

Review

The evolution and genetics of cerebral asymmetry

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Handedness and cerebral asymmetry are commonly assumed to be uniquely human, and even defining characteristics of our species. This is increasingly refuted by the evidence of behavioural asymmetries in non-human species. Although complex manual skill and language are indeed unique to our species and are represented asymmetrically in the brain, some non-human asymmetries appear to be precursors, and others are shared between humans and non-humans. In all behavioural and cerebral asymmetries so far investigated, a minority of individuals reverse or negate the dominant asymmetry, suggesting that such asymmetries are best understood in the context of the overriding bilateral symmetry of the brain and body, and a trade-off between the relative advantages and disadvantages of symmetry and asymmetry. Genetic models of handedness, for example, typically postulate a gene with two alleles, one disposing towards right-handedness and the other imposing no directional influence. There is as yet no convincing evidence as to the location of this putative gene, suggesting that several genes may be involved, or that the gene may be monomorphic with variations due to environmental or epigenetic influences. Nevertheless, it is suggested that, in behavioural, neurological and evolutionary terms, it may be more profitable to examine the degree rather than the direction of asymmetry.

Keywords: behavioural asymmetries; bilateral symmetry; cerebral asymmetry; evolution; handedness; genetics

1. INTRODUCTION

The asymmetry of the brain raises something of a paradox, since, in most respects, the brains and bodies of most organisms, including humans, are strikingly bilaterally symmetrical. As Palmer (2004) put it, bilateral symmetry is the default condition. The midplane of the developing organism is defined by two axes, the anteroposterior and dorsoventral axes, but there is no left–right axis. Instead, the left and right halves of the organism are constructed from separate mediolateral axes. Since these axes are mirror images, the resulting organism will be bilaterally symmetrical, unless there is some symmetry-breaking step. Indeed, most organisms, including humans, belong to the phylum known as Bilateria, which goes back some 600 million years (Chen *et al.* 2004). Nevertheless, bilateral symmetry is not restricted to the Bilateria, and has arisen independently in different lineages. It may even precede the Bilateria, since it is also present in some species of the phylum Cnidaria, which is outside the Bilateria. In the sea anemone *Nematostella vectensis*, for example, bilateral symmetry is dependent on the expression of homologous *Hox* genes much as it is in the Bilateria, suggesting that bilateral symmetry arose even before the evolutionary split between the Cnidaria and the Bilateria (Finnerty *et al.* 2004).

For animals that move freely in the natural world, bilateral symmetry is adaptive, because symmetrically placed limbs, be they legs, wings or flippers, provide for linear movement, which is more efficient than motion in an arc. Directional motion creates a back–front asymmetry, so that eyes and mouth are placed forward, but asymmetry tends to be preserved with respect to left and right. Any sensory asymmetry would create an increased risk of predation from the weaker side. In a world in which left–right parity is largely conserved, then, bilateral symmetry is a natural adaptation.

Against this strong background of bilateral symmetry, our brains and bodies exhibit some striking left–right asymmetries. Indeed, asymmetries are widespread in nature, albeit superimposed on a body plan that is fundamentally bilaterally symmetrical. Many asymmetries are so-called fluctuating asymmetries, which are random variations from symmetry, usually slight, and these are not of concern here. Rather, my focus is on cerebral and behavioural asymmetries in which the direction of asymmetry in the majority of individuals in a population is in the same direction. Such asymmetries suggest that bilateral symmetry is readily and systematically broken if asymmetry proves more adaptive. This is true of the internal organs, including the heart, lungs, stomach and liver, which are arranged asymmetrically, presumably in the interests of more efficient packaging, and perhaps also of more effective function. Automobiles, for example, have evolved to be outwardly bilaterally symmetrical, but their engines are arranged asymmetrically—a matter of

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efficiency in both packaging and performance. Internal organs, moreover, are relatively independent of the organism's interactions with the spatial world, so the pressure to symmetry is eased. The brain and nervous system, on the other hand, are more directly concerned with sensorimotor activity, and are, for the most part, organized symmetrically. Superimposed on the fundamental symmetry of the brain, though, are a number of systematic asymmetries.

In humans, at least, the most obvious asymmetry is handedness. In the great majority of the human population, one hand is clearly dominant in activities such as writing and throwing, and, in approximately 90 per cent of the population, the dominant hand is the right hand. This asymmetry is not at all obvious in the actual structure of the hands themselves, although there are some differences in muscle strength and bone density favouring the dominant hand; at least some of these are a consequence rather than a cause of greater use of the dominant hand (see Steele & Uomini 2005, for review). Handedness is much more obviously a matter of differential skill and activity between the hands, reflecting a cerebral asymmetry rather than a mechanical one. Since the pioneering discoveries of Broca (1861), it is well established that the left hemisphere of the brain is also dominant for language, especially those aspects of language concerned with production. It is also clear that there are complementary specializations of the right hemisphere (Sperry 1982; Corballis 1991; Mort *et al.* 2003).

It is widely held that these asymmetries are uniquely human, and perhaps even a defining characteristic of our species. It is often suggested that handedness and cerebral asymmetry resulted from some genetic mutation at some point after the split of the hominins from the other great apes (e.g. Corballis 1991; Annett 2002; McManus 2002), and Crow (2002) has gone so far as to suggest that this mutation was the speciation event that created *Homo sapiens* and other putatively human characteristics such as language, theory of mind and a susceptibility to psychosis. It is probably true that some functions that are lateralized in the human brain, such as language and specialized manual functions, are unique to our species, but it is becoming increasingly clear that cerebral asymmetry itself is not. Furthermore, many of the lateralized functions documented in non-humans are probably precursors to those functions we regard as uniquely human (e.g. Rogers & Andrew 2002; Corballis 2003).

