

The Many Sides of Hemispheric Asymmetry: A Selective Review and Outlook



INS is approved by the American Psychological Association to sponsor Continuing Education for psychologists. INS maintains responsibility for this program and its content.

Michael C. Corballis,¹ AND Isabelle S. Häberling²

¹School of Psychology, University of Auckland, Auckland, New Zealand

²Department of Child and Adolescent Psychiatry and Psychotherapy, University Hospital of Psychiatry, Zurich, Switzerland

(RECEIVED January 31, 2017; FINAL REVISION April 6, 2017; ACCEPTED April 10, 2017)

Abstract

Hemispheric asymmetry is commonly viewed as a dual system, unique to humans, with the two sides of the human brain in complementary roles. To the contrary, modern research shows that cerebral and behavioral asymmetries are widespread in the animal kingdom, and that the concept of duality is an oversimplification. The brain has many networks serving different functions; these are differentially lateralized, and involve many genes. Unlike the asymmetries of the internal organs, brain asymmetry is variable, with a significant minority of the population showing reversed asymmetries or the absence of asymmetry. This variability may underlie the divisions of labor and the specializations that sustain social life. (*JINS*, 2017, 23, 710–718)

Keywords: Language, laterality, Cognitive neuroscience

BACKGROUND

Left–right asymmetry has long been considered part of the human condition. Throughout recorded history, people have shown a preference for the right hand, which is also generally superior in terms of skill, giving rise to the term “dexterity.” So far as we know, right-handedness is common to all cultures (Porac, Rees, & Buller, 1990), resulting in near universal associations of positive connotations with the right and negative values with the left (Needham, 1973). Right handedness is generally not evident in the structure of the hands themselves, but reflects an asymmetry in the brain. More direct evidence for cerebral asymmetry emerged in the 19th century when it was reported that speech deficits generally resulted from damage to the left cerebral hemisphere rather than to the right (Broca, 1863; Wernicke, 1874), a finding since widely confirmed. This led to a strong and persisting view that one side of the brain, usually the left, was dominant, as manifest in control of speech and manual action. For many decades the left hemisphere of the brain was termed the major hemisphere, and the right the minor hemisphere.

There were nevertheless early hints that the right brain might have complementary specialization for nonverbal activity, such

as perception (e.g., Jackson, 1864) or emotion (Luys, 1881). This view gained renewed currency from the 1960s, when a group of patients underwent section of the forebrain commissures for the relief of intractable, multifocal epilepsy. In that respect, the operation proved generally successful, but it also opened up the possibility of assessing the capacities of each side of the brain independently of the other. The research soon demonstrated left-hemispheric dominance for speech, with the production of speech seemingly more strongly lateralized than comprehension (Sperry, 1982), although some studies suggests equal lateralization (e.g., Häberling, Steinemann, & Corballis, 2016). Right-hemispheric advantages were also documented for a host of nonverbal functions, including perceptual judgments, mental transformations, sorting shapes into categories, or perceiving wholes from parts (see Sperry, 1982, for a summary). Both right- and left-hemisphere functions have also been widely documented in patients with unilateral brain injury, as well as in studies using dichotic listening and tachistosopic perception to measure asymmetries in normal participants (see, e.g., Corballis, 1991, for review).

These various findings led to an avalanche of speculation about the dual nature of the brain. Joseph E. Bogen (1969), who with Philip V. Vogel had performed the split-brain operations, wrote of the left brain as *propositional* and the right brain as *appositional*, relating the dichotomy to age-old distinctions such as the Confucian concepts of *Yin* and *Yang*, the Buddhist concepts of *buddhi* and *manas*, or Levi-Strauss's

Correspondence and reprint requests to: Michael C. Corballis, School of Psychology, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand. E-mail: m.corballis@auckland.ac.nz

distinction between the *positive* and the *mystic*. The dual brain was popularized by the psychologist Robert E. Ornstein (1972) in his best-selling book *The Psychology of Consciousness*, with the left hemisphere portrayed as linear, rational, analytic, and fundamentally Western in its style of thought, and the right hemisphere as divergent, intuitive, holistic, emotional, creative, and fundamentally Eastern. The duality may have been exaggerated, even mythologized, by the tumultuous events of the 1960s and early 1970s, with the protests over United States involvement in the Vietnam War, the rise of the feminist movement, and the emergence of a drug culture. The left brain came to be associated with the military-industrial establishment and the right with the creative, peace-loving East (Corballis, 1980).

This duality persists in the public mind, along with calls for greater attention to be given to the creative, emotional right hemisphere in activities as diverse as art, education, history, literature, and even business. *The American Heritage*® *Dictionary of the English Language* (2008) offers the following definitions

Left-brained *adj*: 1. Having the left brain dominant. 2. Of or relating to the thought processes, such as logic and calculation, generally associated with the left brain. 3. Of or relating to a person whose behavior is dominated by logic, analytical thinking and verbal communication, rather than emotion and creativity.

Right-brained *adj*: 1. Having the right brain dominant. 2. Of or relating to the thought processes involved in creativity and imagination, generally associated with the right brain. 3. Of or relating to a person whose behavior is dominated by emotion, creativity, intuition, nonverbal communication, and global reasoning rather than logic and analysis.

Another recent example is Iain McGilchrist's (2009) book *The Master and His Emissary*, portraying the history of Western civilization as shaped by the counter-forces of the left and right brains. McGilchrist reverses the traditional notion of the left hemisphere as the dominant or major hemisphere, anointing the right brain as the master and the left brain the emissary.

