Laterality and Human Speciation

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Summary. Although cerebral asymmetries abound in non-human animals, there are still reasons to suppose that there may have been a single-gene mutation producing a 'dextral' (D) allele, which created a strong bias toward right-handedness and left-cerebral dominance for language at some point in hominid evolution. The alternative 'chance' (C) allele is presumed directionally neutral, although there may be other influences producing weak population manual and cerebral asymmetries in the absence of the D allele. It is unlikely that this laterality gene is located in homologous regions of the X and Y chromosomes, as suggested by Crow (1998), but there is a case for supposing that it is located solely on the X chromosome. I argue that language evolved from manual gestures, and the D allele may have served to guarantee manual and vocal control in the same (left) hemisphere in the majority of humans. The 'speciation event' that distinguished *Homo sapiens* from other large-brained hominids may have been a switch from a predominantly gestural to a predominantly vocal form of language.

IT IS OFTEN ARGUED that one of the characteristics distinguishing humans from other apes, and perhaps other species generally, is laterality, that we are, in other words, the lopsided apes (Corballis, 1991). Of course, asymmetries abound in nature, but what may be unique to our species is the strong bias toward right-handedness and left-cerebral dominance for language. This view has been strongly endorsed by Crow (1993, 1998), who has argued for a 'speciation event' that gave rise to laterality, language itself, theory of mind, and a proneness to thought disorders such as schizophrenia. It was this event that gave rise to the emergence of our own species, *H. sapiens*, perhaps 150,000 years ago. Crow also argues that the gene responsible for these changes is located in homologous regions of the X and Y chromosomes. In this chapter, I shall be mainly concerned with the role that laterality has to play in this scenario.

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ARE WE REALLY THE LOPSIDED APES?

Laterality in non-human species

Over the past decade or so there has been growing resistance to the idea that handedness and cerebral asymmetry are uniquely human attributes. In a recent review, Vallortigara *et al.* (1999) note that functional and structural asymmetries of the brain are widespread in vertebrates, including fish, reptiles, amphibians and mammals. All species so far tested that show gregarious behaviour display evidence of cerebral lateralisation at the population level, with the evidence generally consistent with a left-hemisphere specialisation for stimulus categorisation and a right-hemisphere specialisation for attack and agonistic behaviour. It is not difficult to see how these asymmetries might underlie the left-hemispheric specialisation for language and the right-hemispheric specialisation for emotional and spatial behaviour in humans. Some 40% of the species tested that do not show gregarious behaviour also show some degree of complementary lateralisation. The population bias is typically not as extreme as that of left-hemispheric speech dominance in humans, but one extreme case was recently claimed by Gannon *et al.* (1998), who reported that the left temporal planum was larger than the right in 17 out of 18 chimpanzees. This proportion is actually larger, even significantly so,[1] than that reported in humans (Geschwind & Levitsky, 1968).

Population-level preference for one or other limb, be it hand, foot or paw, also appears to be quite widespread. It has long been known that parrots show a preference for the left foot in picking up small objects (Friedman & Davis, 1938), and the population bias of about 90% is about the same as that in humans. Evidence from other species usually shows less extreme biases, and they are typically contingent on the actual activity performed with the hand or paw. For example, although Collins (1970) found no overall bias among mice for one or other paw in reaching into a glass tube for food, a more recent study has shown a right-paw preference on one test and a left-paw preference on another (Waters & Denenberg, 1994). Among primates the evidence is mixed, and somewhat controversial. MacNeilage *et al.* (1987) suggested that primates tend to be left-handed in reaching, but those that became less arboreal evolved a complementary right-hand preference for fine motor acts. Hopkins (1996) has documented evidence that about two-thirds of captive chimpanzees are consistently right-handed for a number of activities, such as extracting peanut butter from a tube, and, as shown in more recent work, gestural communication (Hopkins & Leavens, 1998). Byrne (1996) has also reported a population-

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[1] The proportion in humans is about 67% (Geschwind & Levitsky, 1968), leading to an expected value of 12 out of 18. Comparing the observed value of 17 out of 18 in chimpanzees to this expected value yields a chi-square of 6.25, which is significant at $P < 0.05$.

level hand preference among gorillas preparing vegetable matter for consumption, with about two-thirds showing a right-hand preference for the more intricate components.

