

Laterality in living beings, hand dominance, and cerebral lateralization

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SUMMARY

To date, lateralization in living beings is a phenomenon almost mythologically unexplored. Scientists have proved that lateralization is not exclusively a human feature. Investigations in molecular biology, protein structure, mobility of bacteria, and intracellular lateralization in ciliates, shows important and universal nature of lateralization in living systems. Dominant lateralization implies the appearance of a dominant extremity, or a dominant sense during the performance of complex psychomotor activities. Hand dominance is usually defined as a tendency to use one hand rather than another to perform most activities and this is considered to be the most obvious example of cerebral lateralization and exclusive characteristic of humans. However, there are some exceptions in other species. The dominant hand is able to perform more complex and subtle manual tasks than the non-dominant hand, and this behavioral superiority is the absolute result of additional cerebral support. The asymmetry of brain organization was confirmed in rats, chimpanzees, dogs and birds, some fishes and lizards. The relationships between hand dominance with brain structure and function remain far from clear. For a long time, lateralization was considered unique to humans, but recently it has become clear that lateralization is a fundamental characteristic of the organization of brain and behavior in all vertebrates. It has been questioned to what extent lateralization in humans and other vertebrates may be comparable.

Keywords: laterality; handedness; cerebral dominance

LATERALITY IN LIVING BEINGS

Lateralization may be defined as a localization of function, or activity on one body side which is dominant over the other [1]. To date, lateralization in living environment is a phenomenon not explored satisfactorily. Scientists have proved that lateralization is not exclusively a human feature. Investigations in molecular biology, protein structure, mobility of bacteria, and intracellular lateralization in ciliates, show important and universal nature of lateralization in living systems [2]. Morphological asymmetry is a common feature of animal body plans, from shell coiling in snails to organ placement in humans [3]. Left–right asymmetries of brain and behavior are now known to be widespread among both vertebrates and invertebrates and can arise through a number of genetic, epigenetic, or neural mechanisms. A right-hemisphere dominance for emotion seems to be present in all primates so far investigated, suggesting an evolutionary continuity going back at least 30 to 40 million years [4]. Based on the current body of literature, the general perception remains that while other animals may demonstrate some lateralized behaviors, no other animal shows this trait to an equal level of significance as population-level right-handedness in humans [5].

Dominant lateralization implies the appearance of a dominant extremity, or a dominant sense during the performance of complex psychomotor activities. The lateralization ap-

pears as right and left at the same time, equal by function, symmetrical in the performance of activities [1]. Dominant lateralization appears as right, which is most often, or left, which is much rarer. Lateralization in humans is determined at the level of upper extremities, at the level of the senses of sight and hearing and at the level of lower extremities [1].

A fundamental question which as yet remains unanswered is why laterality evolved at all. One of the explanations proposes that lateralization may serve a double purpose. It maximizes the skill and strength level and reduces duration of dependence of children. Secondly, it expedites or facilitates the “fight and flight” reflex response for dexterous individuals [6]. No satisfactory explanation has been offered as to why and how laterality in living beings evolved [6]. Laterality is one of the central topics of the development of neuropsychology and it is an inexhaustible inspiration for researchers.

HAND DOMINANCE

Hand dominance is usually defined as a tendency to use one hand rather than the other to perform most activities, and this is considered to be the most obvious example of cerebral lateralization and exclusive characteristic of humans [7]. As always, every rule has its exceptions – parrots that live in Australia, on the Indonesian archipelago, and on the Pacific islands, as well as one species of frogs. Both

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species show a surprising dominance of the right extremity, which can only be represented by “blind street” in evolution [8]. Around two thirds of chimpanzees are right-handed, especially in gesturing and throwing [6]. In essence, primates generally exhibit mixed handedness. The reason that primates do not exhibit consistent handedness is due to the fact that they use their hands and arms for locomotion. It is also observed that when the supporting limb tires, chimpanzees change hands. Sometimes the fishing-dominant hand becomes the supporting hand and vice versa. In this context, having a dominant handedness would be dangerous and would impair food-gathering [6]. Human/animal partition is no longer tenable, and scientists are reviewing the following four (nonexclusive) possible drivers for the origin of population-level right-handedness: skilled manipulative activity, as in tool use; communicative gestures; organizational complexity of action, in particular hierarchical structure; and the role of intentionality in goal-directed action. Fully testing these hypotheses will require developmental and evolutionary evidence, as well as modern neuroimaging data [9].

