomalous functional and anatomical connectivity of the primary motor cortex was discovered with the assumption that network anomalies affecting the basic motor execution

had gone well beyond socio-communicative concepts. Added to this, in right-handed ASD-adolescents, typical left hemisphere dominance is reduced, both anatomically and functionally, with an unusual degree of right hemisphere motor participation.^[23]

In a patient with left brain lesion, transcranial magnetic stimulation of the right motor cortex had evoked contractions of muscles of both hands while no responses were observed from the left hemispheric stimulation. There was an evidence of sensori-motor dissociation and asymmetry of the corticospinal projections, suggestive of reorganization after early unilateral left brain lesion. In certain rare conditions, good hand function is possible with ipsilateral corticospinal reorganization, supporting the role of unexplored mechanisms of motor recovery.^[24]

The ventral temporal cortex (VTC) contains several areas with selective responses to words, numbers, faces, and objects. The temporal fusiform gyrus (FG) had been found to respond to faces. Using electrocorticography (ECoG), electrical brain stimulation (EBS) inpatients implanted with intracranial electrodes in either the left or right hemisphere had disrupted the conscious perception of faces only when it was delivered in the right, but not left, FG.^[25]

It has been agreed that in our daily life we constantly exert sustained and phasic cognitive control processes to manage multiple competing task sets and rapidly switch between them. A variability in the prefrontal hemispheric asymmetry in the intrinsic (i.e., resting-state-related) brain dynamics has been postulated to reflect individual differences in preferentially engaging of either the left-lateralized, phasic or the right-lateralized, sustained cognitive control processes to regulate behavior in response to changing task demands, regardless of the specific cognitive domain involved.^[26]

Corticobasal syndrome is a dysfunction of both cerebral cortex and basal ganglia. In a classical presentation of the corticobasal syndrome, aphasia was observed to be associated with motor dysfunction of the right side of the body, pointing to the involvement of the left cerebral hemisphere. Less commonly, aphasia was conjunct to left-sided motor presentation while dysarthria had no preferential correlation.^[27]

In Parkinson's disease (PD), veering while walking

is reported to be vision-based (asymmetrical perception of the visual environment) or motoric (asymmetry in stride length between relatively affected and non-affected body sides). Interventions to correct walking abnormalities such as veering in PD should incorporate vision-based strategies rather than solely addressing motor asymmetries, and should be tailored to the distinctive navigational profiles of left-side onset of motor symptoms (LPD) and right-side onset (RPD).^[28]

The functional organization of the pre-frontal cortex (PFC) has been explored with a considerable evidence for a left hemisphere (LH) "interpreter". Recent investigations have added evidence for several roles of the right PFC in reasoning, problem solving, and decision-making; focusing on the beneficial complementary role of the right PFC in maintaining and enhancing the role of the left PFC, the "interpreter".^[29]

The type of the nervous system of subjects has been easily demonstrated by the aid of the recently innovated PC software programs. These aids help to differentiate people within groups of the same type of nervous system, to provide an idea about the severity of the hemispheric asymmetry, and to show the results of performance of certain testing tasks. The academic performance of the examinees within a strong type of nervous system is significantly higher than those within a weak type.^[30]

Brain frontal electroencephalogram (EEG) and functional magnetic resonance imaging (fMRI) measures may similarly capture PFC functioning during reward anticipation tasks. Increased left frontal activity is associated with increased left anterior cingulate cortex (ACC)/medial prefrontal cortex (mPFC) and left orbito frontal cortex (OFC) activation. These two measures suggest the role of such regions in reward anticipation processing and point out the pathophysiology of some disorders like depression and schizophrenia.^[31]

In Alzheimer's disease, asymmetric amyloid- β deposition is associated with asymmetric hypometabolism and clinical symptoms. Stronger leftward asymmetry of amyloid- β deposition is associated with more severe language impairment while stronger rightward asymmetry with more severe visuospatial impairment. Similarly, patients with predominance of language deficits have shown more left-lateralized amyloid- β burden and hypometabolism

than patients with predominant visuospatial impairment and vice-versa in several cortical regions.^[32]