McGrew & Marchant (1997: 201) have expressed some scepticism as to the generality of this work; in a review of handedness in primates, they conclude that 'only chimpanzees show signs of a population bias … to the right, but only in captivity and only incompletely'. It is possible that the bias in captive chimpanzees is culturally determined. For example, there is no evidence, despite extensive observation, that chimpanzees ever use pointing gestures in the wild, but pointing has been widely adopted among the 115 captive chimpanzees studied by Hopkins & Leavens (1998), as well in other captive apes (reviewed by Leavens *et al.*, 1996). This suggests that chimpanzees readily acquire manual actions from human contact, and may also be influenced by predominance of right-handedness among their human captors.

What is unique about human laterality?

Although some of the evidence is rather conflicting, there is little doubt that there are population-level cerebral and manual asymmetries in many non-human species, including primates. We must therefore ask whether it is reasonable to conclude that there is still some aspect of laterality that is unique to humans, perhaps to the point of defining a speciation event. It was probably never realistic to suppose that human laterality appeared *de novo*, as a result of a single genetic mutation, say, and even the characteristic asymmetries of the internal organs depend on a cascade of influences rather than on the actions of a single gene (Garcia-Castro *et al.*, 2000). It is not out of the question that there *are* aspects of human laterality unique to our species, perhaps dependent on a single genetic mutation, but any such mutation would surely have operated against a background of existing asymmetries (Corballis, 1997). Let us consider, then, what aspects of human laterality might be considered unique, and what their genetic basis might be.

In most people, articulate speech is controlled by the left cerebral hemisphere, and language itself is generally considered uniquely human (Chomsky, 1980; Pinker, 1994; Calvin & Bickerton, 2000). It follows, even if only secondarily, that the left-hemispheric dominance for speech and other aspects of language is uniquely human. There are also manual activities typically carried out with the right hand, or with different contributions from the two hands, that are at least arguably uniquely human, again bestowing a uniqueness on the asymmetries themselves. One is throwing. Marzke (1996) has argued that as far back as *Australopithecus afarensis* changes in the structure of the hand, the steady bipedal stance, and control of the trunk were adapted for accurate and potentially lethal throwing. Chimpanzees, by contrast, are capable only of a crude

form of underarm propulsion that is better described as a fling. Indeed, the ability to throw with precision, as a means of both attack and defence, may well have been necessary to ensure survival on the savanna, especially for a species previously restricted to a largely arboreal existence. Most people throw with the right hand, and few if any can throw equally well with either hand. Most people, too, use tools preferentially in the right hand, or with the right hand performing the critical operation while the left hand serves a holding function; for example, the left hand holds the nail while the right wields the hammer, or the left hand holds the bow while the right hand pulls back the arrow for accurate aim. Although other species have been shown to use improvised tools, the systematic manufacture of tools is generally attributed to the genus *Homo*.

Distinctively human activities like speaking, throwing, and manufacturing and using tools, may be better programmed within a cerebral hemisphere, so that interhemispheric conflict is eliminated (Corballis, 1991). Wilkins & Wakefield (1995) also point out that lateralisation might facilitate internally generated manual activities, like manipulation and throwing, by shortening the feedback from sensorimotor to motor areas. These considerations may well have favoured the selection of one or more further mutations to enhance, and perhaps guarantee, cerebral asymmetry for the programming of complex action sequences in our species.

However, it may not have been simply a matter of lateralising a number of independent activities. The importance of a consistent lateralising influence may derive from the fact that it guaranteed the lateralisation of speech and manual control in the *same* cerebral hemisphere. Calvin & Bickerton (2000) have proposed that the origins of syntax may lie, at least partly, in the neural mechanisms involved in accurate throwing; if this is so, then it would follow that the two might be located in the same hemisphere, as proposed by Calvin (1983). But there is perhaps more compelling evidence for a link between language and *gesture* (of which throwing might be considered just an example). There are cells in area F5 in the pre-motor cortex of the macaque that fire when the monkey makes specific grasping movements, and a subpopulation of these cells, known as 'mirror neurones', also fire when the animal observes a person making the same grasping movement (Rizzolatti & Gentilucci, 1988). Because this system maps a programmed movement onto the perception of the same movement, it has been suggested as a precursor to language, and as implying that language evolved from manual gestures (Rizzolatti & Arbib, 1998). There are many other reasons to suppose that language may have evolved from a system of manual gestures rather than vocal calls (Hewes, 1973; Corballis, 1991, 1999; Armstrong *et al.*, 1995; Givon, 1995).

