



Invited Review Article

The Dual Coding Hypothesis of Human Cerebral Asymmetries

Onur GÜNTÜRKÜN, Markus HAUSMANN

Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-University Bochum, 44780 Bochum, Germany



Abstract

This review attempts to formulate a new hypothesis on the neuronal organization of human cerebral asymmetries. In short, we claim that left-right differences of diverse functions are constituted by two different mechanisms. One are neuroanatomical asymmetries of different cortical and subcortical areas. It is assumed that these features develop according to principles laid down in early ontogeny and are established by tight interactions between genetic and epigenetic constraints. We suppose that neuroanatomical asymmetries do not change importantly in adults and thus represent an invariant feature over time. The second mechanism is constituted by dynamic factors that are capable to importantly alter the balance between the hemispheres. As outlined below, we suppose that commissural interactions, which can be asymmetrical by themselves, mediate this effect. In addition, since the efficiency of synaptic transmission at commissural synapses can be altered by gonadal steroids, interhemispheric interactions are sex-dependent and change in women over the menstrual cycle, thereby leading to alterations of functional hemispheric asymmetries. Thus, the degree of lateralization of diverse human functions is equal to the net result of the two factors, a time-invariant and a time-variant one.

Key words: lateralization, gonadal steroid hormones, corpus callosum, sex-differences

Introduction

Before embarking into deeper considerations, some sobering prologema seem to be in place. We know since Broca's seminal contribution (8) that our brain is asymmetrically organized. In this span of time scientists could reveal countless lateralized sensory, cognitive, emotional, or motor functions as well as several dozen

neural systems which display anatomical left-right differences. Despite these discoveries which seem to reflect a true scientific success story, our understanding of the fundamental problems in lateralization research has made little progress. We still lack clear knowledge how asymmetries of anatomy are translated into the lateralized functioning of a whole brain. But we nevertheless assume that anatomical

asymmetries somehow directly determine functional left-right differences and that consequently functional asymmetries are invariant over time. This review intends to challenge this view.

Anatomical Asymmetries – The First Century

“It is quite certain that the two hemispheres of the brain are similar; if cerebral convolutions, indeed, display light and incidental variations from individual to individual, there are none which one could notice between either sides of the telencephalon” (8). Despite this pessimistic beginning on the side of anatomical asymmetries, Broca came to note later that the right hemisphere was larger than the left, without being able to correlate this feature with a lateralized function (7,6). In the decades following these discoveries there was probably no easily measurable neural feature for which subtle asymmetries could not be described, among them cortical surface (65), skull length (32), the medullary crossing pattern of the pyramidal tract (15), as well as the cortical petalia, which are frontal and parietooccipital protrusions of the hemispheres (36). The significance of these studies is probably extremely limited. It is virtually impossible to draw a causal link between a lateralized functional system and such gross measures of the brain. It makes more sense to concentrate on functionally defined areas and to search for lateralized anatomical features that are truly linked to function.

This was the approach taken by several authors over the last hundred years when they concentrated on asymmetries of the sylvian fissure to gain a deeper understanding of the neural basis of language asymmetries (for a recent review see (33)). Here, we will not concentrate on the whole fissure but will only present studies on the planum temporale (PT). The PT is a smooth, triangular structure on the supratemporal plane in the depth of the sylvian fissure. Although it is seen easily in every dissection course, its borders are still a matter of dispute, especially for the caudal ending. Largely neglecting older studies on asymmetries of the PT (46), (19) rediscovered a left-side bias in a sample of human brains and postulated a direct link to

language lateralization. This watershed paper is probably the most cited and one of the most influential publications in modern asymmetry research. It marks the beginning of a truly modern analysis of lateralized structure-function relationships. We therefore will selectively overview research on the anatomy of the lateralized language system.

Anatomical Asymmetries as Revealed in Language Systems

The PT involves the core of the Wernicke area and is therefore activated during phonological processing. Although a left side bias in PT-size thus makes a seductive link to speech processing, scientists faced a surprisingly hard time when trying to proof this connection. Foundas et al.(16) found that language lateralization followed the direction of PT asymmetry in a small sample of patients that underwent the intracarotid test to verify their language lateralization. In a much larger sample, however, Janke and Steinmetz (34) found no significant relationship between dichotic listening scores and PT asymmetry. Likewise, Hellige et al. (30) were also not successful to show this link in a similar study. Moffat et al. (44) used the fused dichotic words test and found that lefthanders with left hemisphere speech dominance had a strong leftward PT-asymmetry, while lefthanders with right speech dominance showed no clear left-right PT-pattern. Thus, it might be conceivable that not the asymmetry of PT as such, but the absolute size of the left PT determines language lateralization. A number of further studies could also not reveal meaningful relations between language lateralization measures from imaging data and PT-asymmetry but showed stronger relations to absolute left PT-size (for review see (23)).

