

EVOLUTION AND DEVELOPMENT OF BRAIN ASYMMETRY, AND ITS RELEVANCE TO LANGUAGE, TOOL USE AND CONSCIOUSNESS

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A brain is said to be asymmetrical or lateralised if one hemisphere is structurally different from the other, or if each hemisphere controls a different set of functions. If the majority of individuals in a population have asymmetries of the same kind and in the same lateral direction, we say that there is hemispheric specialisation. For a long time Western science argued that lateralisation or hemispheric specialisation was a unique characteristic of humans, explaining our "superior" abilities in tool use and language (reviewed by Bradshaw & Rogers, 1992). Indeed, there are still some who essentially adhere to this notion at the present time, seeing cerebral asymmetry as unique to humans at least in its extent, pattern and bias within the population (Corballis, 1991). Brain lateralisation has also been considered as providing a possible basis of consciousness (Eccles, 1989; and reviewed by Rogers, 1995a). Furthermore, group differences in brain asymmetry have been variously used in attempts to provide biological explanations for sex differences in behaviour (see below), schizophrenia (Gruzelier & Floor-Henry, 1979; Nasrallah, 1982), stuttering, dyslexia (Dunlop & Dunlop, 1974), alcoholism (Nasrallah, Keelor & McCalley-Whitters, 1983; Ellis & Oscar-Berman, 1989) and, as a current fashion, sexual orientation (Geschwind & Gallaburda, 1987; McCormick, Witelson & Kingstone, 1990; Dellatolas, Annesi, Jallon, Chavance, & Lellouch, 1990). In every case, the behaviour in question is tied to a difference in brain asymmetry said to be caused biologically by the action of genes or hormones on the

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brain. These simplistic explanations need much closer scrutiny.

One of the earliest theories linking brain asymmetry to sex differences in behaviour suggested that, because women are more emotional than men, they must be more right-hemisphere dominant (reviewed by Star, 1979). This theory ignored the fact that women have superior verbal ability, and that this function is located in the left hemisphere. Another hypothesis, known as the Levy-Sperry hypothesis, argued that women have *less* lateralised brains than men, whereas yet another (proposed by Buffery & Gray, 1972) claimed that women have *more* lateralised brains. The latter two hypotheses were based on *ad hoc* deductions made about sex differences in performance of spatial tasks (for more detail see Star, 1979; Rogers, 1988).

Similarly, in the case of schizophrenia some claim that there is impaired functioning of the right hemisphere (Bellini, Gambini, Palladin, & Scarone, 1988). Others suggest that the impairment is in the left hemisphere (Gur, 1978; Nasrallah, 1982), thus causing more dependence on the right, "dark" or sinister hemisphere. Attempts have also been made to link schizophrenia, as well as a number of other neurological conditions, to disturbed asymmetries in neurotransmitter levels (Glick, Ross & Hough, 1982), but again there is no conclusive evidence on this matter.

In all of the other behavioural conditions to which brain asymmetry has been applied, there are similar contradictory views, and a lack of convincing evidence. Brain asymmetry is thus a scientific concept with broad ramifications into social attitudes.

The presence of asymmetry in the human brain has been recognised for more than a hundred years. In 1836 Dax noticed that patients suffering from disturbances of speech had damage to the left hemisphere, and not the right. Soon after, Broca associated right side paralysis with aphasia, the inability to produce speech, and located the damage to a region in the left hemisphere now known as Broca's area. In 1874 Wernicke found that damage to another region in the left hemisphere, now called Wernicke's area, caused loss of language understanding while not affecting speech production. Today we can visualise activity in these brain regions using computer imaging techniques, which allow determination of regional activity in the living brain as it performs certain functions. Positron emission tomography, for example, allows imaging of changes in blood flow as a person hears, sees, speaks or generates words. Each of these processes leads to increased blood flow, and nerve cell activity, in different regions of the left hemisphere. Incidentally, the same regions of the left hemisphere are specialised for both spoken and signed language in humans (Bellugi,

Poizner & Klima, 1989).