2. LATERALITY IN NON-HUMAN SPECIES

(a) *Handedness*

The illusion that cerebral asymmetry is uniquely human may stem from the fact that the most obvious manifestation is handedness. At least among mammals, humans are unique in that they are bipedal, freeing the hands from involvement in locomotion. As a consequence, humans are supremely manipulative, and manipulative actions of the hands are an outward manifestation of cerebral asymmetry. This makes human cerebral asymmetry uniquely transparent. Nevertheless, there is now some evidence for consistent handedness in other species. The work of Hopkins and

colleagues has revealed a population-level preference for the right hand in captive chimpanzees, at least for certain activities such as extracting peanut butter from a glass tube (Hopkins 1996), using an anvil (Hopkins *et al.* 2007), gestural communication (Hopkins & Leavens 1998) and throwing (Hopkins *et al.* 2005).

The incidence of right-handedness in chimpanzees in these studies is typically approximately 65 per cent, considerably less than the incidence of right-handedness in humans, which is approximately 90 per cent. These estimates may not be truly indicative, however, since, within each species, hand preference does vary with task, and the tasks themselves are somewhat species-specific. One activity common to tests on both species is throwing, and the proportion of chimpanzees throwing with the right hand is higher than that for other measures (Hopkins *et al.* 2005). In a sample of over a million humans in the USA, the incidence of right-handed throwing was 89.9 per cent for men and 92.4 per cent for women (Gilbert & Wysocki 1992), considerably higher than the values observed in a chimpanzee sample, where 53 animals were reported as right-handed, 16 as ambiguous and 23 as left-handed (Hopkins *et al.* 2005). Of course, even throwing may not be strictly comparable in the two species. Humans have developed throwing to a more precise and intricate level, and more than half of the chimpanzees in the sample observed by Hopkins *et al.* did not throw at all. Even so, it seems unlikely that the incidence of right-handedness in chimpanzees approaches that in humans.

Curiously, one study of 22 bonobos, which along with common chimpanzees are our closest living non-human relatives, revealed no evidence for species-level handedness (Harrison & Nystrom 2008). Palmer (2002) has suggested that the findings of Hopkins and colleagues may be due to statistical artefacts, and has shown the results to be marginal when assessed using funnel plots, which show scatter plots of right-hand use against sample size, although the more recent studies do reveal significant species-level right-handedness using this technique (e.g. Hopkins *et al.* 2005).

Another difficulty is that field research suggests little or no population-level asymmetry in non-human primates, including chimpanzees. Sugiyama *et al.* (1993) examined handedness in chimpanzees for nut-cracking, a lateralized task in which one hand manipulates the anvil and the other the hammer, but left-handers were as frequent as right-handers. McGrew & Marchant (2001) found no evidence for handedness across a variety of activities in chimpanzees observed in the wild, and suggested that the bias in captive chimpanzees is a consequence of contact with right-handed humans. Hopkins *et al.* (2004) have disputed this, claiming that right-handedness occurs in three distinct populations of captive chimpanzees and is unrelated to the proportion of animals raised by humans. Yet, a recent study of well-digging in wild chimpanzees again has suggested a lack of any population bias in handedness (McGrew *et al.* 2007). To confound matters further, Corp & Byrne (2004) studied the dominant hand used by wild chimpanzees when eating *Saba florida*, and found that females were predominantly right-handed and males predominantly left-handed.

Whether there is true species-specific right-handedness in chimpanzees may remain unresolved until there is unequivocal evidence for population-level handedness in chimpanzees in the wild.

Evidence from other primates is inconsistent. There have been claims that monkeys show a slight population-level preference for reaching with the left hand (MacNeilage *et al.* 1987), but subsequent evidence has been mixed (see commentaries to the article by MacNeilage *et al.* 1987), but if true, the asymmetry may reflect a right-hemispheric bias for spatial perception—as also documented in humans (for a review see Corballis 1983). At least one study has shown a slight *right-hand* advantage in a bimanual task in rhesus monkeys, but no bias in capuchins (Westergaard & Suomi 1996). In a sample of baboons, too, nearly 80 per cent were reported to prefer the right hand in making specific communicative gestures (Meguerditchian & Vauclair 2006).

Oddly enough, the clearest case of limb asymmetry in non-human animals comes not from primates but from birds. Most species of parrot show a strong preference for the left foot in picking up objects, and the proportion of left footers is close to 90 per cent, comparable with the proportion of humans who are right-handed (Rogers 1980). Given that the bill is the main manipulative organ in the parrot, the use of the left foot as the holding device could be regarded as the equivalent of the use of the left hand by right-handed humans. This result might be taken as evidence that manual specialization arises in species, such as parrots, that use their limbs for manipulation, as proposed by Walker (1980). Consistent with this, Güntürkün *et al.* (1988) gave pigeons, which do not use the feet in a manipulative fashion, the task of scratching a piece of tape from the bill, and found no preference for one or other foot at either the individual or species level. Rogers & Workman (1993), though, found that 31 out of 38 chicks, given the same task, chose the right foot. Chicks make use of the feet in scratching the ground for food, whereas pigeons do not, suggesting to Rogers and Workman that involvement in feeding rather than manipulation *per se* may be the critical factor underlying limb preference in birds. This may generalize to other species. For example, Levermann *et al.* (2003) reported that some 77 per cent of walrus show a preference for the right flipper when feeding. The direction of the asymmetry may vary between species, though, since Sovrano (2007) reported a *left-forelimb* feeding bias in toads.