However, the story is more complicated, since Schlaug et al. (53) showed professional musicians with absolute pitch perception to have extraordinary large left PTs. Zatorre et al. (68) were unable to replicate the speciality of absolute pitch perceivers but came to the principally same conclusion for a group of musicians. Professional musicians usually start musical training early in life (usually

before primary school) and remain practicing many hours per day for decades. Thus, they might alter their brain shape in a few critical areas as shown for string players with respect to the motor cortex contralateral to the left hand (14). The fact that musicians show larger left PT-scores casts serious doubt on the initial assumption that PT-asymmetry could be an anatomical fundament of language asymmetry. These doubts are underlined by numerous studies showing PT to be activated not only by speech but also by nonspeech sounds. The biggest problem, however, comes from anatomy itself. The posterior border of PT is defined by the onset of the posterior ascending ramus of the sylvian fissure. This definition has no clear scientific reasoning but simply follows the knife-cut direction as published by Geschwind and Levitsky (19). If the bank of cortex within the posterior ramus would be included into the measurements, the aforementioned asymmetries disappear (23). However, neither the inclusion nor the exclusion of the posterior planum makes any sense without having first shown that the superficial topography under consideration follows cytoarchitectonic delineations. According to Witelson (66) PT as defined in most imaging studies is only a portion of a cytoarchitectonic area that includes parts of the ramus ascendens posterioris of the fissura sylvii. By Von Economo and Horn (13) are, at least to some degree closer to a simpler PT-definition as often used and also find in a very small sample leftward asymmetries. This is supported by Galaburda et al. (17), while Braak (5) was more cautious due to problems in defining the borders of the higher-order auditory cortices. Taken together, the seemingly obvious link proposed by Geschwind and Levitsky (19) turned out to be in no way obvious. The human temporal lobe has some anatomical asymmetries in its external anatomy, but their connection to underlying cytoarchitectonics and to function are still unknown.

The situation is more settled for cytoarchitectonic details. Seldon (55,56) was able to show a number of morphological asymmetries of Wernicke's area in Golgi stains: 1) The Wernicke area and its homotopic counterpart on the right are

constituted by vertically oriented equidistant cellular columns (13) that might correspond to auditory frequency-specific modules; 2) these columns are more wide on the left side; 3) horizontally oriented dendrites are also longer on the left without being able to compensate for the wider intercolumnar distances on this side. These observations might reveal that the horizontal area covered by single neurons allows for a greater input on the left without intermingling with the input from neighbouring columns. Additionally a single auditory axon from primary auditory cortex might innervate less columns on the left side allowing for greater specialization in Wernicke's area. Galuske et al. (18) moved beyond Seldon (55,56) by showing that neuronal clusters in Wernicke's area are spaced about 20% further apart and are "cabled together" with longer interconnecting axons than clusters in area 22 of the right brain. Due to a larger interdigitation of clusters on the left side, left area 22 contains about 30% more distinct subsystems within the same volume of tissue. Because area 22 is larger in the dominant than in the nondominant hemisphere (17), interdigitation of more columnar subsystems can be achieved without reducing the number of columns constituting a particular subsystem. Thus, if these subsystems are tuned to different features, more feature domains could be represented in the left than in the right area 22 without reduction of the number of neurons devoted to a particular feature. This anatomical characteristic may permit a more fine-grained analysis of feature domains, e.g., for the analysis of speech. Not only the posterior, but also the anterior speech area (area 44) shows conspicuous cytoarchitectonic asymmetries. Analyzing 192 neurons from 8 brains, Scheibel and coworkers (51,52) showed that proximal basal dendrites were longer on the right than on the left side, while the reverse was true for distal dendrites in the operculum frontale (Broca's area). Moreover, a detailed analysis revealed that area 44 was more voluminous and more densely packed with neurons on the left side (2). Additionally, Albanese et al. (1) found in 15 of 24 postmortem brains a left and in 3 a right predominance in both weight and cortical surface of Broca's area.