Other forms of neural processing, such as listening to chords and tones without analysing them, increases activity predominantly in the right hemisphere. When the subject analyses the chord structure, left hemisphere activity is greater (Peretz & Morais, 1988). Broadly speaking, the left hemisphere is used for analytical, sequential thinking, whereas the right is used for parallel, or holistic, thinking. It must be emphasised nevertheless, that the left-right dichotomy is not absolute, and varies amongst individuals, partly depending on past experience, and between tasks (Kinsbourne, 1978).

In the human brain this division of function between the hemispheres is manifest in structural asymmetries and in lateralised motor behaviours. Each hemisphere controls the opposite side of the body, including the muscles of the face. Thus, the fact that emotions are expressed more strongly on the left side of the face (Christman & Hackworth, 1993) reflects control by the right hemisphere. We also pay greater attention to expressions on the left side of another person's face or a photograph of a face. By contrast, during speech, which is under left hemisphere control, the right side of the mouth moves more than the left (Wolf & Goodale, 1987).

Gross anatomical asymmetry of the brain is visible even to the naked eye. The left hemisphere is wider in the posterior region, where visual inputs are processed, and the right is wider in the anterior region. This skewed anatomy of the brain impresses itself on the interior side of the skull, and so can be seen in endocasts of the skulls of fossil hominids. They too had asymmetrical brains.

Other evidence indicates that the hominids were right handed. For example, the fracture patterns of prehistoric stone tools indicate that the tool being made was rotated clockwise, suggesting that it was held in the left hand while being struck with a hammer stone held in the right hand, just as a right-handed person would today (Toth, 1985). From this and other evidence for right handedness in early humans, together with the predominance of stone axes that can be most effectively used by the right hand, anthropologists have drawn an association between the evolution of tool use and language ability (Bradshaw & Rogers, 1992). Neurobiologists have added the third side to the triangle, by including brain asymmetry as the basis for both behaviours.

As all of these attributes (brain asymmetry, tool use and language) were considered to be unique to the human species, a conceptual divide had been constructed between humans and other animals. Those who adhered to this view were saying in essence that, although we evolved from monkeys and apes, we made a huge evolutionary leap away from

them. But, there is now overwhelming evidence that asymmetry of brain function occurs in a wide number of species, and that lateralised biases in behaviour may have evolved at least as early as fish. For example, Reist, Bodaly, Fudge, Cash, & Stevens (1987) have reported that whitefish, *Coregonus sp.*, have more superficial scars on the left side of the body. These scars are attributed to lampreys and the lateral bias suggests that the whitefish is better able to remove lampreys from its right side by rubbing them against surfaces or that the lampreys have a lateral bias that leads them to attach to the left side of the whitefish more readily. This population bias might possibly reflect a bias for turning or a side preference. There is other evidence for a turning bias in fish; *Girardinus falcatus* exhibits a significant population bias to turn right when first presented with the shape of a simulated predator and to the left on subsequent presentations (Cantalupo, Bisazza, & Vallortigara, 1994). The early evolution of lateralisation of brain function is also supported by a report of lateralised neural control in an amphibian: the frog, *Rana pipiens*, controls its alarm vocalisation by the left side of the brain (Bauer, 1993). Examples of lateral biases in other species are discussed below, but for a more comprehensive summary see Bradshaw and Rogers (1992).

For tool use too, humans are not unique. There is a growing list of examples of tool use by animals. Chimpanzees use sticks to "fish" termites from their nest (McGrew & Marchant, 1992), and rocks to crack open nuts placed on a tree root or another rock as an anvil (Boesch, & Boesch, 1982). Moreover, the chimps appear to *be aware of* the function of the stones as tools because they immediately place the nut on the hardest spot of the anvil (Sakura, & Matsuzawa, 1991). Sea otters too use a rock as a hammer to crack open shell fish (Kenyon, 1969), and some species of finches on the Galapagos Islands use cactus spines to probe into crevices and impale insects (Millikan & Bowman, 1967). Elephants have been reported to perform 21 types of tool use, with 22 acts per hour in captive animals and half as often in wild ones (Chevalier-Skolnikoff, & Liska, 1993). The latter authors conclude that tool use is so common that, of course, not only did it appear well before humans evolved, but it may well have originated a number of times in different phylogenetic groups, each time for a different purpose.