There may also be precursors to handedness in postural asymmetries. For example, horses tend to stand with the left foreleg in front of the right rather than vice versa, which has been taken as evidence that the right foreleg tends to be the weight-bearing one, and therefore the stronger of the two (McGreevy & Rogers 2005). Similar asymmetries are present in zebras and impalas (McGreevy *et al.* 2007). Horses also gallop asymmetrically, with one hindhoof striking the ground before the other. One study of two species of thoroughbred race horses, Arabians and American Quarter horses, showed that 90 per cent led with the right hoof, and only 10 per cent with the left hoof

(Williams & Norris 2007)—estimates very close to those for hand and foot dominance in humans.

(b) Cerebral and behavioural asymmetries

Asymmetries in non-human species are also clearly observed in behaviours other than those to do directly with hands or limbs, providing further evidence of cerebral asymmetry. Many species also show biases in overt behaviour, such as turning to escape predators or to attack prey. Faced with a barrier through which a predator was visible, some species of fishes showed population-level biases to turn left or right, while others did not (Bisazza *et al.* 2000). Tadpoles have a bias to turn left when escaping a predator, but a bias to turn right when turning to take in air at the surface (Rogers 2002b). Dogs tend to wag their tails to the left, implying right-hemisphere dominance, when faced with an unfamiliar, dominant dog, but wag to the right, implying left-hemisphere dominance, when faced with their owners (Quaranta *et al.* 2007). These findings are broadly consistent with the suggestion by Davidson (2004), based on human research, that the left hemisphere tends to be specialized for approach and the right hemisphere for avoidance.

A right-hemisphere bias has also been documented for social responses in a number of species of fishes (Sovrano *et al.* 2001), chicks (Vallortigara & Andrew 1994), sheep (Peirce *et al.* 2000) and monkeys (Vermeire *et al.* 1998), and may relate to the right-hemispheric involvement in social understanding in humans (e.g. Sperry *et al.* 1979). Chicks also show a right-hemisphere bias in processing the gaze direction of a predator (Rosa Salva *et al.* 2007), which is interesting because it involves both response to a predator and social cognition—the ability to respond to social cues. The right hemisphere may also be the dark side, as there is also evidence that it is the more specialized for aggressive behaviour in a number of species, including toads (e.g. Rogers 2002b), lizards (Deckel 1995), chicks (Howard *et al.* 1980), baboons (Casperd & Dunbar 1996) and humans (Devinsky *et al.* 1994). Right-handed boxers typically hold a stance in which their opponents are in their left visual fields, perhaps to ratchet up the aggression in their right hemispheres, but also, of course, to give greater momentum to the stronger right hand.

Complementary to the right-hemispheric dominance for attack is a left-hemispheric dominance for feeding. Chicks (Deng & Rogers 1997), pigeons (Güntürkün 1985), zebra finches (Alonso 1998) and toads (Vallortigara *et al.* 1998) look preferentially with the right eye in responding to prey or feeding matter, and we saw earlier that some species, at least, show a right-hand preference for feeding-related activities. Andrew *et al.* (2000) have also suggested that this asymmetry may be related to left-hemispheric control of the mouth structures, an asymmetry that may be widespread in vertebrates and may relate to the left-hemispheric control of vocalization, also documented in frogs (Bauer 1993) and canaries (Nottebohm 1977; Halle *et al.* 2004). Hook-Costigan & Rogers (1998) found that marmosets opened the right side of the mouth wider when making social contact calls, again implying left cerebral dominance, but the left side of

the mouth wider when expressing fear, implying right cerebral dominance for emotion. This finding mimics that found in humans, with the right side of the mouth more prominent for speech and the left for emotional expression (e.g. Graves & Goodglass 1982; Graves & Potter 1988). These asymmetries are also evident in 5- to 12-month-old human babies, who open the right side of the mouth wider when babbling and the left side when smiling (Holowka & Petitto 2002).

Asymmetries for vocalization apply to perception as well as to production. A left-hemispheric advantage for the perception of species-specific vocalizations has been demonstrated in mice (Ehert 1987), rhesus monkeys (Hauser & Anderson 1994), Japanese macaques (Heffner & Heffner 1984) and rhesus monkeys (Poremba *et al.* 2004). In chimpanzees, the left temporal planum is larger on the left than on the right (Gannon *et al.* 1998; Hopkins *et al.* 1998), an asymmetry that seems to be absent in rhesus monkeys and baboons (Wada *et al.* 1975), but is well documented in humans (Geschwind & Levitsky 1968; Jäncke & Steinmetz 1993; Foundas *et al.* 1996). These asymmetries may well be precursors to left cerebral dominance for language processing in humans.

This review is by no means exhaustive, but shows overwhelmingly that cerebral asymmetries abound in non-human species, and at least some of these asymmetries were almost certainly precursors to handedness and left cerebral dominance for language, and to right-hemisphere specializations, in humans. Of course, language itself is widely supposed to be uniquely human (e.g. Chomsky 1966; Pinker 1994; Hauser *et al.* 2002), and we humans have also exploited manipulative skill to a level far beyond that evident in any other species—consider, for example, throwing, writing, playing musical instruments or even tying shoelaces. However, the mechanisms by which these accomplishments were achieved were built from the mechanisms that were probably lateralized in our forebears, and the added complexity may well have exacerbated the earlier asymmetries. Indeed, there are even glimpses of cognitive asymmetries in non-human animals in functions that might have served as precursors to the evolution of language. For example, pigeons tend to discriminate patterns projected to the left hemisphere in a categorical fashion, and those projected to the right hemisphere in a more holistic ('coordinate') fashion (Yamazaki *et al.* 2007). The same appears to be true of humans (Kosslyn *et al.* 1989), and may well have set the stage for language to be lateralized to the left hemisphere.