The question emerges on what is the main discriminating agent between *Homo sapiens* and other mammals, which made the human species predominantly right-handed during the course of evolution [10]. Handedness, particularly right-handedness prevalence of up to 93%, has been demonstrated in the 35,000-year-old remains of a Neanderthal and 500,000-year-old tools of hominids [6].

In any case, the dominant hand is able to perform more complex and subtle manual tasks than the non-dominant hand, and this behavioral superiority is the absolute result of additional cerebral support [2]. One meta-analysis, examining the incidence of sinistrality involving 81 studies from Africa, America, Asia, and Australia, showed that the proportion of left-handedness ranged from 5% to 30% [6]. One study of a large sample ($n = 2,546$) of primary schoolchildren in Belgrade, Serbia, reports a prevalence of left-handedness as 7.6% [11]. Another study among Belgrade high school students ($n = 1,189$) found a slightly lower prevalence of 6.8% [2]. The proportion of strongly left-handed persons was only 3.3% among university students in Belgrade ($n = 1,113$) [12]. Our fourth study was performed on adult residents of the Stari Grad municipality in Belgrade ($n = 1,202$), which reported the proportion of left-handedness of 5% [13].

Some people do not consistently use the dominant hand, i.e. they prefer one hand for one manual activity, and the other one for another activity. This situation is described as “mixed-handedness” [1]. In contrast to this, “ambiguous handedness” is inconsistent use of the dominant hand for the same manual activity [1]. There is also an inconsistency between the hand dominance and feet or eye dominance [1]. Intuitively mixed-handedness may seem advantageous in almost every context, as if a person had two equally dexterous hands. No satisfactory explanation has been offered as to why and how single-handedness evolved. Mixed-handedness and ambidexterity are exceedingly rare. Some studies report that 3.7% of the population is mixed-handed; ambidexterity is very

rare with no reported prevalence in the literature [6]. To study handedness variations in humans, it is important to choose typical tasks among human populations from different cultures. Thus, some tasks commonly used in Western societies to measure handedness, such as writing or teeth brushing, are meaningless in other cultures [14]. Despite strong neuropsychological correlates for handedness, methods of assessment are not uniform or consistent across development [5]. What is currently lacking is a way to clearly identify the left-hander categories in order to better estimate fitness costs and benefits associated with each category [14].

Certain studies have shown that social and cultural factors may alter the “natural” dominant hand in three ways: a) changing hand dominance for one activity without changes in hand dominance for other activities that are carried out with one hand; b) reducing the degree of hand dominance; c) completely changing hand dominance, which results in reducing the prevalence of left-handedness in the population [15]. For example in China, there is a strong social pressure for right-handed writing and eating, which has drastically decreased the proportion of left-handers for these tasks compared with other tasks [14]. Studies show that there are 13% of left-handers in their late twenties, and less than 1% of left-handers among persons in their eighties [2]. This finding could be explained by the fact that the socio-cultural pressure against left-handed people was much more pronounced in the past than it is today, when this attitude is much more liberal. Another possible explanation is based on the assumption of a shortened lifespan of left-handed people [16]. The first study that tested the possibility of social modulation affecting behavioral lateralization in animals was the study on chicks [17]. An ancient debate between Plato and Aristotle on handedness is well-known. Plato, a right-handed Greek philosopher, argued that the hand dominance was a learned trait, whereas Aristotle, his left-handed student, claimed in his *Metaphysics* that people are either right-handed or left-handed by nature [18].