A further reason to suppose that mirror neurones may be part of a system that is a precursor to language is that area F5 in macaques is roughly homologous to Broca's area in humans. There is an important difference, though:

mirror neurones are located bilaterally in the macaque whereas in the great majority of humans Broca's area, at least in so far as it is involved in speech, is confined to the left hemisphere. Moreover, there is also evidence that there is a system for recognising gestures in humans that is similar to that in macaques, and that it is left-hemispheric and may well overlap with Broca's area (Rizzolatti *et al.*, 1996). This suggests that, at some point in the evolution of our species, what was initially a bilateral system became predominantly unilateral, perhaps when the programming reached a certain level of complexity, and when it co-opted oral as well as manual sequencing. The enlargement of the left temporal planum in chimpanzees (Gannon *et al.*, 1998) may suggest that this had already occurred in the common ancestor of humans and chimpanzees, although there is as yet no evidence that this anatomical asymmetry is accompanied by a functional asymmetry. Moreover, an asymmetry of the temporal planum need not imply a corresponding asymmetry in the language-mediating areas of the prefrontal cortex. There is evidence that Broca's area is first discerned in hominid skulls in *Homo habilis*, suggesting that the lateralised circuits for language, whether gestural or vocal, might have evolved with the emergence of the genus *Homo* (Tobias, 1987).

According to this scenario, then, what is unique to humans may be a lateralised system for the programming of language that couples manual and vocal control. The direction of lateralisation may have been determined by pre-existing cerebral asymmetries, or perhaps by underlying developmental gradients that dictate different rates of development on the two sides of the brain (Corballis, 1991). Whatever the case, it does not seem unreasonable to suppose that it was governed by a mutation, perhaps involving a gene governing rate of growth, at some point in hominid evolution.

GENETIC THEORIES OF HANDEDNESS

The most compelling genetic theories of handedness are based on the insightful suggestion of Annett (1972), that human handedness may depend on two genetic influences, one creating a bias toward right-handedness and the other creating no disposition towards either right- or left-handedness. That is, the genetic influence is not over whether a person will be right- or left-handed, but is over whether a person will be right-handed *or not*. These may be considered as alleles of a single 'right-shift' gene, and Annett (1993) has labelled them RS+ and RS–, respectively. In her model, differences in performance between the two hands are subjected to random environmental influences, producing a normal distribution, but in those homozygotic individuals inheriting a double dose of the RS+ allele, this distribution is shifted markedly to favour the right hand. In heterozygotes inheriting one of each allele, the distribution is also shifted to

the right, but to a lesser extent. In those homozygotic for the RS– allele, there is no genetic disposition towards either left- or right-handedness, although cultural pressures may induce a small shift to the right. Annett also proposes that a heterozygotic advantage in terms of fitness has resulted in balanced polymorphism, ensuring that both alleles remain in the population.

McManus (1985, 1999) has proposed a similar single-gene model, with two alleles, one labelled D for 'dextral' and the other C for 'chance'. In his scheme, handedness is defined in terms of preference rather than performance, and is considered to be a dichotomous variable. Hence *all* DD homozygotes are considered to be right-handed, while CC homozygotes are considered to be divided equally into right- and left-handers. Among CD heterozygotes, it is proposed that the proportions lie midway between those of CC and DD homozygotes, so that 75% will be right-handed and 25% left-handed.