This conclusion should be treated with caution, though, since there is considerable phylogenetic distance between pigeons and humans. These and other asymmetries may well have come about through convergent evolution, rather than common descent. As another example, left-hemisphere dominance in the control of vocalization has been shown in both canaries and humans, as noted above, but in canaries appears to derive from a leftward bias in the syrinx, the vocal organ itself (Halle *et al.* 2004), rather than in the brain, as in humans. Comparative psychologists have made extraordinary progress in documenting cerebral asymmetries in non-human species, but the challenge now is to

determine which are true homologies and which mere analogies. Two of the most prolific investigators of animal asymmetries, Vallortigara & Rogers (2005), write that '...the overall similarities across species strongly support the hypothesis of a common origin of lateralization in vertebrates (p. 578)', but they go on to suggest that the evolutionary pressures for lateralization are indifferent as to whether it is the product of homology or convergent evolution. The issue becomes critical, though, to the question of whether the cerebral and manual asymmetries in humans somehow set our species apart in a fundamental way from all other species (e.g. Crow 2002).

The asymmetries reviewed above are in a consistent direction in the majority of the population, but there are always some individuals in which the direction is reversed, or in some cases seemingly absent. Ghirlanda & Vallortigara (2004) noted that, in animal studies, the proportion of individuals that reverse the population-level bias ranges from approximately 10 per cent, as in human handedness, to approximately 35 per cent, as in chimpanzee handedness. Both extremes are also evident within our own species. Previc (1991) has summarized evidence for what he termed 'natural' forms of auditory and motor asymmetries in humans, and these favour one side over the other in a ratio of 2 : 1. They include the right-ear advantage in dichotic listening, right-eye dominance, a host of postural asymmetries and a tendency, especially among newborns, to turn the head to the right. These asymmetries may relate to the fact that about two-thirds of human foetuses are confined to an asymmetrical foetal position, with the right side facing towards the mother's front, during the final trimester. This leaves approximately 33 per cent of people with the reversed asymmetry. One possibility is that the 90 per cent bias evident in human handedness and cerebral asymmetry reflects a genetic influence superimposed on a more general bias of approximately 67 per cent (Corballis 1997).

3. GENETIC THEORIES

Variations in laterality suggests the possibility of genetic influences. Genetic theories of laterality have focused on human handedness, and, as noted above, have typically incorporated the assumption that handedness is uniquely human and involved some genetic mutation since the split of the hominins from the great apes (e.g. McManus 1999; Annett 2002; Crow 2002). The ubiquity of cerebral and behavioural asymmetries calls into question the notion of some uniquely human laterality gene, but the examination of contemporary genetic theories of handedness may nevertheless provide insights into the more general nature of genetic control over lateral asymmetries, and may apply widely across species and different manifestations of asymmetry.

(a) *Single-gene models*

Approximately 36 years ago, Annett (2002) proposed that the important genetic distinction, at least with respect to handedness, was not between left- and right-handers, but between those carrying a 'right-shift'

(RS) factor and those not carrying this factor—in more recent terminology, there is a RS allele, RS+, and an allele without directional specification, RS−. It should be emphasized, though, that, in Annett's model, most of the variation in handedness is considered to be random, and the RS+ allele shifts a normal distribution of intermanual differences to the right. For individuals homozygous for the RS+ allele, designated RS++, the shift is approximately two standard deviations to the right of neutrality, for heterozygotes, designated RS+−, the shift is approximately one standard deviation to the right, and for those homozygous for the RS− allele, designated RS−−, the distribution is centred on the point of neutrality—that is, the direction of handedness is essentially assigned at random. (Since the proportion of left-handers is slightly lower in women than in men, Annett (2002) proposed that the shifts are slightly larger in women.)

The idea that genes can influence the presence versus the absence of an asymmetry, rather than the direction of the asymmetry, may be a general principle in the genetics of asymmetry (Morgan & Corballis 1978), and applies, for example, to the asymmetry of the heart and other visceral organs (Layton 1976; Supp *et al.* 1997). In mice, a mutation on a single gene, known as *iv*, can cancel a left–right gradient and the asymmetry of the heart is randomized. Half of the affected mice show *situs inversus* (left–right reversal of the heart and other visceral organs; Layton 1976; Supp *et al.* 1997). This provides a plausible precedent for the single-gene models of human handedness and cerebral asymmetry developed by Annett (2002). Nevertheless, it does not lead to the identification of the gene itself, since *situs inversus* in humans appears to be unrelated to handedness or cerebral dominance for language (Kennedy *et al.* 1999). The actual gene or genes involved must be different.

The same principle is embodied in Klar's (1996) and McManus's (1999, 2002) genetic models of handedness. Similar to Annett, McManus proposed a two-allele gene, with a dextral (D) allele specifying right-handedness and a chance (C) allele that does not specify the direction of handedness, but leaves it to chance. Unlike Annett, McManus proposed that handedness is fundamentally dichotomous, so that all DD individuals are right-handed, 75 per cent of CD individuals are right-handed and 25 per cent left-handed, and CC individuals are equally divided between left- and right-handers.