CEREBRAL LATERALIZATION

Initially, it was thought that the entire left hemisphere was dominant for most neurological functions and that the right hemisphere was subdominant [19]. This standpoint was based on the first series of studies revealing that lesions in the left hemisphere were responsible for the impairment of such an important and visible task such as speech [1]. In the following phases of the research it was observed that the right hemisphere could be dominant in left-handers. Speech and laterality movement are noted as a whole and are determined by each other. In addition, where a predominance of hand and speech appears, the dominance for all other functions of the brain is also expected [2]. The asymmetry of brain organization was confirmed in rats [20], chimpanzees [21], dogs [22], and birds [23, 24]. It was even found among some fishes [17] and lizards [25]. Inconsistent asymmetry of brain orga-

nization was found in cats [26]. Chimpanzees also show left-sided enlargement in two cortical areas homologous to the main language areas in humans, i.e. in Broca's and in Wernicke's area. Even chimpanzees and dogs, as well as many other species can learn to respond to simple spoken instructions, but cannot produce anything resembling human speech [4]. After Broca's investigations, interest flagged for a while, but was revived a century later, in the 1960s, with the study of a patients who had undergone split-brain surgery, in which the main commissures connecting the two hemispheres were cut as a means of controlling intractable epilepsy [4]. Testing of each disconnected hemisphere again revealed that the left hemisphere is specialized for language and the right hemisphere for emotional and nonverbal functions [4]. This work won Roger W. Sperry the Nobel Prize for Physiology and Medicine in 1981. Evidence that the right hemisphere was more specialized for perception and emotion also led to speculation, some of it far-fetched, about the complementary roles of the two sides of the brain in maintaining psychological equilibrium [4].

Until the 1960s it was believed that the functional asymmetry is an exclusive characteristic of the human species. However, studies have shown that canaries stop singing as a consequence of lesions only in the left hemisphere [23]. Left-hemisphere dominance for vocalization has been shown in mice and frogs, and may well relate to the leftward dominance for speech – although language itself is unique to humans and is not necessarily vocal, as sign languages remind us [4]. Sherman and collaborators have shown the asymmetry in the rat cerebral hemispheres, or other functional asymmetry, such as the position of their tail and their activities in the open air [27]. In the house mouse, the ultrasonic calls emitted by young mice to evoke maternal caring behavior are preferentially recognized by the left hemisphere [28].

Some progress in the study of cerebral dominance was achieved in the second half of the 20th century by the introduction of non-invasive techniques that are now commonly applied, such as the functional transcranial Doppler sonography and functional magnetic resonance imaging. Functional transcranial Doppler sonography measures cerebral blood flow in accordance with the neuronal activity in the anterior, middle, and posterior cerebral arteries [2]. This method continuously registers blood flow in accordance with brain activity, provides an excellent temporal resolution compared to other neuroimaging techniques, and is simple for use. It is applicable for patients with whom good cooperation cannot be established, as well as for children. This method has shed light on the organization of the hemisphere itself, within the cognitive, motor and sensory function in adults and children [29]. Post-mortem studies were carried out and have shown an initial substrate for functional asymmetry [30]. It is interesting to mention that several of the gross anatomic asymmetries in both fetal and mature human brain were demonstrated in the fossil skulls of our ancestors [19]. Scientists have shown that *planum temporale*, a triangular area situated on the superior temporal gyrus, represents a structural marker

for asymmetry of the cerebral hemisphere, and believe that their study will contribute to a better understanding of the origin of lateralization [31]. Neurochemicals as well as structural asymmetry must be taken into account if one is to understand lateral differences in function [31].