CEREBRAL ASYMMETRY AND AGING

On comparing motor performance of the dominant and nondominant hands, older adults have shown a tendency to be less asymmetric compared to young adults, suggesting decreased motor lateralization and functional compensation within the aging brain. It has been also hypothesized that the older the age, the less is the motor asymmetry, and that 'old old' individuals (aged >80 years) tend to have less motor asymmetry than 'young old' individuals (aged <80 years).^[33] Age-related decline in higher cognitive function is also defined. Laterality, reflected as right ear preference for dichotic stimuli, has been found to be increased in persons above 60 years of age.^[34] During adverse acoustic conditions (noise), "cocktail party" listening skills depend on the quality of speech representations in the left cerebral hemisphere rather than compensatory recruitment of right hemisphere mechanisms.^[35]

Episodic memory is a cognitive function that appears to be more susceptible than others to the effect of aging. Young individuals and high-performing older adults, obtaining higher scores on the memory tasks, are reported to exhibit similar performances on episodic memory tasks and both groups have shown symmetrical recruitment of both left and right hemispheric areas during memory retrieval. In contrast, low-performing older adults have demonstrated a greater engagement of the left hemisphere during verbal memory task.^[36]

Acquisition of language skills depends on the progressive maturation of specialized brain networks that are usually lateralized in adult population. Diffusion tractography has been utilized to study the three segments of the arcuate fasciculus connecting Wernicke's to Broca's region (long segment), Broca's to Geschwind's region (anterior segment), and Wernicke's to Geschwind's region (posterior segment). The long and anterior arcuate segments are lateralized before adolescence and their lateralization remains stable throughout adolescence and early adulthood. Conversely, the posterior segment shows right lateralization in childhood but becomes progressively

bilateral during adolescence.^[37]

Adolescents with idiopathic scoliosis (AIS) have been observed to exhibit morphological vestibular asymmetry that is probably determined well before birth. Since the vestibular system influences the vestibulospinal pathway, the hypothalamus, and the cerebellum, it has been assumed that it is a possible cause of later morphological, hormonal and neurosensory anomalies observed in adolescent idiopathic scoliosis. Moreover, the simple lateral semicircular canal (SCC) MRI measurement could be used for early detection of AIS, selection of children for close follow-up, and initiation of preventive treatment before the occurrence of spinal deformity.^[38] Some highly specific visual tasks have been shown to depend on hemispheric specialization. There is a general lateralization of cerebral activation towards the right hemisphere of early visual cortical areas and areas of higher-level visual processing especially in top-down attentional processing. The right hemisphere lateralization of the early visual areas is mentioned to be partly due to an increased volume of grey matter in the right hemisphere. Difference in activation of the superior parietal lobule has been correlated with subject age, suggesting a shift towards the left hemisphere with increasing age.^[39]

CEREBRAL ASYMMETRY AND SEX

Women show less functional asymmetries than men particularly on right hemisphere tasks^[14]. Men with right-hemisphere ventromedial prefrontal cortex (vmPFC) damage and women with left-hemisphere vmPFC damage have demonstrated significantly reduced aversion to risk and ambiguity. Men with damage to the left vmPFC and women with damage to the right vmPFC have shown aversion to risk and ambiguity comparable to participants with left or right-sided brain damage outside the vmPFC, and to participants without brain damage.^[40]

In some recent Russian investigations, the neurons of the central nucleus of the amygdala complex have been studied in histological sections of the brain. The average values of neurons in the left hemispheres of females were insignificantly greater than in the right hemispheres and the reverse happened in males. An association of these gender-related differences to emotional perception in both sexes has been

sometimes attempted.^[41,42]

Mental rotation is a visuospatial task associated with pronounced sex differences. Performance is also affected by gonadal hormones such as testosterone and estradiol. Using fMRI, ten premenopausal women were tested on a 3D mental rotation task during the early follicular and late follicular phases of the menstrual cycle. Change in estradiol between the two phases was confirmed by hormone assays. Brain activation patterns were similar across the two phases, given that the right hemisphere is the dominant hemisphere in visuospatial processing.^[43]

CEREBRAL ASYMMETRY, CEREBRAL BLOOD FLOW AND EXERCISE

During hand motor task performance, the dominant human primary motor cortex is demonstrated to have a stronger blood oxygen level dependent (BOLD) response over the other non-dominant motor cortex. This is accompanied by a higher vascular reactivity in the dominant motor cortex. These reported observations demonstrate a cerebral vascular asymmetry between the left and right primary motor cortices; the origin of which arises from the contribution of large draining veins.^[44]