Annett's and McManus's models provide essentially indistinguishable fits to the data on the inheritance of handedness. Table 1 shows how McManus's version fits the data accumulated by McManus & Bryden (1992), with the proportion $p(D)$ of D alleles in the population estimated at 0.76. This estimate might seem high, but perhaps reflects a largely literate society in which dextrality, or left cerebral dominance, has greater adaptive fitness than the lack of consistent handedness or cerebral dominance. Variations in this parameter might explain cultural differences in handedness.

In more recent formulations of her model, Annett (e.g. 2002) has proposed that the bias is cerebral rather than manual, so that right-handedness implies a dominance of the left hemisphere. (In these terms, the

Table 1. Percentage of left-handed offspring by parental combination based on the data summarized by McManus & Bryden (1992) and prediction from McManus's model.

	parental handedness		
	R–R	R–L	L–L
per cent left-handed offspring	9.5	19.5	26.1
predicted by McManus's model with $p(D)=0.76$	9.45	20.24	28.87

Table 2. Expected numbers of right- and left-handed individuals with left and right cerebral dominance for language in a hypothetical population of 100, according to McManus's model of handedness^a.

	language-dominant hemisphere	
	left	right
right-handers	83	7
left-handers	7	3

^a The numbers are based on $p(D)=0.8$. DD individuals are assumed to be right-handed and left-cerebrally dominant for language. In DC individuals, the proportions of right-handed and left-cerebrally dominant individuals are both 0.75, and are assumed to be uncorrelated. CC individuals are assumed to be equally divided among all combinations of right- and left-handedness and left and right cerebral dominance.

right shift is better described as a *left* shift.) There is also a weak correlation between handedness and the lateralized representation of language in the human brain. Studies based on the Wada test (Rasmussen & Milner 1977), electroconvulsive therapy (Warrington & Pratt 1973) and brain imaging (Pujol *et al.* 1999; Knecht *et al.* 2000) are reasonably consistent in showing that over 90 per cent of right-handers are left-cerebrally dominant for language, compared with approximately 70 per cent of left-handers. These estimates can be matched by McManus's model with $p(D)=0.8$, on the assumption that handedness and cerebral dominance for language are subject to the same biases in the three genotypes, but that the biases are applied independently (table 2). It may therefore be reasonable to suppose that a single two-allele gene may underlie variations in both handedness and cerebral dominance for language, and perhaps other asymmetries, both human and non-human, as well.

(b) *Where is the gene?*

Genetic models are unlikely to be widely accepted until the putative gene is located. The evidence so far is not especially convincing. One specific claim is that of Crow (2002), who has argued that the laterality gene is located in the Xq21.3/Yp11.2 region of homology on the X and Y chromosomes, and suggested protocadherin XY as a likely candidate. These claims are based largely on evidence that individuals with Turner's syndrome, who lack an X-chromosome, have deficits in performance associated with the right hemisphere, while those with an extra X chromosome (XXY, as in Klinefelter's syndrome, or XXX syndrome) have relative deficits in verbal IQ, suggesting a left-hemisphere deficiency. Further evidence comes from a study

showing a higher concordance of handedness in siblings of the same sex than in opposite-sex siblings, as expected from linkage to homologous X–Y loci (Corballis *et al.* 1996), but the effect was weak.

One argument against this theory is that polymorphisms are unstable on the Y chromosome (Corballis 1997), yet variations in handedness seem to have been fairly constant for at least 5000 years (Coren & Porac 1977) and probably longer. Evidence from the prehistoric record is necessarily indirect, but in a careful analysis of skeletal evidence and material cultural markers, Steele & Uomini (2005) suggested that the predominance of right-handedness was probably present in early species of our own genus, *Homo*, approximately 2 Myr ago. Following McKeever (2000), I have suggested that the gene may be on the X chromosome alone (Corballis 2001; see also Jones & Martin 2000). However, a genome-wide search for the handedness gene has since offered little support for X-linkage, and suggests that the region 2p11.2–12 on chromosome 2 may be a more likely candidate (Francks *et al.* 2002). Although this failed to replicate in an independent sample, a further analysis has revealed significant paternal linkage within this site (Francks *et al.* 2003), suggesting that imprinting may play a role.

Further investigation has narrowed the locus to the leucine-rich repeat transmembrane neuronal 1 (*LRRTM1*) gene on chromosome 2p12, a maternally suppressed gene that appears to be associated paternally with handedness and schizophrenia (Francks *et al.* 2007). The effect was observed in a sample of dyslexic siblings but not in a set of twins, and the same haplotype was over-transmitted paternally in a large sample of individuals with schizophrenic and schizoaffective disorders, which are, in turn, known to be related to the anomalies of handedness and cerebral asymmetry. Paternal inheritance is something of a puzzle, since surveys on phenotypic handedness have suggested a stronger maternal than paternal influence (e.g. Annett 2002). It seems unlikely, then, that *LRRTM1* is the only gene involved in handedness and cerebral asymmetry—indeed, it may have more to do with conditions such as dyslexia or schizophrenia, with only an indirect influence on laterality.

There are other reasons to suppose that several genes may be involved, perhaps with additive effects. Besides suggesting 2p12 as a likely candidate, linkage analyses have pointed to other regions of interest, including 17p11–q23 (Francks *et al.* 2003), 10q26 (Van Agtmael *et al.* 2002) and 12q21–23 (Warren *et al.* 2006). Inconsistencies between these reports might be due to the differences in the way handedness is defined, differences in populations, or the vagaries of statistical analysis. Furthermore, if the models proposed by Annett and McManus are correct in the assumption that chance plays a major role, especially in the determination of left-handedness, the gene or genes will be difficult to detect using linkage analyses.