ORIGINS AND ASSOCIATION BETWEEN HAND DOMINANCE AND CEREBRAL LATERALIZATION

The simplest theory of lateralization, which is widely accepted, is that patterns of asymmetry are strongly determined genetically. It is well-known that the left hemisphere of the brain is typically dominant for speech and motor activity, while the right hemisphere is responsible for the artistic aptitude, spatial orientation, attention, and many aspects of emotional life [19]. According to this, the patterns of anatomical, biochemical, and functional asymmetry of brain organization in humans, as in the animal kingdom, are strictly genetically determined [19]. Two left-handed parents produce the highest proportion of left-handed children, i.e. approximately 30–40% [32]. The incidence of left-handedness is higher when the mother is left-handed and the father is not, than when the father is left-handed and the mother is not [17]. One of the most influential and widely cited genetic models was called the Right Shift Theory or Theory Shift to the Right by Marian Annett [33]. One of the key settings of Annett's theory is the distribution of the manual dexterity between the left and the right hand. In the world of other primates and lower animal species, the distribution is in the form of a normal curve. Simply put, chimpanzees, cats, birds, etc. are equally skilled with both left and right extremities, which are equally frequently used. The distribution is normal and identical to *Homo sapiens*, except that it is "moved" to the right (right shift). That distribution shift to the right is genetically coded, and the specific gene responsible (the so-called Right Shift Gene) was not destined to produce the dominance of the right hand, but to induce a specific cerebral asymmetry, i.e. to induce a neurological speech center in the left cerebral hemisphere during the earliest stages of development. As a result, the right hand appears as dominant in relation to the left [33]. If left-handedness were purely genetically caused, both identical twins would have identical dominant handedness. Studies have reported that left-handedness occurs in only 76% of twins [34]. Therefore, large studies with better genome coverage are needed to clearly identify the genes involved in the relative hand skills and hand preferences [14]. This may either suggest that the specific deviations, such as the twin, sex, and maternal effects, may be best explained by the environmental factors, as suggested in the literature [17]. The associations between left-handedness and various health problems have often led to a distinction between the pathological left-handedness, which would arise from developmental stresses, and the familial left-handedness which would be due to genotype [35]. This hypothesis considered that some people are left-handed because they have suffered different types of pathology. The in-

creased proportion of lefthanders in clinical populations with central nervous system disorders (e.g. schizophrenia, epilepsy, mental retardation or learning disabilities) can be explained by the claim that early brain insult may cause the individual to switch to the opposite hand for unimanual activities [36].

The modification of dominance by intrauterine environmental changes increases diversity to a far greater extent than a rigid genetic mechanism would allow [19]. Geschwind and Galaburda [19] pointed out that “the lateralization is a central topic in biology and medicine, not simply a secret interest in a small number of researchers.” If living beings were genetically predestined to be right-handed, then left-handedness, as some believe, may be considered the failure to be right-handed. Scientists have tried to explain what type of development mistakes have been made. They suggested the possible factors that lead to developmental abnormalities and irregular, or “anomalous” brain dominance; the anomaly is considered to be everything that does not fit the majority and different from the usual standards [19]. Particular attention was paid to the intrauterine environment and factors acting during intrauterine development. In the womb, male and female fetuses share the same maternal and placental hormones. It has been found that sex hormones, such as testosterone, may affect the proliferation and migration of neurons in the brain of the fetus in the critical periods of the development, by acting on the appropriate hormone receptors and enzymes [19]. Testosterone receptors have been identified in the nerves and other tissues in the body. In experimental studies, plasma testosterone in male rat fetuses increases rapidly when mother is exposed to stress [19]. A sudden increase in the level of testosterone in the womb under the influence of stress, combined with an additional testosterone from the testicles, can cause a slow and irregular development particularly of the left hemisphere, because it develops more slowly than the right [19]. This may be one of the explanations why left-handed people are more frequent in men. It is proposed that left-handedness in females can be associated with increased sensitivity of testosterone receptors, but with elevated levels of this hormone in utero [19]. This model has also undergone numerous criticisms [37].

The birth-stress model is the most controversial explanation for the origin of left-handedness [38]. This model radicalized previous interpretation of pathological left-handedness, noting that each case of non-right-handedness is pathological. According to this, non-right-handedness originates from stress at birth, primarily in the firstborn child and in fourth and subsequent births; according to this model, all types of non-right-handedness can be considered pathological side-effect of this stress [38]. This finding is supported by the higher incidence of left-handedness in twins compared with singletons, simply because twins may be more exposed to birth stress [17].

Some studies have shown that the energy that the brain of the male fetus receives during exposure to ultrasound can affect the migration of neurons and consequently produces anomalous cerebral dominance [39]. One study

also confirmed the association between exposure to ultrasound in pregnant mothers and later left-handedness in boys [40].

It could also be interesting and easy to study the effects of pregnancy during different seasons and under differing conditions of light, temperatures, and other variables [2]. There are studies that have examined the effect of light on bird eggs and later development of behavioral lateralization [17]. Research in Serbia has shown that maternal cigarette smoking during pregnancy and APGAR score less than 7 at birth were significant risk factors for left-handedness [41].