To fashion a tool for a particular use is considered to require a higher cognitive ability. The chimpanzees carefully select the sticks that they use for termite fishing and they break them to the desired length (McGrew & Marchant, 1992). Wild orang-utans similarly probe holes with sticks that they fashion so that they have a spatulate form at one end, to be held firmly in the mouth, and are chewed at the other end, to

be inserted in the hole possibly to soak up honey (van Schaik & Fox, 1994).

There are many other examples of tool use in wild and captive primates (Bard, 1990; Brewer & McGrew, 1990; Galdikas, 1982; Rogers & Kaplan, 1994; Visalberghi, 1987), but few studies have consistently reported whether the tool use involves handedness, as in humans. Westergaard (1991) has reported left handedness in capuchins, *Cebus apella*, and lion-tailed macaques, *Macaca silenus*, for holding and manipulating dipping sticks. McGrew and Marchant (1994) have reported a weak, but significant, bias for left handedness in wild chimpanzees performing termite fishing. For holding the hammer when cracking nuts, chimpanzees display individual hand preferences but there appears to be no consistent handedness in the population (Boesch, 1991; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993). There is a need to collect more information on hand preferences in tool use, and it is premature to conclude that, unlike humans, nonhuman primates do not have strong handedness for tool use.

Contrary to earlier indications, there is now ample evidence that many primate species exhibit handedness for picking up and holding food (reviewed by Bradshaw & Rogers, 1995; Ward & Hopkins, 1993). Early investigations of hand preferences in primates seemed to show that there were hand preferences at an individual level but no predominant bias for use of the same hand (i.e. handedness). These reports, however, were dogged by small sample sizes and poor data sampling, and a reanalysis of the original findings has indicated the presence of handedness (MacNeilage, Studdert-Kennedy & Lindblom, 1987). For instance, the lower primates, prosimians, are left handed for holding food (reviewed by Ward, & Hopkins, 1993). The right hand may have a stronger a grip and thus it may be used for holding on to the tree branches. According to MacNeilage et al. (1987), as primates evolved to being less arboreal, the right hand was freed for use in manipulating, and a shift to right handedness for fine motor acts could occur. Such right-hand preferences have been reported in some studies of chimpanzees (Bard, Hopkins, & Fort, 1990 ; Hopkins & Bard, 1993; Hopkins, Bard, Jones, & Bales, 1993) and gorillas (Olson, Ellis, & Nadler, 1990). In orang-utans, there is no predominant handedness for food holding and manipulation in the population as a whole, possibly because orang-utans are arboreal, although older females are more likely to be right-handed (Rogers & Kaplan, 1995) and this is inconsistent with the hypothesis of MacNeilage et al. (1987), which predicts left handedness in arboreal species. In fact, apparently like humans, orang-utans have a preference for touching the face with the left hand, in their

case when they manipulate parts of the face as in cleaning the teeth, eyes or nose (Kaplan & Rogers, 1994; Rogers & Kaplan, 1995).

The other branch of the primate evolutionary tree, that of the New World monkeys, has been less well studied for handedness. Most emphasis has been on hand preferences in the common marmoset, *Callithrix jacchus*. For holding food, individuals of this species are either left or right hand preferent or have no hand preference but there are more left-hand preferent individuals, even though this bias towards left handedness is not strong (Box, 1977; Hook-Costigan & Rogers, 1995). This species appears never to have evolved, or possibly to have lost, a strong bias for handedness within the population, but nevertheless individuals retain hand preferences, and thus lateralised brains.

It should be mentioned here that, although preferred use of a particular hand reflects lateralisation of the brain, it does not in itself indicate how that lateralisation is determined. It may have come about by the process of evolution, as suggested for populations in which there is a consistent preference for all or most individuals to use the same hand to perform similar functions, or the preference may be learned and thus the learning establishes brain lateralisation.