In temporal lobe epilepsy (TLE) with and without mesial temporal sclerosis (MTS and no MTS), an asymmetry of quantitative cerebral blood flow (CBF) values over non-TLE controls has been elucidated. Hypoperfusion regions in the right TLE-MTS patients have been mainly clustered in the bilateral temporal lobes, frontal lobes, insular lobes, and left caudate nucleus. The right TLE-noMTS have shown hypoperfusion in the bilateral temporal lobes, frontal lobes, right insular lobe, parietal lobe, occipital lobe, and caudate nucleus.^[45]

Exercise is mentioned to induce hemodynamic changes in the bilateral prefrontal cortex (PFC). Asymmetric changes in right and left hemispheric PFC have been detected via continuous measurement of the respiratory exchange and concentrations of oxy-, deoxy- and total hemoglobin during incremental cycling exercise.^[46]

COMPARATIVE STUDIES OF CEREBRAL ASYMMETRIES

Species-related behavioral and brain asymmetries evidently exist in nonhuman species. Specifically, evidence has been given that genes play specific roles in determining left-right differences in behavioral, perceptual, cognitive, functional, and neuroanatomical asymmetries in nonhuman primates. It is hypothesized that hemispheric specialization evolved as a by-product of increasing brain size relative to the surface area of the corpus callosum indifferent primate species.^[47] The presence of handedness asymmetry in non-human animals is debated. However, a recent study has provided evidence for handedness in bipedal - but not quadrupedal - marsupials.^[48]

Magnetization transfer ratio (MTR) has been often used for imaging myelination but it does not possess a high specificity because tissues with nonmyelin such as muscle can also show high MTR. A new magnetization transfer (MT) indicator termed MT asymmetry (MTA) has been utilized as method of myelin imaging in rat brain. High signals in white matter and significantly low signals in gray matter and muscle have indicated that MTA has higher specificity than MTR. MTA could be considered a good biomarker for imaging myelination.^[49]

Grooming is the most common innate behavior in animals. In rodents, it consists of sequences of movements organized in four phases, executed symmetrically on both sides of the animal and creating a syntactic chain of behavioral events. The grooming syntax can be altered by stress and novelty, as well as by several mutations and brain lesions. In mice, induced unilateral lesion of the medial forebrain bundle had resulted in an incompleteness of grooming bouts, decreased number of transitions between grooming phases, and asymmetry in grooming behavior with reduced tendency to groom the contralateral side.^[50]

METHODS OF DETECTING FUNCTIONAL ASYMMETRIES

Techniques for studying functional brain asymmetries include:

1. Analyzing the consequences of damage (e.g. stroke, tumor, degenerative, epilepsy, gunshot, congenital) to an area allows the identification of its function(s).
2. Unilateral injection of barbiturate into the carotid artery leads the ipsilateral hemisphere to be "put to sleep".

3. Using susceptibility weighted imaging (SWI) allows visualization of asymmetric deep medullary veins (DMV) in patients with acute middle cerebral artery (MCA) stroke.^[12]
4. Functional lateralization for language production has been assessed using the well-established verb generation task, fMRI and diffusion-weighted MRI.^[21]
5. Diffusion tractography is used to follow pathways, e.g. of the corticobulbar tract.^[21]
6. Transcranial magnetic stimulation of the cerebral cortex helps to know their functions.^[24]
7. PC software programs are utilized for analysis of data obtained from other methods.^[30]
8. Electroencephalography (EEG) can be used for electrical brain stimulation (EBS) in patients implanted with intracranial electrodes^[25] and usage of electroencephalogram (EEG).^[31]
9. Callosal or other commissures sectioning is used in animals. A part or more of corpus callosum may be congenitally missing in man. All these lead to the "split brain syndrome".^[51]

MECHANISMS UNDERLYING CEREBRAL ASYMMETRIES

The mechanisms that underlie cerebral asymmetry largely operate prenatally since the human brain exhibits morphological asymmetries as early as the second trimester of the intrauterine life and it shows functional lateralization in neonates. The genetic role of a gene model with autosomal dominant inheritance is extensively raised.^[22] Role of environmental factors is also attracted in the processing of cerebral asymmetry; they may modify the development of asymmetry and handedness. Gonadal hormones have been also claimed to underlie some cerebral asymmetries.^[43] Testosterone in early life is thought to slow the development of the left cerebral hemisphere; thus influencing cerebral asymmetry.^[52] Integrity of the corpus callosum is postulated to play a role in the ontogenesis of cerebral asymmetry as it is related to the absence of callosal connections between the asymmetric cortical areas.^[53] Structural asymmetry of the cerebral hemisphere is primarily restricted to small, not large, cortical areas and to areas possessing large population number of neurons.^[54]

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