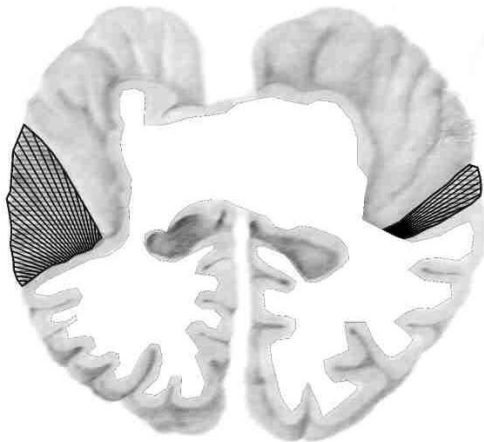


Fig. 1. Size asymmetry of the planum temporale (hatched) on the left and the right hemisphere.

Anatomical Asymmetries – Summary

It is beyond the scope of this review to dwell on all asymmetrical neuroanatomy issues. There are similar studies showing, e.g., asymmetrical patterns at cortical (2) and spinal level (43) that are possibly related to handedness. These studies show that like for speech systems, all analyses that concentrated on measuring the size of certain cortical fields and comparing them between left and right encountered multiple challenges are related to two problems: 1) The interindividual variation is larger than the left-right effect; 2) Cortical fields as seen on MRI do not necessarily coincide with cytoarchitectural boundaries. Only studies that took these boundaries into account or directly used cytoarchitectonic analyses were able to show that the adult human brain is left-right different in a systematic fashion.

At least some of these asymmetries seem to emerge early in life, suggesting an early and genetically determined fate that drives the premature brain into a lateralized architecture (62,64). Human and animal studies were successful in showing how tight interactions between genetic and epigenetic factors are able to constitute structural left-right differences during ontogeny (37,38,58,61). Once these

asymmetries are established, they do not change anymore to an important extent (21). Thus, cerebral asymmetries seem to emerge early in life, changing the local connectivity and the size of functional fields in a lateralized fashion. These structural changes are probably sufficient to alter the processes of the left and the right hemisphere to thereby enable a complementary cognitive architecture. Looking at brain asymmetry from this perspective it seems to be 'static' as soon as the dramatic changes of early ontogeny cease. As shown below, the story of changes never ends.

3.1 Changes of Asymmetry During the Menstrual Cycle

A large number of studies shows that cerebral asymmetries of diverse functional systems are sex dependent (57,28; spatial orientation: (67); face recognition: (48)). Although not all lateralization studies have shown this gender effect, the pattern of a more symmetrical lateralization in females but a more pronounced asymmetry in males pervades in many studies (63). In addition to this more symmetrical lateralization, the data for women also show larger variance (28), supporting the assumption that females display a more heterogeneous pattern of functional cerebral organization (41).

The results of several studies make it likely that these sex effects are at least in part related to gonadal steroid hormone differences between genders. One implication of this finding is that alterations during steroid fluctuations in the menstrual cycle should lead to changes in cerebral asymmetries. Thus, if lateralization in women is modulated by gonadal hormonal fluctuations, it is very likely that female data are on the average less asymmetric and more variant, since women participating in lateralization experiments are very likely to be tested at different phases of their menstrual cycle. These results would further imply that cerebral asymmetries are not static but change dynamically over time.

Indeed, asymmetry changes during the cycle have been shown, but different authors have provided a remarkably controversial picture of the lateralized events

during menstrual cycle. Some studies showed greatest asymmetries in figure recognition (4), dichotic listening (50), and spatial bisection (40) during the high steroid hormone phase, while others found during the same timeframe no asymmetry in face processing (4) and lexical decision (10). Other studies have revealed strongest lateralization patterns during the low steroid menses in face decision (29), figural comparison (49) and dichotic listening with verbal (42) or with musical stimuli (50). This study (50) found complementary shifts in asymmetry with a greater right ear advantage for the verbal task during midluteal phase, and a greater left ear advantage for the music task during menses.

Some contradictions arise due to the lack of hormone assessment in most studies, which inevitably increases the data pool with women tested outside the optimal time window. The extent of this problem is shown in a study by Gordon et al.(20), in which half of the female subjects had to be eliminated from the analyses when post hoc hormone assays revealed these subjects not to have been in their expected cycle phase. An important variable further confounding the issue is the repeated measures design itself. As shown by Hausmann and Gunturkun (27) women show hemisphere-specific changes from the first to the second session, independent of gonadal hormones. Without statistically controlling such session effects, unreliable data patterns are likely to occur.

The first study controlling all of these confounding factors tested cerebral asymmetries in three visual half-field tasks, usually revealing a right hemisphere- (face discrimination, figural comparison) and a left hemisphere-advantage (lexical decision) (26). Three groups of subjects were tested: A group of normally cycling young women, a group of men, and a group of postmenopausal women. All subjects were tested twice: normally cycling women once during menses and once during the midluteal phase (day 20 – 22); men and postmenopausal women in temporally corresponding sessions. This study revealed that young women only show asymmetrical performance measures during menses, but less pronounced functional asymmetries during the midluteal phase. Men and

postmenopausal women evinced stable asymmetries for all three tasks. At least for the figural comparison task we showed an increase of progesterone to correlate with a decrease of functional asymmetry by way of enhancing the performance of the visuospatially subdominant left hemisphere.