The split-brain operation was subsequently carried out in other medical centers, along with psychological analysis of its effects, but as an avenue into the study of cerebral asymmetry the split-brain era itself is now largely over, with the advent of more effective drugs and the development of more limited surgery for the relief of epilepsy. There was always the suspicion that the results from split-brain patients may have been confounded by the patients' medical condition, and by side-effects of the operation itself. Evidence is now focused more on brain imaging, allowing for testing of people without adverse medical conditions, and at the same time, interest has spread to broader questions about the nature, incidence, and evolution of structural and behavioral asymmetries. A possible disadvantage of brain imaging is that it identifies areas activated by a given task, but that may not be necessary

for the task. Nevertheless, these developments have led to a view of cerebral asymmetry that is at once more complex and more widely understood. They question the notion of a simple dichotomy, and dispel many of the myths about brain duality that still persist in popular culture.

BEYOND DUALITY

The idea that the two sides of the brain somehow represent opposite polarities was due more to the human propensity to categorize in binary manner, or what has been termed *dichomania* (Whitaker, 1982), than to the neurological or psychological evidence. The brain is much more obviously symmetrical than asymmetrical, and the various right-hemisphere specializations outlined by Sperry (1982) are not absolute. The most lateralized of functions are language, and especially speech, and a right-hemispheric specialization for spatial attention. The asymmetry of spatial attention is most apparent in the phenomenon of left hemispatial neglect following right-sided lesions (Heilman & van den Abell, 1980). Right-sided neglect following equivalent damage to equivalent regions of the left hemisphere does occur in some individuals, but is typically transient (Ogden, 1985). These asymmetries bear little relation to handedness. One brain-imaging study, for example, showed "typical" left-hemisphere dominance for speech in 88% of right-handers and as many as 78% of left-handers (Mazoyer et al., 2014), while another showed right-hemispheric specialization for spatial attention to be unrelated to handedness (Badzakova-Trajkov, Roberts, Häberling, & Corballis, 2010).

Brain-imaging provides the opportunity for a more fine-grained analysis of cerebral asymmetries, increasingly focused on networks rather than localized regions of the brain. Liu, Stufflebeam, Sepulcre, Hedden, and Buckner (2009) used fMRI to measure intrinsic brain activity in a sample of 300 people, who were simply asked to stay awake and watch a blank screen. They computed laterality indices over wide areas of the brain; factor analysis of these indices yielded four orthogonal factors, suggesting four independently lateralized networks. Two were lateralized to the left hemisphere; based on previous evidence from functional imaging, the authors identified one as the language circuit, and the other the *default-mode network*, associated with mind wandering and internal thoughts (Buckner, Andrews-Hanner, & Schacter, 2008). The other two were lateralized to the right hemisphere, one identified by the authors as concerned with vision, and the other as a network for the detection of unattended events. These networks almost certainly do not capture the totality of asymmetries in the brain, since they were evident only in the brain "at rest," in default mode. Even so, they take us well beyond the dual brain.

Using a similar factor-analytic approach, Häberling, Corballis, and Corballis (2016) computed laterality indices when people were engaged in active tasks, including production and comprehension of words and observation of manual gestures. Factor analysis resulted in three orthogonal

factors, all biased to the left hemisphere. The most strongly lateralized was the language factor, and the other two were linked primarily to gesture, with one strongly correlated with handedness and the other independent of handedness. These three networks were contained within a larger system known as the *mirror-neuron system*. In nonhuman primates, this system has been associated with the production and understanding of manual action, such as grasping an object (Rizzolatti & Sinigaglia, 2010). Brain imaging suggests that the system is also present in humans, but is relatively enlarged (Caspers, Zilles, Laird, & Eickhoff, 2010).

In the course of evolution, the system may have lateralized and fissioned into the three networks identified in the factor analysis, with the language network perhaps the first to separate. Of special interest is the finding that the network associated with handedness was independent of the language network, and represented primarily in the parietal lobe, and may have co-evolved with the development of tools. The other gestural network may be the residual of the original primate mirror system. This account lends some support to the view that language itself evolved from manual gestures rather than from vocal calls (Corballis, 2002; Hewes, 1973; Meguerditchian, Vaclair, & Hopkins, 2013), originating in the primate mirror system (Rizzolatti & Arbib, 1998).

It is likely that similar research with a wider variety of tasks will elicit evidence for further lateralized networks. Nevertheless we can see already that the brain probably harbors many different networks with varying degrees of asymmetry. Since the factors on which they are based are orthogonal, we can suppose that they are mutually independent, suggesting that brain asymmetry depends on multiple influences.

Yet symmetry remains the default condition. Humans, along with the other primates, belong to a vast clade of animals known as the *bilateria*, characterized by near bilateral symmetry about the plane orthogonal to the distinctive anterior–posterior (front–back) and dorsal–ventral (up–down) axes. This fundamentally symmetrical body plan was probably driven in part by the absence of consistent differences in contingencies affecting the left and right sides of the body, and by the greater economy of programming duplicate structures on either side of the body. Like the rest of the body, the brain is more obviously symmetrical than it is asymmetrical, but asymmetries emerge when symmetry is restrictive or otherwise maladaptive. In complex brains, some relaxation of the principles of symmetry permitted increased specialization of functions. But even the human brain retains a high level of symmetry, since we live in a world largely without left–right bias, and those biases that do exist are often the creations of our own species, such as the manufacture and use of tools, and the invention of reading and writing.

UNIQUELY HUMAN?

It is commonly supposed that cerebral asymmetry is unique to humans, perhaps even a defining characteristic of our species (e.g., Corballis, 1991; Crow, 1998). It is increasingly clear that this is not the case. Consistent asymmetries in behavior and brain function have now been well documented

in nonhuman species (Rogers, Vallortigara, & Andrew, 2013). Even population-level handedness seems to be widespread among primates. It is now well established that some 65 to 70% great apes favor the right hand in various tasks (e.g., Hopkins et al., 2011), although the incidence is lower than that in humans, which stands at around 90%. Orangutans seem to be an exception, with some 72% showing a left-hand preference in scratching and fine manipulation of the face, but no consistent asymmetry evident in other manual tasks (Rogers & Kaplan, 1996). Earlier, MacNeilage, Studdert-Kennedy, and Lindblom (1987) reported a left-hand advantage for reaching in Old World monkeys, but a weak right-hand preference for manipulation.