In contrast to their weak lateralisation for handedness, marmosets have a strong population bias for processing certain forms of visual information: they prefer to use the right eye for peeping through a hole to view food and a range of other stimuli (Hook-Costigan & Rogers, 1995). "Eyedness" has also been shown in a lower primate species, *Otolemur garnettii*, but in this case the preferred eye for viewing food is the left eye (Rogers & Ward, 1994). There is evidence to suggest that these eye preferences reflect perceptual rather than motor lateralisation (Rogers & Ward, 1994) and, therefore, marmosets may have retained lateralisation for perceptual processing but not motor performance. The eye preferred for viewing depends on the stimulus being viewed and the state of arousal of the subject (Rogers & Ward, 1994). These variables have not been considered in studies of humans that have used shifts of eye dominance from the right to the left eye as indicators of neurochemical imbalances underlying, for example, schizophrenia and alcoholism (see above).

Other New World primates do, however, display handedness. As mentioned above, capuchins are left handed for holding dipping sticks and squirrel monkeys, *Saimiri sciureus*, are right-hand and right-foot preferent for scratching and touching their bodies (Aruguete, Ely, & King, 1992), to give just two examples.

Thus, nonhuman primates display lateral biases on a range of behaviours, but some of the best examples of lateralisation are for birds.

Knowledge of "footedness" in parrots (most prefer to hold food objects in the left foot) has a history three centuries long (Harris, 1989), but this was ignored until recently. Now it is recognised that parrots exhibit strong footedness equivalent to that of handedness in humans (Rogers, 1980; reviewed by Bradshaw & Rogers, 1992).

In the early 1970s Nottebohm (1971) demonstrated that many species of songbirds, such as the chaffinch and canary, have brain asymmetry for control of singing by the left hemisphere only. Many songbirds have individually characteristic songs, which can be analysed in a linguistic framework to contain elements, syllables and phrases. The song is produced by the syrinx in the trachea, and each side of the syrinx is controlled by a branch of the hypoglossal nerve from the ipsilateral side of the brain. Sectioning the right nerve has no effect on an individual's ability to sing, but sectioning the left nerve mutes the bird. Nottebohm described the latter birds as performing like actors in a silent film. They stood on the perch performing all of the beak, wing and body movements used in singing but uttered no more than an occasional click or a short phrase. A similar loss of song was obtained if the higher vocal centre in the left hemisphere was lesioned, but not if the same region in the right hemisphere was lesioned. This was the first clear example of brain asymmetry being present in a nonhuman animal.

Evidence for asymmetry of brain function in the chicken first became available in the late 1970s (Rogers & Anson, 1979). When a hungry chick searches for grains of food scattered on a background of small pebbles, it will soon learn to discriminate between the two stimuli if it is tested binocularly or monocularly with the right eye open, but when it is tested monocularly with the left eye open it takes much longer to find the food and often gives up the search altogether (Mench & Andrew, 1986; Zappia & Rogers, 1987). As each eye sends its visual information to the thalamus and optic tectum on the contralateral side of the brain and from there most projections go to the forebrain hemisphere on the same side, it is the left hemisphere which is able to categorise food from "nonfood". Recently, it has been shown that the left-hemisphere of the chick is also used to categorise other stimulus types, including members of the same species (Rogers, 1995b; Vallortigara & Andrew, 1991, 1994). The left eye and right hemisphere, by contrast, attends to the details of each individual stimulus. For example, when given a choice between a familiar cage-mate and a strange chick, chicks tested monocularly using the left eye discriminate between the companion and the stranger, whereas those using the right eye discriminate less clearly or not at all (Vallortigara & Andrew, 1994). In other words, the left eye and right hemisphere recognises and responds

to chicks as individuals, rather than as a category, much as the right hemisphere of humans recognises faces. In fact, one cannot fail to be struck by the similar functions performed by each hemisphere in chicks and humans.