In all studies reviewed up to now women were tested twice or triple. Such a design pays no regard to the individual cycle length and is unable to monitor alterations outside the timepoints of testing. Therefore, Hausmann et al.(25) analyzed functional cerebral asymmetries over a period of 6 weeks with 15 testing sessions by concomitantly measuring progesterone, estradiol, testosterone and the gonadotropins LH and FSH. Again the data of this study showed especially progesterone to reduce asymmetries for the figural comparison task by increasing left hemisphere performance. One important prediction from these studies is that aging subjects should show sex-dependent changes in their cerebral asymmetries since women should display a different pattern before vs. after menopause while no comparable alterations are to be expected in men. Indeed, as Hausmann et al.(24) tested 92 participants (50 young [mean age: 26.3 years]: 23 males, 27 females, 42 old [mean age: 63.8 years]: 22 males, 20 females) for visual-field asymmetries, they revealed that on a figural-comparison task, a left-visual-field advantage was marginally decreased with age in the men, but significantly increased in the women. This is exactly what would be expected if especially left hemisphere performance as tested in the figural comparison task is decreased due to a reduction of progesterone levels after menopause.

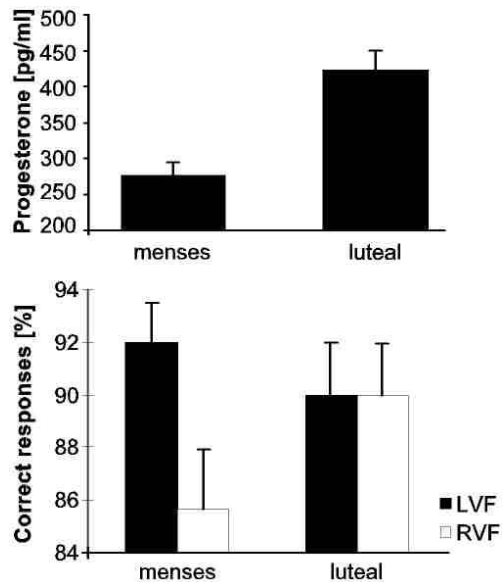


Fig. 2. Changing saliva progesterone levels during the menstrual cycle (upper graph) coincide with alterations of functional cerebral asymmetries in women (lower graph). During menses (cycle day 2), female subjects evince a significantly higher percentage of correct responses in the left visual field (LVF) than in the right visual field (RVF), indicating a right-hemisphere advantage in the figural comparison task. During the luteal cycle phase (cycle day 22), these functional asymmetries are reduced in the same subjects. Thus, the typical left visual field advantage, indicating a right-hemispheric specialization, is only significant during menses, while no hemispheric differences are present during the luteal phase.

3.2 The Hypothesis of Progesterone-Mediated Hemispheric Decoupling

Overall, these results demonstrate a reduction of lateralization during the luteal phase, at least for some lateralized tasks. The repeated demonstration of a progesterone-effect makes it likely that it is this gonadal steroid hormone which exerts a prime role for the changes in asymmetry level. Progesterone is known to suppress the glutamate-induced excitatory responses

of neurons by an attenuation of non-NMDA glutamate-receptor (59). Physiological doses of progesterone reduce the excitatory glutamate responses by 87% (60). Progesterone also augments the inhibitory neuronal response to GABA (59). Thus, an increase of progesterone during the luteal phase decreases the first excitatory EPSP by decreasing non-NMDA receptor efficiency and by augmenting the GABA responses.

But how would these progesterone-effects ultimately alter functional asymmetries? Several neuropsychological models suggest that interhemispheric cross-talk is one of the most essential mechanisms in causing cerebral asymmetries (31). The most widespread view in explaining cerebral asymmetries by callosal mechanisms is reciprocal inhibition in which a stimulus-specific activation of one of the hemispheres inhibits the other one during task processing (11, 9). Thus, it is possible that the progesterone-effect on left-right interactions is mainly due to changes in callosal transfer.