Marsupials also typically show a population-level-preference for one or other forelimb in operations such as feeding, catching insects, or collecting nest material, and the degree of lateralization increases between species with the degree of bipedality (Giljov, Karenina, & Malashichev, 2012). Many marsupials are bipedal and show consistent paw preference. Among brush-tailed bettongs, for instance, the incidence of left-paw preferences was estimated at between 82 and 92%. Although the left paw is generally preferred for manipulation, the right paw seems to be preferred for postural support. Directional paw preference appears to be unrelated to phylogenetic relations between species, suggesting that it was driven by ecological influences rather than genetics (Giljov, Karenina, Ingram, & Malashichev, 2015), although the consistency of direction, curiously opposite to that in humans and great apes, suggests an underlying biological gradient.

Bipedality frees the forelimbs from locomotion, allowing them to become specialized for manipulation; indeed, in evolutionary terms, it may have been the adaptiveness of enhanced manipulation that drove bipedality itself, in humans as in marsupials. Manipulation may have been enhanced through the forelimbs becoming specialized differentially, with the two hands or paws working cooperatively. Even so, the forelimbs still retain a high degree of symmetry even in humans, since many actions require the capacity to operate unimanually on either side of space, as in reaching or plucking. Effective manual action is perhaps always a tradeoff between symmetry and asymmetry.

A left-hemispheric dominance for vocalization has been reported even in frogs (Bauer, 1993) and mice (Ehert, 1987), suggesting precursors to the left-hemispheric control of speech in humans. Chimpanzees, our closest nonhuman relatives, show enlargement of the left hemisphere in homologues of Broca's (Cantalupo & Hopkins, 2001) and Wernicke's (Gannon, Holloway, Broadfield, & Braun, 1998) areas, the two major cortical language areas in humans. These asymmetries are tantalizing because there is no indication that great apes can produce anything resembling speech. They might be taken as further, indirect evidence that language evolved from manual gestures, since Broca's and Wernicke's areas are contained within the mirror system described above.

The representation of emotion is also biased toward the right hemisphere in primates as well as in humans, suggesting that it may go back at least 30 to 40 million years (Lindell, 2013).

Indeed it probably goes back further, since evidence from birds and fish suggest that the right hemisphere is associated with both positive and negative emotion, and the left with the inhibition of emotion (Andrew, 2002). Many other examples of lateralized behavior are covered by Rogers et al. (2013). Lateralization appears to have emerged where adaptive in many, perhaps most, species, and may be idiosyncratic to particular species or may be conserved with modification through different lineages. Human laterality no doubt retains behavioral and cerebral asymmetries evident in many other species, with some asymmetries sharpened or modified as adaptation to specific human aptitudes, such as language and tool use. At the same time we humans, like other bilateria, have retained a fundamentally symmetrical body plan. Sexual selection may play a role here, since facial symmetry is one mark of attractiveness (Rhodes & Zebrowitz, 2002); one study shows that men with more symmetrical faces have more sexual partners than do those with less symmetrical faces (Thornhill & Gangestad, 1994)!

INDIVIDUAL DIFFERENCES

A ubiquitous aspect of cerebral asymmetry is its variability. Despite the prevalence of human right-handedness, some 10% of the population are left-handed, or in a few cases ambidextrous. The incidence of left-cerebral dominance for language is if anything higher than that of right-handedness, with perhaps only approximately 6% showing departure from left-hemispheric dominance (Corballis, Badzakova-Trajkov, & Häberling, 2012). This variability persists across the animal kingdom, where asymmetry consistently favoring one side over the other lies within the range of approximately 65 to 90% (Ghirlanda & Vallortigara, 2004).

Because of its ubiquity, it seems likely that this variability is itself adaptive. Ghirlanda and Vallortigara propose a game-theoretic analysis in which there is an advantage to be gained in belonging to a minority, but only so long as it is a minority. In flocks of birds that wheel away from a predator, the minority that peels off in the opposite direction may escape because the invader prefers to attack where the prey are more numerous. In the case of humans, left-handers may carry an advantage in sports such as tennis, baseball, or boxing, perhaps deriving from warfare (e.g., sword-fighting) because of the surprise element.

As noted earlier, creativity is often associated with the nonverbal right side of the brain, leading to the popular idea that left-handers are more creative than right-handers. The evidence cited for this is typically based on selected cases, such as Leonard da Vinci or the five recent Presidents of the United States (Ford, Reagan, George H.W. Bush, Clinton, Obama) who happened to be left-handed, and it is sometimes simply assumed that creative people must be left-handed. For example, the Pulitzer-Prize winning author James Michener was once declared “Southpaw of the Year,” but wrote back to say the only thing he did with his left hand was scratch his right elbow (McManus, 2002).

Brain-imaging suggests that creativity activity depends more on collaboration between the hemispheres than on a single hemisphere (Lindell, 2011), and there is some evidence

that mixed handers may show higher levels of creativity than either right- or left-handers (Badzakova-Trajkov et al., 2011; Shobe, Ross, & Fleck, 2009); however, they also show a higher disposition to magical ideation (Badzakova-Trajkov et al., 2011; Barnett & Corballis, 2002), schizotypy (Somers, Sommer, Boks, & Kahn, 2009; Tsuang, Chen, Kuo, & Hsiao, 2013), schizophrenia (DeLisi et al., 2002; Orr, Cannon, Gilvarry, Jones, & Murray, 1999), and other problems of mental health (Rodriguez et al., 2010; Rodriguez & Waldenstrom, 2008). Lack of cerebral dominance, as reflected in mixed handedness, has long been associated with language problems, including dyslexia and stuttering (Orton, 1937), although the evidence has often been equivocal. One large-scale study of 11-year-olds showed a dip in academic performance in mixed handers relative to left- or right-handers (Crow, Crow, Done, & Leask, 1998). Mixed handedness may be a mixed blessing.