It has also been suggested, though, that handedness is a facultative trait, with no genetic variation. Laland *et al.* (1995) have shown how a model incorporating a single dextral gene can explain the data on inheritance of right handedness, on the assumption that facultative right-handedness can be negated or reversed by

parental and cultural influences. For example, the advantage of being in a left-handed minority in fighting or in sport might be maintained through non-genetic parental inheritance; the successful left-handed warrior might train his sons also to be left-handed. Laland and colleagues also suggested that handedness can be transmitted from parent to infant through imitation or through the tendency of the parent to place objects in the hand corresponding to their own hand preference. An alternative possibility is that the action of the dextral gene is itself silenced by an epigenetic event, such as methylation (Klar 2004). Such events can even be transmitted between generations, but they do not involve mutations, and so would not be evident in the genome (Bird 2007). Models in which variation is non-genetic might after all be consistent with Crow's (2002) claim that the laterality gene is located in a homologous region of the X and Y chromosomes.

4. EVOLUTIONARY THEORIES

(a) *Why asymmetry?*

As a general rule, although there are noteworthy exceptions, the advantages of symmetry seem to apply more strongly to motor output than to sensory input (for a review see Corballis 1998). As an example, Watson & Kimura (1989) showed that right-handers were much better able to throw with the right hand, but equally adept with either hand at intercepting rapidly moving targets. In sports such as cricket, fielders can typically throw much further and more accurately with the dominant hand, but there is relatively little difference between the hands in catching a ball. Studies of patients following commissurotomy indicate that the production of speech typically depends exclusively on the left hemisphere, but that both hemispheres are capable of comprehending speech—although the left is usually superior (Sperry 1982). In general, then, there may be a stronger evolutionary imperative to preserve at least a degree of symmetry in reactions to the environment, which can impinge on either side, than in actions on the environment, where the organism is free to reposition itself to take advantage of any asymmetry (Corballis & Beale 1976). Complex motor patterns, such as speech or skilled manual performance, are generated within the brain and are relatively impervious to environmental input, so bilateral symmetry can be relaxed.

There may also be adaptive advantages to unilateral control. One suggestion is that bilateral control would be constrained by the relatively slow conduction time between hemispheres, so that unilateral computations can be carried out with greater speed (Ringo *et al.* 1994). Another advantage of hemispheric specialization is that it avoids duplication, and this may be especially important in complex functions, such as language, which require extensive neural circuitry. Duplication may therefore be wasteful of neural space, and complementary specialization in the two hemispheres results in a gain in overall computational efficiency. The left-hemispheric dominance for language, for example, is matched by a right-hemispheric dominance for spatial attention (Mort *et al.* 2003). Duplication of programming in the two

hemispheres might also lead to interhemispheric conflict (Corballis 1991). Stuttering, for example, has been associated with anomalies in cerebral dominance (Foundas *et al.* 2003).

These arguments, though, do not explain cases in which direction of asymmetry is the same in the majority of the population. One possibility is that there are group pressures for conformity in lateralized functions. In human societies, manufactured objects are often intrinsically asymmetrical and constructed for the convenience of right-handers and inconvenience of left-handers—these include scissors, books, magazines, musical instruments and even the placement of door handles. Convention demands that we shake hands and salute with the right hand. Of course, these asymmetries may be the consequence rather than the cause of right-hand dominance, and conformity in lateralized behaviour need not depend on biological asymmetry, except perhaps in the sense that asymmetry is a necessary requirement for the ability to tell left from right (Corballis & Beale 1970). In driving, for example, our very survival demands that we keep to the appropriate side of the road, but, in some countries, this is the left side and some the right.

If conformity does play a role in the shaping of directional asymmetries, we might expect asymmetries to be more pronounced in gregarious species than in those in which individuals are relatively isolated. There is some evidence that this may be so. In fishes, shoaling is a means of protection, and it is adaptive if all fishes in a shoal turn in the same direction when confronted with a predator, particularly if the predator is directly in front and turning in either direction would be equally effective. Bisazza *et al.* (2000) found that, among species of shoaling fishes, all six demonstrated a turning bias at the population level, whereas, among 10 species of non-shoaling fishes, six did not show a population-level bias, although all showed a bias at the individual level. Other pertinent evidence is difficult to find, and Vallortigara & Rogers (2005) pointed out that the gregariousness may change over time, and the conditions that led to population-level lateralization in the first place may no longer apply to extant species.

It is also possible that population-level asymmetries are based on some underlying property of living matter, such as the helical coiling of amino acids. For some speculation along these lines, see the final chapter of McManus (2002).

(b) *Why the variation in lateralization?*

If cerebral asymmetry were clearly adaptive, one might ask why it varies between individuals, and is sometimes even reversed. We have seen that the variation, in humans at least, may be best described in terms of the presence versus the absence of a population-level lateralizing influence, such as the RS+ or D allele, rather than in terms of opposite directions of asymmetry. If asymmetry were the sole consideration, then one might expect the entire population to show the same direction of asymmetry (e.g. all people right-handed and left-cerebrally dominant for language), or perhaps equal numbers of individuals showing opposite directions of asymmetry (e.g. half the population left-handed and half right-handed). This state of affairs has

been called antisymmetry and applies to the asymmetry of the claws in male fiddler crabs—one claw is larger than the other, but the larger one is as likely to be on the left as on the right. But the behavioural and cerebral asymmetries evident in both humans and non-human species apply only to a majority, with a significant minority showing either reversed asymmetry or a lack of asymmetry.