The corpus callosum is mostly constituted by excitatory and glutamatergic fibers that terminate on pyramidal neurons which then activate GABAergic interneurons (12). These activated inhibitory cells then induce a widespread inhibition in homotopic regions of the contralateral hemisphere. Thus, the corpus callosum does not simply exert an excitatory or inhibitory action on the contralateral hemisphere, but rather induces brief excitatory postsynaptic potentials (EPSP), followed by prolonged inhibition (IPSP). We therefore propose that progesterone reduces cortico-cortical transmission by suppressing the excitatory responses of neurons to glutamate, as well as by enhancing their inhibitory responses to GABA. The combined effect should result in the functional hemispheric decoupling and thus to a temporal reduction in functional asymmetry.

It is even possible that the corpus callosum is composed of different channels that are asymmetrically organized by themselves. Experiments with animals have already shown this to be the case (22,35). In humans, Marzi et al.(39) performing a meta-analysis of different lateralized reaction time tasks also concluded that visuo-motor

information transmission was faster from the right to the left hemisphere. This finding has recently been supported by Nowicka et al.(46), who showed that, for certain stimuli, interhemispheric transmission time was shorter for information transfer from the unspecialized hemisphere to the specialized one, than transfer in the opposite direction. A convincing electrophysiological demonstration of this effect comes from Nalcaci et al.(45) who analyzed the frequency components of visual evoked potentials elicited by the reversal of checkerboard patterns presented in visual half fields. Especially the activation of fibers contributing to the theta band were significantly faster from the right to the left hemisphere.

3.3 The Dual Coding Hypothesis of Cerebral Asymmetries

The first part of this paper reviewed studies from the language system that clearly showed multiple anatomical asymmetries which constitute the neuronal fundament for the functional asymmetry of the human speech system. Similar results exist for other lateralized systems. Thus, cerebral asymmetries seem to result from structural left-right differences that develop very early in ontogeny to then determine functional asymmetries. The second part provided a considerably different picture. Here, functional asymmetries were variable over relatively short timeframes, driven by cellular changes exerted by gonadal steroid hormones, particularly progesterone. This view of asymmetries is a much more dynamic, complex, and variable one. We suppose that both aspects together determine the architecture of asymmetries. Thus, lateralized systems would be dually coded. One code is (relatively) static and would result from the continuing asymmetry resulting from anatomically lateralized streams of processing. The second code is dynamic and changes asymmetries by altering interhemispheric interactions. If these commissural crosstalk is already asymmetrically organized, it might even be possible that dynamic factors would be able to modify some of these lateralized interhemispheric channels without changing others. Functional cerebral asymmetries

would then be constituted by static factors established in ontogeny and by multiple dynamic factors changing over short times during the whole lifetime.

İnsan Beyin Asimetrilerinin İkili Kodlama Hipotezi

ÖZET

Bu derleme insan serebral asimetrilerinin nöronal düzenlenmesi ile ilgili yeni bir hipotezin formüle edilmesi üzerine hazırlandı. Kısaca, biz değişik işlevlerin sol-sağ farklılıklarının iki ayrı mekanizma ile oluştuğunu iddia etmekteyiz. İlki farklı kortikal ve subkortikal alanların nöroanatomikal asimetrileridir. Bu özelliklerin erken ontogeni sırasında ortaya konan ilkeler doğrultusunda genetik ve epigenetik baskılama arasındaki sıkı etkileşimden ortaya çıktığı varsayıldı. Nöroanatomik asimetrilerin erişkinlerde çok önemli değişikliklere uğramadığı savındayız ve böylece zamanla sabit bir özellik olarak süregelmektedir. İkinci mekanizma ise hemisferler arası dengeyi önemli ölçüde etkileyebilecek dinamik faktörlerden oluşmaktadır. Aşağıda belirtildiği gibi, tek başına asimetric olabilen kommissural etkileşimin bu sonucu doğurduğunu varsayıyoruz. Buna ek olarak, komissural sinapslardaki sinaptik iletimin etkisinin gonadal steroidler ile değiştirilebileceğinden, hemisferler arası etkileşim cinse bağlıdır ve kadınlarda adet siklusünce değişmektedir ve böylelikle fonksiyonel hemisferik asimetrilerin değişmesine yol açmaktadır. Bu sonuçla, farklı insan işlevlerinin lateralizasyon dereceleri, biri zaman-sabiti diğeri zamanla-değişen iki faktörün net sonucuna eşit olmaktadır.

ANAHTAR SÖZCÜKLER: lateralizasyon, gonadal steroid hormonlar, corpus callosum, seks-farklılıkları

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Correspondence

Onur Güntürkün, Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-University Bochum, 44780 Bochum, Germany
Phone: 0049-234-3226213
Fax: 0049-234-3214377
Email: onur.guentuerkuen@ruhr-uni-bochum.de

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