Although rather different in terms of underlying assumptions about handedness, these two models provide good, and essentially equivalent, fits to data on the proportions of left- and right-handers born to parents of differing handedness. Both Annett and McManus also assume that the gene influences not only handedness, but also cerebral asymmetry for language. McManus (1999) points out that his model readily accounts for the observed relation between handedness and language dominance if it is assumed that the D and C alleles influence language dominance in exactly the same way but in a statistically independent fashion. Thus DD individuals are all right-handed and left-language dominant, while in CC homozygotes handedness and language dominance are assigned independently and at random, so that there are equal proportions in each combination of handedness and language dominance. DC heterozygotes are 75% right-handed and 75% left-language dominant, but the two asymmetries are independent, so that the breakdown is as follows:

right-handed and left-language dominant	56.25%
right-handed and right-language dominant	18.75%
left-handed and left-language dominant	18.75%
left-handed and right-language dominant	6.25%

It follows from these last two figures that left-handers should be more often left- than right-language dominant, although the difference is attenuated slightly by the addition of CC left-handers. The evidence has consistently shown that, among right-handers, the incidence of left-language dominance is at least 96%, while among left-handers it is lower but is still around 70% (Warrington & Pratt, 1973; Rasmussen & Milner, 1977; Pujol *et al.*, 1999), almost exactly as predicted.

Annett and McManus have both proposed that this laterality gene is uniquely human. In view of the evidence for a weak population-level right-handedness in primates (Hopkins, 1996), I have suggested that the D allele

may operate against a background, not of equal proportions of left- and right-handers, but against a pre-existing bias of about 67% in favour of right-handers (Corballis, 1997). That is, CC individuals who lack the D allele may be 67% right- and 33% left-handed, and the proportions of right- and left-handers among CD heterozygotes might be recalibrated accordingly to 83% and 17%, respectively. This also accords with evidence that human asymmetries other than handedness and language dominance, such as the asymmetries of the face, the right-ear dominance in dichotic listening, or the fetal position of the final trimester in which the right hand faces towards the mother's front, are in a ratio of approximately 67 : 33 rather than 90 : 10; these and other asymmetries are summarised by Previc (1991). [Ironically, one such asymmetry is the enlargement of the left temporal planum relative to the right, which makes the more pronounced ratio (17 : 1) reported in chimpanzees (Gannon *et al.*, 1998) all the more striking, and perhaps difficult to accept as a true estimate of the population ratio.] The assumption that the background asymmetry is 67 : 33 rather than 50 : 50, when incorporated into Annett's and McManus's models, provides a slightly better fit to aspects of the data on inheritance (Corballis, 1997).

IS THE GENE ON THE SEX CHROMOSOMES?

Crow (1998) suggested that the laterality gene is not only responsible for language and theory of mind, thereby further defining *H. sapiens* as a distinct species, but that it might be located in homologous regions of the sex chromosomes. If true, this might not only explain the slight differences in cerebral asymmetry, but could also suggest that the gene was subject to sexual selection. Crow's reasons for suggesting that the gene is located on the sex chromosomes are based on certain genetic disorders. He cites evidence that people lacking an X chromosome, a condition known as Turner's syndrome, have deficits that may be described as deficits of the right hemisphere, while those with an extra X chromosome, whether XXY (Klinefelter's syndrome) or XXX, have deficits that appear to be deficits of left-hemispheric functioning. This suggests that a gene on the X chromosome influences cerebral dominance. As males, like females with Turner's syndrome, also carry only one X chromosome, yet do not show deficits associated with right-hemisphere malfunction, a gene on the Y chromosome must balance that on the X. According to Crow, then, this identifies the gene as one of the select class of X–Y homologous genes.

This theory suggests that siblings of the same handedness should be more often of the same sex than of opposite sex, and the reverse should be true of opposite-handed siblings. This follows because fathers can pass on their Y chromosomes only to sons and their X chromosomes only to daughters. The

expected concordance is weak, in part because mothers pass on their X chromosomes to either sons or daughters, and in part because the C allele (or RS– allele in Annett's terminology) does not determine the direction of hand- edness, so that two sons, for example, might receive the C allele from the father's Y chromosome yet be of opposite handedness. Nevertheless, the concordance was demonstrated in a large-scale study of handedness in sibling pairs (Corballis *et al.*, 1996), although there was an anomaly in that the relatively small numbers of left-handed pairs were more often of opposite than of same sex.

There are, however, two serious difficulties. The first is that of explaining how the gene came to be present on both the X and the Y chromosome. As there is no recombination, there would have to be a second event, such as a transposition, for the gene to be copied over to the other chromosome. The problem may not be insuperable, as there is evidence that such transpositions do occur, and there is at least one sequence that occurs only on the X chromo- some in gorillas and chimpanzees, but is duplicated with more than 99% homology on the Y chromosome in humans (Bickmore & Cook, 1987). But even if the gene exists on both chromosomes, there is still the question of how the mutation that produced the D allele could have resulted in that allele being present on both chromosomes.