The variability in handedness and cerebral asymmetry contrasts markedly with the stability of asymmetries of the internal organs. Normally, the heart, stomach, and spleen are displaced to the left and the liver to the right, and the lung on the left has two lobes and only one on the right. In cases of *situs inversus* these are reversed (in some cases incompletely), but this condition occurs only in around 1 person in 10,000 (Torgersen, 1950), whereas reversals of handedness in approximately 1 in 10, and perhaps even less in the case of cerebral asymmetry for language. This relaxation of asymmetry in the brain further suggests that variability has some adaptive function within the population.

GENETICS OF ASYMMETRY

Handedness is weakly inherited. According to one survey, the probability of being left-handed depends on parental handedness, rising from 9.5% among the offspring of two right-handers to 19.5% when just one parent is right handed to 26.1% when both parents are left-handed (McManus & Bryden, 1992). The data are quite well accounted for in terms of a hypothetical gene with one allele producing a shift toward right-handedness, and a second allele in which the direction of handedness is simply a matter of chance (see Annett, 2002, and McManus, 2002, for different versions). This model can also provide an adequate fit to data on the relations between handedness and the cerebral asymmetry for language, on the assumption that one allele of the gene produces a shift toward left-hemispheric control, with right-cerebral control a matter of chance (Corballis et al., 2012). The model also provided a fit to data from twins, while also indicating no special mirroring effect in the case of monozygotic twins of opposite handedness (Badzakova-Trajkov, Häberling, & Corballis, 2010).

While a single-gene model can provide plausible if not always exact fits to the data, attempts to locate such a gene have been largely fruitless. In a large-scale study that included both twins and singletons, Medland et al. (2009) concluded that genetic variation accounted for 23.6% of the variation in handedness, but also advocated a polygenic model.

McManus, Davison, and Armour (2009) suggest that as many as 40 genes may be involved, although they also affirm that phenotypic predictions from a polygene model are “barely distinguishable” from those of a single-gene model. Whatever the number of genes, although, it remains likely that the genetic influences are unidirectional, with no such influence toward systematic reversal. Left-handedness, then, is due to the absence or cancellation of a genetic right shift, and even *situs inversus* appears to be a matter of chance rather than a genetically induced reversal (Afzelius, 1976; Douard, Feldman, Bary, Loric, & Delmas, 2000). If there are indeed many genes involved, the chances of locating them through linkage analysis may be low, especially if there is also a nongenetic influence, including sheer chance. The harvest, although, has not been wholly fruitless, with a few candidates showing some relation to functional asymmetries.

The strong association of language and cerebral asymmetry raises the possibility of language-related genes influencing laterality, or *vice versa*. One candidate is the *FOXP2* gene. A mutation of this gene resulted in a severe speech impediment in approximately half the members of an extended English family (Enard et al., 2002). Handedness seems to be largely unaffected, since one study showed 12 of the 15 members of the family to be right handed (Alcock, Passingham, Watkins, & Vargha-Khadem, 2000), but there is some evidence for anomalies in cerebral asymmetry. Brain imaging revealed that members of a family affected by the mutation, unlike their unaffected relatives, showed no activation in Broca’s area while covertly generating verbs (Liégeois et al., 2003); instead, activation was scattered and seemed not to be more dominant on one or other side. Two single-nucleotide polymorphisms (SNPs) on the *FOXP2* gene (rs6980093 and rs7799109) have been associated with variability in brain activation in the left frontal cortex (Pinel et al., 2012), and two further SNPs (rs2396753 and rs12533005) have been linked to cerebral asymmetry for speech as determined by dichotic listening (Ocklenburg et al., 2013b).

Another candidate is *LRRMT1*, a gene reported to be associated with handedness, but apparently only in samples of individuals classified as dyslexic; when inherited through the father a particular haplotype consisting of minor alleles at three locations significantly shifted handedness toward the left (Francks et al., 2007). This same haplotype was over-transmitted paternally in those with schizophrenia. These effects were not evident in non-dyslexic samples, including a Chinese sample and other samples. Ludwig et al. (2009) found the same haplotype to be paternally associated with schizophrenia, but at best only weakly with handedness. Ocklenburg et al. (2013a) found an association of language lateralization, using the dichotic-listening task, with genetic variation in *CCKAR*, another gene related to schizophrenia.

A growing possibility is that handedness and cerebral asymmetry is related to the *situs* of the internal organs, despite the fact that *situs* is more uniformly determined than either handedness or cerebral asymmetry. One question is whether *situs inversus* of the internal organs also reverses

brain asymmetry. Given the rarity of *situs inversus*, evidence is fairly scarce, but one study showed 15 out of 16 individuals with *situs inversus* to be right-handed (Matsumoto et al., 1997), while another showed three people with *situs inversus* to be left-cerebrally dominant for language, with a larger temporal planum on the left, as in the majority of individuals with normal *situs* (Kennedy et al., 1999). Intriguingly, though, all three showed reversed petalia; that is, they showed protrusion of the right frontal lobe relative the left and of the left occipital lobe relative to the right, the opposite of that normally observed. This suggests some influence of *situs* on brain asymmetry, but this is overridden by asymmetry for language.