Regardless of whether these variations in the direction of asymmetry are of genetic or non-genetic origin, it is of interest to speculate that variation itself might be adaptive. Vallortigara & Rogers (2005) have suggested that directional asymmetries may have been subjected to frequency-based selection, such that there is an adaptive advantage to being in a reversed minority only if it remains a minority. Suppose, for example, that members of a group tend to stick together to avoid predation, and run off to the left when a predator threatens. By being one of many, each individual is less likely to be singled out by the predator. The predator may nevertheless choose to attack the mob rather than the strays, since the chances of catching at least one victim is maximized. Some individuals may therefore benefit from belonging to a minority that veers off to the right—a strategy that works only if this group remains a minority. This may have resulted in a subtle selection dynamic that held left- and right-turning in balance (see also Ghirlanda & Vallortigara 2004), but with left-turning, implying a right-hemisphere dominance for this behaviour, maintained for the majority. One might argue similarly that left-handers hold an advantage in fighting, but only so long as they are in the minority (Raymond *et al.* 1996). In genetic terms, this theory implies an allele that reverses the prevalent asymmetry, but it is also consistent with a model, such as that of Annett (2002) or McManus (2002), in which one allele cancels, rather than reverses, the asymmetrical influence of the other.

A more general possibility is that of a trade-off between bilateral symmetry and asymmetry—perhaps too much symmetry leads to difficulties in the neural programming of complex action, and too much asymmetry leads to a vulnerability in an even-handed world where impediments, such as attack from predators, may occur on either side of the organism. The balance may be achieved simply by developmental mechanisms in which tendencies to asymmetry are held in check by those conforming to the basic bilateral symmetry of the body plan. In this case, variations might be attributed simply to environmental influences. But balance may also be accomplished through genetic influences. In terms of single-gene models, for example, balance may be accomplished through a heterozygotic advantage (Annett 2002); that is, RS+ – individuals may have slightly greater biological fitness than either RS++ or RS– – individuals. This ensures that both alleles are preserved in the population. Annett herself has documented evidence that, in the human population, left-handers may be especially susceptible to reading disorders, while extreme right-handers may be relatively disadvantaged in spatial or some sporting activities. She also noted a preponderance of left-handers among surgeons.

The more interesting and relevant comparisons, though, may be between the presence and absence of asymmetry rather than between opposite directions of asymmetry. A study of 12 770 eleven-year-olds in the UK suggests that those without clear handedness performed worse than either left- or right-handers on tests of verbal ability, non-verbal ability, reading comprehension and mathematical ability (Crow *et al.* 1998). This suggests that those lacking the directional allele (RS+ or D) may run the risk of what Crow *et al.* called 'hemispheric indecision', to the detriment of certain intellectual activities. Of course, chance influences will ensure that some of these individuals will be left-handed and some right-handed, so the overall risk of falling into the susceptible group is small. Crow and colleagues result was not replicated in a sample of 530 younger boys (Mayringer & Wimmer 2002), but similar deficits associated with ambidexterity in adults have been reported by Peters *et al.* (2006) and Corballis *et al.* (2008).

The disadvantages of cerebral symmetry may apply also to non-human species. In chicks, cerebral asymmetry is determined by asymmetrical exposure to light prior to hatching, and chicks raised without this pre-hatching asymmetry are at a disadvantage relative to lateralized birds in a situation where they monitor a hovering predator while, at the same time, discriminating grain from non-edible grit (Rogers 2002a). A similar result has been obtained in pigeons. As with chickens, pigeons show a right-eye advantage in discriminating grain from grit, and Güntürkün *et al.* (2000) reported a positive correlation between the degree of asymmetry, as determined under monocular viewing, and the discrimination performance under binocular conditions, suggesting that visual foraging is accomplished more effectively if mediated by a single hemisphere.

Given the advantages of an asymmetrical brain, the question arises as to why asymmetry has not become fixed in the population. One possibility, suggested earlier, is that reversed asymmetry may be advantageous so long as it is a minority condition. Reversed asymmetry may result from the lack of any genetically induced bias, and its advantages may offset any penalty owing to the risk of a lack of asymmetry. Alternatively, there may be compensatory advantages more directly associated with the lack of asymmetry. These may have to do with the more general benefits that drove the evolution of bilateral symmetry in the first place, resulting in a more balanced awareness and disposition to movement. Sexual selection may also have played a role; symmetry is seen as more attractive than lopsidedness, and people judge symmetrical faces to be more attractive than asymmetrical ones (e.g. Gangestad *et al.* 1994; Rhodes & Zebrowitz 2002).

(c) *Symmetrical oddity?*

It is of interest to speculate, though, that cerebral symmetry, or a relative lack of consistent lateralization, might have cognitive consequences that are adaptive, but only if a minority condition, creating kinds of cognitive oddity that may lead to creativity or enhanced charisma. In what may appear as an unpromising lead,

Barnett & Corballis (2002) found that mixed-handers were more prone to magical ideation, characterized by mild paranoia and superstition, than either left- or right-handers—a function that was essentially the inverse of the relationship between academic achievement and handedness reported by Crow *et al.* (1998). A similar result was reported by Nicholls *et al.* (2005), although Jaspers-Fayer & Peters (2005) found no relationship between handedness and magical ideation, which was nevertheless more prevalent in females with a tendency to left–right confusion, perhaps suggestive of cerebral symmetry. In a similar vein, there is evidence that mixed-handedness is associated with a greater sensitivity to sensory illusions (Niebauer *et al.* 2002) and a higher risk of schizophrenia (Claridge *et al.* 1998; Upadhyay *et al.* 2004), and strong belief in the paranormal seems to be associated with symmetrical brain activity (Pizzagalli *et al.* 2000).