The second difficulty is that polymorphisms on the Y chromosome are unstable under any selection regime, including a regime in which there is a selec- tive advantage to heterozygotes, as postulated by Annett (1993). This is shown algebraically by Clark (1987), and is consistent with empirical evidence that Y chromosome polymorphisms are rare (Spurdle & Jenkins, 1992). A simulation also shows that if a mutation does result in the D allele occurring on both X and Y chromosomes and there is an ensuing heterozygotic advantage favouring CD genotypes, then the probability of the D allele will at first increase on both chromosomes under the selection regime. A balanced polymorphism will even- tually stabilise on the X chromosome, but the alleles on the Y chromosome will eventually regress to a state in which only one of them remains (Corballis, 1997). The D allele will prevail if DD homozygotes are fitter than CC homozy- gotes, and this is reversed if CC homozygotes are the fitter. Polymorphisms may persist on the Y chromosome if there is no selective regime, but it is diffi- cult to imagine why a laterality allele would appear unless it were associated with some increase in fitness.

Jones & Martin (2000) have argued that the Y chromosome may indeed carry only the C allele, leaving the X chromosome to carry both C and D alle- les. The difficulty with this proposal is that it predicts too large a sex difference to fit the facts. By manipulating parameters, Jones & Martin (2000) show that, in an extreme case, the resulting estimates of the incidence of left-handedness are 13.02% for males and 8.07% for females, which they consider reasonably

close to empirical estimates of 11.64% and 9.79%, respectively, as reported by McManus & Bryden (1992). But in reality it is not a good fit, because the measured sex difference is less than half that predicted, and the parameters that Jones & Martin (2000) used are unrealistic. For example, to achieve this fit they assume that the proportion of left-handedness in CC individuals is 0.21, which is far removed from the value of 0.5 assumed by McManus (1985), or even the value of 0.33 assumed in my own revised version of McManus's model (Corballis, 1997). They also assume that the D allele is dominant, so that DC individuals are all right-handed. This means that the model can no longer fit the data on relations between handedness and language dominance as described by McManus (1999) and outlined above. Moreover, if there is no phenotypic difference between DD and CC individuals, this raises questions about how the heterozygotic advantage, which is necessary to ensure polymorphism, is achieved.

Is the gene on the X chromosome only?

An alternative possibility is that the laterality gene is located solely on the X chromosome, with no counterpart on the Y chromosome. McKeever (2000) has recently reported data on the handedness of parents and their offspring in a large sample that are largely consistent with this possibility. In particular, couples in which the mother was left-handed and the father right-handed produced more left-handed offspring, especially in the case of sons, than did couples in which both were right-handed. Couples in which the mother was right-handed and the father left-handed produced more left-handed daughters than did right-handed couples, but no more left-handed sons. This last result is to be expected according to the X chromosome hypothesis, because fathers can pass on the X chromosome only to their daughters.

Rather surprisingly, perhaps, this model need not predict a sex difference in handedness. In males, there are only two genotypes, which we can label 0C and 0D, where '0' stands for the absence of a corresponding gene on the Y chromosome. We can suppose that the 0D genotype always results in right-handedness, and never in left-handedness, while the 0C genotype results in left-handedness with a probability of 0.5. If we suppose that the incidence of the C allele is c, then the overall incidence of left-handedness in males is simply $c/2$. In the case of females, there are three genotypes: CC, CD and DD. Following McManus (1985), we assume that the probability of left-handedness is 0.5 in CC individuals, 0.25 in DC individuals, and 0 in DD individuals. The overall incidence of left-handed CC females is therefore $c^2/2$, while that of left-handed CD females is $2c(1 - c)/4$, which reduces to $c/2 - c^2/2$. As none of the DD females is left-handed, we can add over CC and CD individuals to get the overall incidence of left-handedness in females, which gives $c/2$. This is exactly the same as that

predicted for males. The slight sex difference might then be attributed to a higher susceptibility to birth stress in males (Bishop, 1990).