The genetic determination of *situs* itself is complex. The asymmetries of the internal organs are governed at the earliest stages by an asymmetry of the cilia, asymmetrical hair-like organelles on the surface of cells, and this directs the asymmetry of a genetic sequence (the *Nodal-Lefty-Pitx2* cascade), which guides the asymmetrical morphogenesis of internal organs through a cascade of genetic influences (Dasgupta & Amack, 2016). One gene in this complex is the *PCSK6* gene, which activates *Nodal*, and a genome-wide assay across three independent samples of individuals with dyslexia showed one allele of *PCSK6* to be significantly associated with increased right-handedness (Scerri et al., 2011). The effect was not present (and if anything slightly reversed) in the general population. Another large-scale study also showed no effect of this allele in the general population, but revealed that a repeat polymorphism at another locus was associated with the degree, but not the direction, of handedness (Arming et al., 2013), and this same repeat has also been associated with attention deficit hyperactivity disorder (ADHD) (Kebir & Joover, 2011). Shore et al. (2016) demonstrated an effects on gene expression regulation for the associated SNP but not the repeat polymorphism.

Several other genes in the pathway that leads to anomalies of left–right development in mice proved to be associated as a group with human handedness in the general population (Brandler et al., 2013). Integrating these and other findings, Brandler and Paracchini (2014) appeal to the cilia themselves, arguably the very source of bodily asymmetries. They discuss genes reported in the literature suggesting that additional genes contributing to left/right asymmetries or ciliopathies, beyond *PCSK6*, are also associated with handedness. The same pathways, therefore, could be implicated in different types of asymmetries and be relevant to disorders like dyslexia. Five genes showing an association with handedness are also involved in ciliogenesis (development of the cilia), two of which are also critical to development of the corpus callosum. Four of the five genes were linked to handedness in the dyslexia cohort that features in much of this research. Brandler and Paracchini suggest that “the mechanisms for establishing LR asymmetry in the body are reused for brain midline development, which in turn influences traits such as handedness and reading ability” (p. 1489).

Left-right asymmetries of brain, body and behavior seem to depend on a complex cascade of genetic influences.

Genetic anomalies or environmental intervention at different levels may lead to a variety of disorders, ranging from *situs inversus* and callosal agenesis at the organic level, and dyslexia, schizophrenia and ADHD at the psychological level. At present, then, we can suppose that cerebral asymmetry depends on multiple genes and multiple levels of causality, and that these also have roles to play in cognitive development. This seems consistent with the growing evidence that cerebral asymmetry is itself multidimensional, and woven into the multiple circuits that underlie human cognition.

CONCLUSIONS AND OUTLOOK

Thirty-seven years ago, I wrote in protest against the dual brain, the notion of a dichotomy between left and right brains (Corballis, 1980). Dual-brain theory has nevertheless continued to be remarkably persistent, especially in popular culture. The terms “left-brained” and “right-brained” are still entrenched in folklore, and perhaps even in neuropsychology, but must be considered metaphoric rather than scientific. As documented in this article, neuropsychologically and genetically, hemispheric asymmetry is increasingly linked to multiple networks in the brain, which may be differentially lateralized and subject to different genetic influences. This means that there are individual differences in psychological function that are likely to be manifest in variations in hemispheric specialization.

One generalization that may well hold is that genetic influences may alter the degree of asymmetry but not its direction. In the case of cerebral asymmetries, the individual qualities long related to relative dominance of the left- and right-brains might be due instead to degree of lateralization rather than its direction. As we have seen, there are already indications that ambilaterality is associated with creativity, as well as with disorders such as schizophrenia, dyslexia, mental health problems, and academic performance. So far, though, ambilaterality has been measured in terms of handedness or, more rarely, the representation of language; relatively little is known about ambilaterality in the context of other functions that are usually lateralized, such as spatial attention or face perception.

This raises the question, though, as to whether disorders associated with lateralization are truly “disorders,” or simply part of the normal web of existence. Even mental illnesses may be adaptive, or once were so. Kauffman (2016) points out that hallucinations were once considered normal, and played a part in the lives of visionaries such as Jesus of Nazareth, St Paul of Tarsus, and even Socrates, and suggests that it was through the writing of Voltaire, Darwin, and Freud that they began to be associated with psychiatric illness. Creativity itself has long been associated with schizophrenia and bipolar disorders, and research also suggests a genetic link (Power et al., 2015). Laterality, or its absence, may be one of the markers of adaptive individual variation.

In evolutionary terms, variations in demeanor, cognition, and personality provide for effective social living, allowing individuals to take multiple specialized roles. Szathmáry

(2015) writes that language, itself strongly lateralized and subject to individual variation, was one of the seven major transitions in evolution, offering something unprecedented, the “negotiated division of labor.” But that division, so critical in the evolution of complex societies, depends not only on language but also on individual differences in other domains as well.

The outlook is for increased understanding of the complexity of brain asymmetries and their genetic underpinning and interrelations with psychological function and individual differences. Laterality remains key to the understanding of the human variation, but in ways far more complex and interesting than implied by simple “dual-brain” models.

ACKNOWLEDGMENT

Funded in part by Grant No. 3701584 to M.C.C. from the Marsden Fund, administered by the Royal Society of New Zealand.