The left eye and right hemisphere also attend to the position of the stimulus in space. Thus, a chick using its left eye has better spatial learning ability than one using its right eye (Rashid & Andrew, 1989). A chick using the left eye is also more fearful (emotional) and shows elevated copulation levels following treatment with the male sex hormone testosterone. It is well-known that chicks tested binocularly following treatment with testosterone show elevated copulation at a precocious age, but remarkably those tested monocularly using the right eye behave as if they had never been treated with the hormone (Rogers, Zappia, & Bullock, 1985). Therefore, only those neural circuits connected to the left eye have access to the region of the brain which has a lowered threshold for copulation following the testosterone treatment.

A large amount of evidence for such asymmetries is now available for the chick. In fact, the chick, with its laterally placed eyes and very small area of binocular overlap in the visual field, is surrounded by two different visual worlds. It responds differently to stimuli perceived in its left or right monocular fields. Another chick might be less likely to be attacked if it approaches an aggressive chick on its left side.

Although the evolutionary significance of these asymmetries may lead some to believe that they are genetically determined, this is not so. Environmental factors have a crucial influence on various forms of brain asymmetry. For example, I have shown that the asymmetries in the visually guided behaviour of the chick are not solely the result of genetic determinants. During the last few days before hatching, the chick embryo is oriented in the egg so that its left eye is turned against its body and is therefore occluded, whereas the right eye is placed next to the air sac. Light entering the egg through the shell and membranes reaches the right eye at a stage when its visual connections to the forebrain are forming, and promotes growth of those visual pathways that are connected to the right eye (Rogers & Sink, 1988; reviewed in Rogers, 1995b). Thus, the lateralisation of various visual functions, although not all functions, may occur as a consequence of asymmetrical light stimulation from the environment (Rogers, 1982). The direction of the asymmetry can be reversed by pulling the embryo's head out of the egg before hatching, occluding the right eye and exposing the left eye to light. These chicks learn better when they use the left eye and right hemisphere, and they control attack and copulation with the left hemisphere (Rogers, 1990). Chicks hatched from eggs incubated in

darkness have no asymmetry for control of these behaviours.

These results show clearly that the asymmetry results from an interaction between genetic and environmental factors. We have shown that hormonal factors also have an influence (Rogers & Rajendra, 1993; Schwarz & Rogers, 1992). The light-dependent growth of the visual pathways connected to the right eye occurs only if there are low circulating levels of the sex hormones, testosterone and oestrogen, in the embryo. In fact, in male chick embryos the testes reduce their production of testosterone just at the time when the light stimulation has its effect.

The chick provides us with a model system which demonstrates that one cannot speak of unitary causes for brain asymmetry. The development of asymmetry is not determined just by the action of a hormone, the genes or environmental factors, but by all of these influences contributing in a completely integrated way. Therefore, popular attempts to explain sex differences in human behaviour simply in terms of the action of sex hormones on the development of brain asymmetry are inadequate (e.g. Geschwind & Galaburda, 1987). It is not possible to separate biological from environmental determinants (that is, genetic or hormonal influences from learning/social influences).

Learning itself can impose neurochemical asymmetries on the chicken brain. When a young chick imprints on or forms a strong attachment to an attractive stimulus, usually its mother but in the laboratory it can be a coloured box or the like, neurochemical changes occur in its left hemisphere as the memory is laid down (Johnston, Rogers, & Johnston, 1993; McCabe & Horn, 1988). Thus, the early learning experience imposes new asymmetries on the developing brain. Similar effects of early learning may effect brain asymmetry in humans.