The idea that only a quarter of CD females will be left-handed also follows naturally from X inactivation. For most of the genes on the X chromosome, one of each pair of X genes in females is inactivated very early in embryonic development (Willard, 1995). This inactivation is random, so that in some cells it is the X chromosome received from the mother that is inactivated, and in some the inactivated chromosome is the one received from the father. This ensures equal dosage of the gene product in both sexes, so that in the CD genotype half of the cases will resemble the 0C male genotype and half will resemble the 0D genotype. We therefore expect the incidence of left-handedness in females inheriting the CD genotype to lie midway between those of the 0C and 0D male genotypes, in other words, a quarter.

On the face of it, this model seems more plausible than a model postulating a gene in homologous regions of the X and Y chromosomes, as the great majority of genes on the X chromosome are not paired with homologous genes on the Y. Moreover, it removes the problem of explaining how the D allele came to be located on both sex chromosomes in the absence of recombination. However, it does not square with Crow's (1998) argument that the gene must be on both chromosomes, because males do not show the 'right-hemisphere' deficits shown by 0X females with Turner's syndrome. It is possible, perhaps, that in Turner's syndrome individuals there is partial deactivation of the remaining X chromosome. Another difficulty with the X chromosome model is that it is in general not supported by large-scale studies of handedness in families, other than that reported by McKeever (2000). McKeever has noted this, and suggested ways in which other studies may have provided distorted information, but this is a matter in need of further resolution.

CONCLUSIONS

There is still reasonable support for the notion that human laterality, in its distinctive aspects, might depend in part on a single gene. It is unlikely that this gene is located in homologous regions of the X and Y chromosomes, but it is possible that it is located on the X chromosome only.

Could this gene be responsible for the 'speciation event' proposed by Crow (1998)? If it is the D allele that was instrumental in this event, then the answer is probably no, because there are individuals lacking this allele who are nevertheless undeniably human, and possessed of normal language abilities, even though the risk of language disorders might be slightly elevated (for a critical review see Bishop, 1990). It is possible that a *population* with this allele had some adaptive advantage over a population, such as the Neanderthals, that did

not possess it, perhaps by virtue of the heterozygotic advantage, or perhaps simply because of a greater diversity of genotype, but one may question whether this could have represented a speciation event on the scale envisaged by Crow.

An alternative scenario, sketched by McManus (1999), is that an earlier form of the D allele, say D*, became dominant perhaps 2 million years ago, so that all members of the genus *Homo* from that point were right-handed. But then a second mutation resulted in the appearance of the present-day C allele, reducing the incidence of right-handedness to 90%. McManus suggests that this mutation may have occurred some time between 100,000 and 10,000 years ago, but it must surely have occurred prior to the migrations of *H. sapiens* from Africa, which may go back at least 125,000 years (Walter *et al.*, 2000). Perhaps it was this second mutation that defined the speciation event, which might be good news for left-handers. In invoking two mutations, however, this model is somewhat unparsimonious and is perhaps too speculative to be considered a serious possibility in the absence of further evidence.

Whatever the nature of the mutations that produced laterality, the bulk of evidence is beginning to weigh against the notion that human speciation itself involved a dramatic change. Arguments for a sudden discontinuity have been based largely on the grounds that language is quite unlike animal communication, and well beyond the capabilities of even our closest relatives, chimpanzees and bonobos (Chomsky, 1980; Bickerton, 1995). Even Bickerton, once a staunch advocate of what has been dubbed the 'big bang' theory of the emergence of syntax (Bickerton, 1995), has more recently argued that the elements of syntax might be found in reciprocal altruism in the great apes (Calvin & Bickerton, 2000). There are other scenarios more consistent with the gradual evolution of language through natural selection than with the notion that language emerged as the lucky outcome of a single mutation (Pinker & Bloom, 1990; MacNeilage, 1998).

From hand to mouth

My own view is that language probably evolved from manual gestures, and that its roots can be traced back to a system of intentional manual activity in our primate ancestors tens of millions of years ago (Hewes, 1973; Corballis, 1991, 1992, 1999; Armstrong *et al.*, 1995; Rizzolatti & Arbib, 1998). No doubt the vocal element would have assumed greater prominence as our hominid forebears gradually achieved greater cortical control over vocalisation, so that by 500,000 years ago, say, language was an approximately equal mixture of manual gesture and vocalisation. The critical event in the evolution of our own species may have been the switch to a system in which the vocal element was dominant, and carried the entire burden of syntax (Goldin-Meadow &

McNeill, 1999), although vocal language is still characteristically accompanied by gesture (McNeill, 1985). The switch from gestural to vocal language may well have been facilitated by the allele that guaranteed that manual and vocal control were located in the left cerebral hemisphere.