REFERENCES

- Afzelius, B.A. (1976). A human syndrome caused by immotile cilia. *Science*, *193*, 317–319.
- Alcock, K.J., Passingham, R.E., Watkins, K.E., & Vargha-Khadem, F. (2000). Oral dyspraxia in inherited speech and language impairment. *Brain & Language*, *75*, 17–33.
- American Heritage Dictionary of the English Language*, 4th edition (2008). New York: Houghton Mifflin.
- Andrew, R.J. (2002). Origins and evolution of lateralization. In L.J. Rogers & A.J. Andrew (Eds.), *Comparative vertebrate lateralization* (pp. 70–93). Cambridge: Cambridge University Press.
- Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Hove, East Sussex, UK: Psychology Press.
- Aming, L., Ocklenburg, S., Schulz, S., Ness, V., Gerding, W.M., Hengstler, J.G., ... Beste, C. (2013). PCSK6VNTR polymorphism is associated with degree of handedness but not direction of handedness. *PLoS One*, *8*, e67251. <http://dx.doi:10.1371/journal.pone.0067251>
- Badzakova-Trajkov, G., Häberling, I.S., & Corballis, M.C. (2010). Cerebral asymmetries in monozygotic twins: An fMRI study. *Neuropsychologia*, *48*, 3086–3093. <http://doi:10.1016/j.neuropsychologia.2010.06.020>
- Badzakova-Trajkov, G., Häberling, I.S., & Corballis, M.C. (2011). Magical ideation, creativity, handedness, and cerebral asymmetries: A combined behavioural and fMRI study. *Neuropsychologia*, *40*, 2896–2903. <http://doi:10.1016/j.neuropsychologia.2011.06.016>
- Badzakova-Trajkov, G., Häberling, I.S., Roberts, R.P., & Corballis, M.C. (2010). Cerebral asymmetries: Complementary and independent processes. *PLoS One*, *5*(3), e9682. <http://doi:10.1371/journal.pone.0009682>
- Barnett, K.J., & Corballis, M.C. (2002). Ambidexterity and magical ideation. *Laterality*, *7*, 75–84. <http://dx.doi:10.1080/13576500143000131>
- Bauer, R.H. (1993). Lateralization of neural control for vocalization by the frog (*Rana pipiens*). *Psychobiology*, *21*, 243–248.
- Bogen, J.E. (1969). The other side of the brain II: An appositional mind. *Bulletin of the Los Angeles Neurological Society*, *34*, 135–162.

- Brandler, W.M., Morris, A.P., Evans, D.M., Scerri, T.S., Kemp, J.P., Timpson, N.J., ... Paracchini, S. (2013). Common variants in left/right asymmetry genes and pathways are associated with relative hand skill. *PLoS Genetics*, *9*, e1003751. <http://dx.doi.org/10.1371/journal.pgen.1003751>
- Brandler, W.M., & Paracchini, S. (2014). The genetic relationship between handedness and neurodevelopmental disorders. *Trends in Molecular Genetics*, *20*, 83–90. <http://dx.doi.org/10.1016/j.molmed.2013.10.008>
- Broca, P. (1863). Localisations des fonctions cérébrales. Siègne de la faculté du langage articulé. *Bulletin de la Société d'Anthropologie*, *4*, 200–208.
- Buckner, R.L., Andrews-Hanna, J.R., & Schacter, D.L. (2008). The brain's default network - Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*, 1–38. <http://dx.doi.org/10.1196/annals.1440.011>
- Cantalupo, C., & Hopkins, W.D. (2001). Asymmetric Broca's area in great apes. *Nature*, *414*, 505.
- Caspers, S., Zilles, K., Laird, A.R., & Eickhoff, S.B. (2010). A metaanalysis of action observation and imitation in the human brain. *Neuroimage*, *50*, 1148e1167. <http://dx.doi.org/10.1016/j.neuroimage.2009.12.112>
- Corballis, M.C. (1980). Laterality and myth. *American Psychologist*, *35*, 254–265.
- Corballis, M.C. (1991). *The lop-sided ape*. New York: Oxford University Press.
- Corballis, M.C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.
- Corballis, M.C., Badzakova-Trajkov, G., & Häberling, I.S. (2012). Right hand, left brain: Genetic and evolutionary bases of cerebral asymmetries for language and manual action. *WIREs Cognitive Science*, *3*, 1–17. <http://doi.org/10.1002/wcs.158>
- Crow, T.J. (1998). Why cerebral asymmetry is the key to the origin of *Homo sapiens*: How to find the gene or eliminate the theory. *Current Psychology of Cognition*, *17*, 1237–1277.
- Crow, T.J., Crow, L.R., Done, D.J., & Leask, S. (1998). Relative hand skill predicts academic ability: Global deficits at the point of hemispheric indecision. *Neuropsychologia*, *36*, 1275–1282.
- Dasgupta, A., & Amack, J.D. (2016). Cilia in vertebrate left–right patterning. *Philosophical Transactions of the Royal Society. Series B, Biological Sciences*, *371*, 20150410. <http://dx.doi.org/10.1098/rstb.2015.0410>