Handedness and cerebral asymmetries are detectable even in the fetus. In photographs of the brains of 16-week-old fetuses one can observe the typical asymmetry similar to the adult brains [4]. A new study shows a leftward asymmetry of the choroid plexus in two thirds of first-trimester human fetuses. This is the earliest brain asymmetry so far identified and may be a precursor to other asymmetries, including that of the *temporal planum*, which is evident from the 31st week of gestation [4]. Ultrasound recordings have shown that by the 10th week of gestation, the majority of fetuses move the right arm more than the left, and from the 15th week, most suck the right thumb rather than the left – an asymmetry strongly predictive of later handedness [4]. Although these data suggest that predispositions for handedness are already present early in ontogeny, they do not exclude a role for environmental factors affecting lateralization later in life [17]. Since both hand preference and language asymmetries are expressed very early, even before birth, a systematic comparison of the very early development of both behavioral traits is needed to understand this relationship. At present, such data are clearly lacking. Fagard [42] concludes that this evidence favors the view that the two asymmetries develop relatively independently.

It has long been thought that speech and language in a broader sense are inseparably linked to the dominance of the hand, but this relationship was never simple and it is not easily explained [1]. Just to illustrate the complexity of these relations it should be said that while almost all (98%) right-handed persons have speech center located in the left hemisphere, which is a fact established in the second half of the 19th century, the vast majority (70%) of left-handed persons also have speech center located in the same hemisphere [43]. Nevertheless, there are also cases with bilaterally positioned speech center. The latter are almost exclusively left-handed individuals, and very rarely right-handed [43]. Some authors believe that about 30% of lefthanders have the speech center in the right hemisphere, or that it extends through both brain hemispheres [44]. Recent studies suggest that neuropsychological substrate for lateralization of speech and hand dominance may not be the same and that there is an independent influence on the development of each of these dominations, which confirms several new genetic and neurological studies [45, 46]. Unfortunately, in animals even less is known about typical development and to what extent early manipulations still exert their effect in adulthood. Such long-term

studies take time, but are very relevant for further progress in the field [46].

CONCLUSION

In general, the relationships between hand dominance and brain structure and function remain far from clear. For a long time, lateralization was considered unique to humans, but recently it has become clear that lateralization is a fundamental characteristic of the organization of brain and behavior in all vertebrates. Animal models open new and exciting insight into the function and evolution and provide the opportunity to experimentally study the causes and consequences of lateralization. It has been questioned to what extent lateralization in humans and other vertebrates may be comparable. It is likely that humans may have species-specific adaptations in their lateralized be-

havior. This may explain the strong human lateralization in handedness, but lateralization of brain and behavior, being such a fundamental aspect of the organization in vertebrates, must share common principles for humans and other vertebrates. There is evidence for both genes and environment to affect the development of behavioral lateralization, but evidence for both, and especially their interaction, is surprisingly incomplete. With the identification of the human genome, and the use of animal models, we believe that substantial progress can be made in the near future.

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Латерализованост живих бића, доминантност руке и церебрална латерализација

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КРАТАК САДРЖАЈ

Латерализованост живих бића до данас је феномен који је готово митолошки неистражен. Научници су доказали да латерализованост није искључиво карактеристика људске врсте. Истраживања у молекуларној биологији, структури протеина, мобилности бактерија и интрацелуларној организацији код цилијата показују значајну и универзалну природу латерализованости у живим системима. Доминантна латерализованост подразумева појаву водећег екстремитета, или водећег чула током обављања сложених психомоторних активности. Доминантност руке се обично дефинише као тежња да се користи једна рука радије него друга за обављање већине активности и ово се сматра најочигледнијим примером церебралне доминације и искључивом карактеристиком људске врсте. Међутим, постоје изузеци

и код других врста. Доминантна рука је у стању да обавља сложеније и суптилније мануелне активности од недоминантне руке, а ова бихевијорална супериорност је апсолутни резултат додатне церебралне подршке. Асиметрија мождане организације потврђена је код пацова, шимпанза, паса, птица, неких риба и гуштера. Односи између доминантности руке са структурама и функцијама мозга још увек су нејасне. Латерализованост се дуго сматрала искључивом карактеристиком човека, али не тако давно постало је јасно да је латерализованост основна карактеристика организације мозга и понашања код свих кичмењака. Остаје питање у којој мери се латерализација код људи и других кичмењака може упоређивати.

Кључне речи: латерализованост; доминантност руке; церебрална латерализација

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