In terms of cognitive capacity, and even linguistic capacity, this may have been a small step, but it may have had large consequences. It would have freed the hands, allowing people to communicate freely while carrying things or tending infants, and to carry out manufacturing and other manual activities while at the same time explaining them to novices. Indeed it may have been this freeing of the hands that led to the cumulative development of technological sophistication that characterises our species. It has been suggested that this did not begin until the so-called 'evolutionary explosion' of some 35,000 years ago (Pfeiffer, 1985), as evidenced by cave drawings, the crafting of ornaments and objects displaying visual metaphor (White, 1989), and more sophisticated manufacture. But this is a Eurocentric view; the advancement of manufacture must have begun earlier than that.

For example, watercraft must have been developed to carry people from the Asian mainland to New Guinea and Australia (once joined) well over 60,000 years ago, as there is evidence that *H. sapiens* had reached south-eastern Australia by about that time (Thorne *et al.*, 1999). Evidence of a sophisticated bone industry, including the manufacture of harpoons, has been discovered in Zaire and dates from 90,000 years ago (Yellen *et al.*, 1995). It therefore seems likely that the evolutionary explosion documented in Europe actually began much earlier in Africa and expanded into Asia, and later into Europe. But it was not the result of a major speciation event, but rather a small change that gave voice to our activities. It is possible, but by no means proven, that a laterality gene had a small part to play in producing this change.

DISCUSSION

Bickerton: If you think that *Homo* had syntactic language, and if you agree with me that syntax is what enables you to have thought, why did we see so little cultural additive to this for thousands of years?

Corballis: Because manual language got in the way. Once speech emerged the hands were free for other activities.

Bickerton: Well couldn't they just stop and make something?

Corballis: This would still be inefficient. Once language was freed from manual activity, technological advance would increase cumulatively.

Questioner: Different populations have different allele frequencies. On the

expectation of a single gene on the X and Y chromosomes, would you then expect to see differences in handedness across populations?

Corballis: We do see differences in the same populations with time. If the frequencies are adjusted across populations for the heterozygous advantage, one gets population differences.

Questioner: Do you require selective pressure to generate frequency differences across populations?

Corballis: It can happen by population drift.

Questioner: Yes, by population drift and since some differences in frequencies are quite high you would expect huge differences in handedness frequencies.

Crow: I'm not clear what your heterozygous advantage is for?

Corballis: It is selecting for language; the advantage is for language. A double dose of this gene gives too much pruning on the right hemisphere and too much is bad for you. You showed a couple of years ago that at the point of equality there is actually a dip in intellectual achievement (Crow *et al.*, 1998). There is a disadvantage for having a double dose of the chance allele. What is being selected for is the right dose, i.e. the heterozygous advantage. So what is being selected for is language, but if you get a double dose of it, you suffer. Marian Annett tried to document this with reading, showing that the heterozygotes could read better than extreme right-handers or extreme left-handers.

Questioner: Can you just clarify the role that brain enlargement plays in your story?

Corballis: What I am assuming is if brain enlargement started about 2 million years ago that it may have been driven by the added complexities that were involved and probably driven by the advantages of more sophisticated language.

Questioner: What about the increase in population of a half million years ago?

Corballis: I'm not sure whether the switch to vocalisation might have had an effect on civilisation … I don't know whether it goes along with my story or not.

Questioner: If there is selection for heterozygosity, I don't see how you can reach equilibrium.

Corballis: If it is 50 : 50 then there is.

Questioner: Could vocal language be at a disadvantage to gestural language?

Corballis: How do you get it off the ground? You are standing there with a creature who can't vocalise: you gesture to him. You have a lot of organisation to do to get the hand and vocalisation together.

Questioner: The difference between gesturing and signing and the difference between signing with right or left hand?

Comment: There is a difference between left- and right-hand signers: a mirror image. Do they reverse: is there mirror reversal?

Corballis: I don't think so.

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