- DeLisi, L.E., Svetina, C., Razi, K., Shields, G., Wellman, N., & Crow, T.J. (2002). Hand preference and hand skill in families with schizophrenia. *Laterality*, *7*, 321–332. <http://dx.doi.org/10.1080/13576500143000294>
- Douard, R., Feldman, A., Bargy, F., Loric, S., & Delmas, V. (2000). Anomalies of lateralization in man a case of total situs inversus. *Surgical and Radiologic Anatomy*, *22*, 293–297.
- Ehert, G. (1987). Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature*, *325*, 249–251.
- Enard, W., Przeworski, M., Fisher, S.E., Lai, C.S.L., Wiebe, V., Kitano, T., ... Pääbo, S. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, *418*, 869–871.
- Francks, C., Maegawa, S., Lauren, J., Abrahams, B.S., Velayos-Baeza, A., Medland, S.E., ... Monaco, A.P. (2007). LRRMT1 on chromosome 2p12 is a maternally suppressed gene that is associated paternally with handedness and schizophrenia. *Molecular Psychiatry*, *12*, 1129–1139. <http://dx.doi.org/10.1038/sj.mp.4002053>
- Gannon, P.J., Holloway, R.L., Broadfield, D.C., & Braun, A.R. (1998). Asymmetry of chimpanzee planum temporale: Human-like pattern of Wernicke's language area homolog. *Science*, *279*, 220–222.
- Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game-theoretical analysis of population structure. *Proceedings of the Royal Society. Series B, Biological Sciences*, *271*, 853–857. <http://dx.doi.org/10.1098/rspb.2003.2669>
- Giljov, A., Karenina, K., & Malashichev, Y. (2012). Does bipedality predict the group-level manual laterality in mammals? *PLoS One*, *7*, e51583. <http://dx.doi.org/10.1371/journal.pone.0051583>
- Giljov, A., Karenina, K., Ingram, J., & Malashichev, Y. (2015). Parallel emergence of true handedness in the evolution of marsupials and placentals. *Current Biology*, *25*, 1878–1884. <http://dx.doi.org/10.1016/j.cub.2015.05.043>
- Häberling, I.S., Corballis, P.M., & Corballis, M.C. (2016). Language, gesture, and handedness: Evidence for independent lateralized networks. *Cortex*, *82*, 72–85. <http://dx.doi.org/10.1016/j.cortex.2016.06.003>
- Häberling, I.S., Steinemann, A., & Corballis, M.C. (2016). Cerebral asymmetry for language: Comparing production with comprehension. *Neuropsychologia*, *80*, 17–23. <http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.002>
- Heilman, K.M., & van den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, *30*, 327–330.
- Hewes, G.W. (1973). Primate communication and the gestural origins of language. *Current Anthropology*, *14*, 5–24.
- Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., ... Schapiro, S.J. (2011). Hand preferences for coordinated bimanual actions in 777 great apes: Implications for the evolution of handedness in hominins. *Journal of Human Evolution*, *60*, 650–611. <http://dx.doi.org/10.1016/j.jhevol.2010.12.008>
- Jackson, J.H. (1864). Clinical remarks on cases of defects of expression (by words, writing, signs, etc) in diseases of the nervous system. *Lancet*, *2*, 604.
- Kauffman, P.R. (2016). Might hallucinations have social utility? A proposal for scientific study. *Journal of Nervous & Mental Disease*, *204*, 702–712. <http://dx.doi.org/10.1097/nmd.0000000000000542>
- Kebir, O., & Joobar, R. (2011). Neuropsychological endophenotypes in attention-deficit/hyperactivity disorder: A review of genetic association studies. *European Archives of Psychiatry & Clinical Neuroscience*, *261*, 583–594.
- Kennedy, D.N., O'Craven, K.M., Ticho, B.S., Goldstein, A.M., Makris, N., & Henson, J.W. (1999). Structural and functional brain asymmetries in human situs inversus totalis. *Neurology*, *53*, 1260–1265.
- Liégeois, F., Baldeweg, T., Connelly, A., Gadian, D.G., Mishkin, M., & Vargha-Khadem, F. (2003). Language fMRI abnormalities associated with FOXP2 gene mutation. *Nature Neuroscience*, *6*, 1230–1237. <http://dx.doi.org/10.1098/rspb.2003.2669>
- Lindell, A.K. (2011). Lateral thinkers are not so laterally minded: Hemispheric asymmetry, interaction, and creativity. *Laterality*, *16*, 479–498. <http://dx.doi.org/10.1080/1357650X.2010.497813>
- Lindell, A.K. (2013). Continuities in emotion lateralization in human and nonhuman primates. *Frontiers in Human Neuroscience*, *7*, 464. <http://dx.doi.org/10.3389/fnhum.2013.00464>
- Liu, H., Stufflebeam, S.M., Sepulcre, J., Hedden, T., & Buckner, R. (2009). Evidence from intrinsic activity that asymmetry of the human brain is controlled by multiple factors. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 20499–20503. <http://dx.doi.org/10.1073/pnas.0908073106>