Birds also have asymmetries for processing auditory information. In chicks the left hemisphere learns to ignore irrelevant auditory stimuli, to categorise them as uninteresting (Rogers & Anson, 1979). The perception of song involves lateralized processes but it is not limited to the left side of the brain. Unilateral lesions placed in the input side of the auditory system (in the left or right nucleus ovoidalis) affect song perception differentially. Following the placement of a lesion in the left nucleus ovoidalis a zebra finch is unable to discriminate between two familiar songs, an ability which the intact bird possesses. Following placement of the lesion in the right nucleus ovoidalis, the zebra finch retains its ability to distinguish two whole songs but has an impaired ability to detect a missing harmonic in a syllable of a song (Cynx, Williams, & Nottebohm, 1992). Thus, as Nottebohm et al. (1990) suggest, the left hemisphere of the zebra finch may be better at

discriminating between stimuli in a 'holistic' sense, whereas the right hemisphere is better at making discriminations which require analysis of components of the song.

What relevance do all these asymmetries in birds have to other species? Since birds diverged from the line to mammalian (and human) evolution at the level of a common reptilian ancestor, the evidence would point again to an early evolution of brain asymmetry. Mention has been made previously about lateralised motor responses in fish. Indeed, it is now known that some form of asymmetry existed at the time of the early trilobites. Fossils of trilobites have a higher incidence of predator-inflicted injuries on the right posterior region of their bodies (Babcock, & Robison, 1989), indicating that they were either more, or less, successful at escape when they moved leftwards, or that their predator had an asymmetry in its direction of attack. Thus, asymmetry of the brain must have evolved very early, soon after the brain structurally duplicated itself.

As we "ascend" the mammalian branch of the evolutionary tree, we find ample evidence for brain asymmetry in rodents (Denenberg, 1981). Although rats and mice show no population bias for right or left handedness (pawedness) when they are tested on a task which requires them to reach into a small tube for a food reward, other tests have shown clear lateralisation of brain function. The right hemisphere analyses spatial information and controls emotional behaviour. The left hemisphere is used for identifying species-specific vocalisations (Ehert, 1987) and for sequential analysis (Bianki, 1988). Rats using the left hemisphere perform better in conditioning situations when a series of stimuli are presented one after the other, and those using the right hemisphere perform better when the stimuli are presented simultaneously (Bianki, 1988). One notices the similarity to the division of function between the hemispheres of the human brain. Also, as shown in the chick, the asymmetry in rats depends on the interaction between sex hormone levels and environmental stimulation during neonatal life (Denenberg, Fitch, Schrott, Cowell, & Waters, 1991).

It is now obvious that brain asymmetry preceded human language and tool use. While it can still be argued that human language evolved as recently as 35,000 years ago (Davidson & Noble, 1989), it can no longer be accepted that it suddenly appeared without neural precursors in other species. Rather, the neural requirements of language and tool use formed over a long evolutionary trajectory (Bradshaw, & Rogers, 1992).

Furthermore, in primates, like humans, the left hemisphere processes the species-specific vocalisations (Petersen, *et al.* 1984). Specialisation

of the left hemisphere for processing species-specific vocalisations in rats, primates and humans may not be coincidental. Moreover, humans process certain language sounds, such as the voicing contrast 'ga' versus 'ka', in the right hemisphere and so too do dogs (Adams, Molfese & Betz, 1987). While primates, and dogs, do not have the vocal apparatus to produce human speech, it is possible that they analyse it much as humans do and that they understand it much better than we think. The ability to analyse language-like vocalisations may have preceded the ability to produce speech by a long period of evolution.

Present knowledge shows that there is a continuum from animals to humans on the attributes once thought to be uniquely human, and that simplistic explanations of human behaviour are not supported by the research on model systems in animals. It is inadequate to opt for biological determinism of complex behaviour, such as schizophrenia, alcoholism or gender differences in behaviour. Genes or hormones do not act alone as biological determinants, but rather they interact with environmental factors to produce the unique pattern of brain organisation within the individual. Furthermore, environmental influences may affect the organisation of the brain throughout the life span. Although exposure to certain forms of environmental stimulation and the formation of memories may have more profound effects during embryonic and neonatal life than in adulthood, older brains can also be modified by environmental stimulation. We now know that the brain is in dynamic interaction with its environment throughout life, and thus its pattern of asymmetry may shift in response to learning, stress factors or other forms of environmental input.

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