Jaynes (1976) speculated that cerebral asymmetry emerged in the second millennium BC, in response to assorted catastrophes, such as floods, invasions, etc. Prior to this, people were governed by hallucinations, invoking the Gods, but cerebral asymmetry allowed the left hemisphere to create a sense of self, so that people took responsibility for their own actions. Jaynes's theory makes little evolutionary sense, since handedness and cerebral asymmetry probably go back at least 2 million years, and perhaps even earlier, in hominid evolution (Corballis 1997; Steele & Uomini 2005). Nevertheless, there may well be some truth to the idea that cerebral asymmetry underlies rational thought, and that a lack of asymmetry may well lead to more delusional and perhaps hallucinatory thought processes.

Although magical thinking may seem counter-productive in terms of biological fitness, it may be related to creativity, with positive implications for science and mathematics. Leonhard & Brugger (1988) noted a link between paranormal thought, delusional thought and creativity, and suggested that these characteristics relate to heightened right-hemispheric activation and relatively coarse semantic activation in that hemisphere. This, in turn, results in a loosening of associations and enhanced creativity. Although Leonhard and Brugger's account focuses on the right hemisphere, it is possible that the profile has to do with the lack of cerebral dominance rather than any specialization of the right hemisphere itself. Despite the evidence that mixed-handers show some deficit in arithmetic ability (Crow *et al.* 1998; Corballis *et al.* 2008), Singh & O'Boyle (2004) reported that mathematically gifted adolescents show no hemispheric asymmetry on tasks involving global–local judgements and matching letters, whereas average-ability adolescents and college students show a left-hemispheric advantage, suggesting that the mathematically gifted may lack consistent cerebral asymmetry. Although Singh and O'Boyle selected right-handers for this study, they also characterize the mathematically gifted as 'typically male, left-handed, and myopic' (p. 371).

At present, then, it remains unclear precisely what advantages accrue to cerebral symmetry rather than the asymmetry observed in most human brains. There are hints that symmetry may lead to enhanced creativity, but this needs further investigation. There is a popular

view that left-handers are overly represented among creative artists or scientists,¹ but this is based more on the idea that the right hemisphere, which controls the left hand, is the more creative of the two sides of the brain, itself a dubious proposition (Zangwill 1976; Corballis 2007). But left-handedness itself may be indicative of the lack of consistent cerebral asymmetry, and any associations with creativity may be a reflection of that rather than of left-handedness *per se*. To my knowledge, there is no comparable evidence from non-human species suggesting that there may be advantages associated with the lack of asymmetry in an otherwise asymmetrical population.

Human societies have often revered the oddball, especially if associated with mystical or even hallucinatory behaviour, and there is at least some evidence that these characteristics may be associated with the lack of consistent asymmetry, as documented above. A symmetrical brain may well provide avenues of thought that do not conform to academic expectations, but may nonetheless provide the impetus for significant discovery and leadership.

5. CONCLUSIONS

Recent research has made it abundantly clear that handedness and cerebral asymmetry are not unique to humans. Nevertheless, activities that are uniquely human, such as language, or that are more highly developed in human than in other species, such as manual skill (*dexterity*), may well have exploited asymmetry in ways not evident in non-human species. Asymmetries are too ubiquitous to be attributed simply to environmental influences, but their genetic bases remain elusive. Single-gene models can provide good fits to phenotypic data, but the location of the putative gene is not known.

A paradoxical feature of the various behavioural and cerebral asymmetries reviewed above is that they do not apply to all members of the species. This suggests that there is some adaptive advantage in maintaining variations in laterality, along with advantages to asymmetry itself. In this respect, these asymmetries contrast with the characteristic asymmetry of the heart and other visceral organs, where reversals and other variations are extremely rare and usually attributed to pathology. In this paper, I have sketched a number of hypotheses as to why variation of lateralization might itself be adaptive. These are not necessarily mutually incompatible, although they do suggest a number of issues that might guide further inquiry. One is whether the genetic component is fixed, and variations arise simply from environmental or epigenetic influences, or whether the variation itself is genetic in origin. If the latter, the question is whether the balance of asymmetries is maintained through frequency-based selection, or through a mechanism such as heterozygotic advantage.

At present, it seems more likely that the balance is one between asymmetry and symmetry, rather than between symmetry and antisymmetry. First, in Bilateria—the phylum to which we and most other animals belong—symmetry is the default condition, and the advantages of

asymmetry must be weighed against the long-standing adaptiveness of symmetry in a world lacking systematic left–right biases. Second, genetic models and genetic evidence suggests that genes rarely determine the direction of asymmetry, but influence instead whether or not an asymmetry will be expressed. In research on lateralization in humans, it has been traditional to compare individuals of opposite laterality, as in comparing left- and right-handers or left and right cerebral hemispheres, but, from both evolutionary and genetic perspectives, it may be more fruitful to compare degrees rather than directions of lateralization. We have seen that those without consistent handedness, for example, may differ from both the left- and right-handers in terms of both intellectual abilities and personality characteristics such as magical ideation, delusional behaviour and possibly creativity. This is one avenue, I suggest, that it might be useful to explore further.

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ENDNOTE

¹This has even led to false claims of left-handedness. For example, Wikipedia lists Albert Einstein, Benjamin Franklin, Pablo Picasso and Leonardo da Vinci among famous scientists and artists who were left-handed. As McManus (2002) documented, the first three were almost certainly right-handed. Wikipedia is right about Leonardo.

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