- Ludwig, K.U., Mattheisen, M., Muhleisen, T.W., Roeske, D., Schmal, C., Breuer, R., ... Cichon, S. (2009). Supporting evidence for LRRMT1 imprinting in schizophrenia. *Molecular Psychiatry*, *14*, 743–745. <http://dx.doi.org/10.1038/mp.2009.28>
- Luys, J.B. (1881). Recherches nouvelles sur les hémiplegies émotives. *Encéphale*, *1*, 644–646.
- MacNeilage, P.F., Studdert-Kennedy, M.G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral & Brain Sciences*, *10*, 247–303.
- Matsumoto, T., Kuriya, N., Akagi, T., Ohbu, K., Toyoda, O., Morita, J., ... Kato, H. (1997). Handedness and laterality of the viscera. *Neurology*, *49*, 1751.
- Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Percey, G., ... Tzourio-Mazoyer, N. (2014). Gaussian mixture modeling of hemispheric lateralization for language in a large sample of healthy individuals balanced for handedness. *PLoS One*, *9*(6), e101165.
- McGilchrist, I. (2009). *The master and his emissary: The divided brain and the making of the western world*. New Haven, CT: Yale University Press.
- McManus, C. (2002). *Right hand, left hand: The origins of asymmetry of brains, bodies, atoms and cultures*. Cambridge, MA: Harvard University Press.
- McManus, I.C., & Bryden, M.P. (1992). The genetics of handedness, cerebral dominance and lateralization. In I. Rapin & S.J. Segalowitz (Eds.), *Handbook of neuropsychology, Vol. 6: Developmental neuropsychology, Part 1* (pp. 115–144). Amsterdam: Elsevier.
- McManus, I.C., Davison, A., & Armour, J.A.L. (2009). Multilocus genetic models of handedness closely resemble single-locus models in explaining family data and are compatible with genome-wide association studies. *Annals of the New York Academy of Sciences*, *1288*, 48–58. <http://dx.doi.org/10.1111/nyas.12102>
- Medland, S., Duffy, D.L., Wright, M.J., Geffen, G.M., Hay, D.A., Levy, F., ... Boomsma, D.I. (2009). Genetic influences on handedness: Data from 25,732 Australian and Dutch twin families. *Neuropsychologia*, *47*, 330–337. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.09.005>
- Meguerditchian, A., Vauclair, J., & Hopkins, W.D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, *55*, 637–650. <http://dx.doi.org/10.1002/dev.21150>
- Needham, R. (1973). *Right and left: Essays on dual symbolic classification*. Chicago, IL: University of Chicago Press.
- Ocklenburg, S., Arning, L., Gerding, W.M., Epplen, J.T., Güntürkün, O., & Beste, C. (2013a). Cholecystokinin A receptor (CCKAR) gene variation is associated with language lateralization. *PLoS One*, *8*, e53643. <http://dx.doi.org/10.1371/journal.pone.0053643>
- Ocklenburg, S., Arning, L., Gerding, W.M., Epplen, J.T., Güntürkün, O., & Beste, C. (2013b). FOXP2 variation modulates functional hemispheric asymmetries for speech perception. *Brain & Language*, *126*, 279–284. <http://dx.doi.org/10.1016/j.bandl.2013.07.001>
- Ogden, J.A. (1985). Antero-posterior interhemispheric differences in the loci of lesions producing visual hemineglect. *Brain & Cognition*, *4*, 59–75.
- Ornstein, R.E. (1972). *The psychology of consciousness*. San Francisco: Freeman.
- Orr, K.G., Cannon, M., Gilvarry, C.M., Jones, P.B., & Murray, R.M. (1999). Schizophrenic patients and their first-degree relatives show an excess of mixed-handedness. *Schizophrenia Research*, *39*, 167–176.
- Orton, S.T. (1937). *Reading, writing, and speech problems in children*. New York: W.W. Norton & Co. Ltd.
- Pinel, P., Fauchereau, F., Moreno, A., Barbot, A., Lathrop, M., Zelenika, D., ... Dehaene, S. (2012). Genetic variants of FOXP2 and KIAA0319/TTRAP/THEM2 locus are associated with altered brain activation in distinct language-related regions. *Journal of Neuroscience*, *32*, 817–825. <http://dx.doi.org/10.1523/jneurosci.5996-10.2012>
- Porac, C., Rees, L., & Buller, T. (1990). Switching hands: A place for left hand use in a right hand world. In S. Coren (Ed.), *Left-handedness: Behavioral implications and anomalies* (pp. 259–290). Amsterdam: Elsevier Science.
- Power, R.A., Steinberg, S., Bjornsdottir, G., Rietveld, C.A., Abdellaoui, A., Nivard, M.M., ... Stefansson, K. (2015). Polygenic risk scores for schizophrenia and bipolar disorder predict creativity. *Nature Neuroscience*, *18*, 953–955. <http://dx.doi.org/10.1038/nn.4040>
- Rhodes, G., & Zebrowitz, L.A. (Eds.). (2002). *Facial attractiveness*. London: Ablex.
- Rizzolatti, G., & Arbib, M.A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188e194.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264e274. <http://dx.doi.org/10.1038/nrn2805>
- Rodriguez, A., Kaakinen, M., Moilanen, I., Taanila, A., McGough, J.L., & Jarvelin, M.-R. (2010). Mixed-handedness is linked to mental health problems in children and adolescents. *Pediatrics*, *125*, e340–e348. <http://dx.doi.org/10.1542/peds.2009-1165>
- Rodriguez, A., & Waldenstrom, U. (2008). Fetal origins of child non-right-handedness and mental health. *Journal of Child Psychology & Psychiatry*, *49*, 967–976. <http://dx.doi.org/10.1111/j.1469-7610.2008.01923.x>
- Rogers, L.J., & Kaplan, G. (1996). Hand preferences and other lateral biases in rehabilitated orang-utans. *Pongo pygmaeus. Animal Behaviour*, *51*, 13–25.
- Rogers, L.J., Vallortigara, G., & Andrew, R.J. (2013). *Divided brains: The biology and behavior of brain asymmetries*. Cambridge, UK: Cambridge University Press.
- Scerri, T.S., Brandler, W.M., Paracchini, S., Morris, A.P., Ring, S.M., Richardson, A.J., ... Monaco, A.P. (2011). PCSK6 is associated with handedness in individuals with dyslexia. *Human Molecular Genetics*, *20*, 608–614. <http://dx.doi.org/10.1093/hmg/ddq475>
- Shobe, E.R., Ross, N.M., & Fleck, J.I. (2009). Influence of handedness and bilateral eye movements on creativity. *Brain & Cognition*, *71*, 204–214. <http://dx.doi.org/10.1080/1357650X.2015.1089879>
- Shore, R., Covill, L., Pettigrew, K.A., Brandler, W.M., Diaz, R., Xu, Y., ... Paracchini, S. (2016). The handedness-associated PCSK6 locus spans an intronic promoter regulating novel transcripts. *Human Molecular Genetics*, *25*, 1771–1779. <http://dx.doi.org/10.1093/hmg/ddw047>
- Somers, M., Sommer, I.E., Boks, M.P., & Kahn, R.S. (2009). Hand-preference and population schizotypy. *Schizophrenia Research*, *108*, 25–32. <http://dx.doi.org/10.1016/j.schres.2008.11.010>
- Sperry, R.W. (1982). Some effects of disconnecting the cerebral hemisphere. *Science*, *217*, 1223–1227.

- Szathmáry, E. (2015). Toward major evolutionary transitions theory 2.0. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 10104–10111. [http://dx.doi/10.1073/pnas.1421398112](http://dx.doi.org/10.1073/pnas.1421398112)
- Thornhill, R., & Gangestad, S.W. (1994). Human fluctuating asymmetry and sexual behavior. *Human Nature*, *4*, 297–302.
- Torgersen, J. (1950). Situs inversus, asymmetry, and twinning. *American Journal of Human Genetics*, *2*, 361–370.
- Tsuang, H.-C., Chen, W.J., Kuo, S.-Y., & Hsiao, P.-C. (2013). The cross-cultural nature of the relationship between schizotypy and mixed handedness. *Laterality*, *18*, 476–490. <http://dx.doi:10.1080/1357650x.2012.720985>
- Wernicke, C. (1874). *Der Aphasische Symptomencomplex. Eine psychologische Studie auf anatomische Basis*. Breslau: Cohn and Wiegert.
- Whitaker, H.A. (1982). Dichotomania: An essay on our left and right brains. *Journal of Visual Verbal Language*, *2*, 7–13.