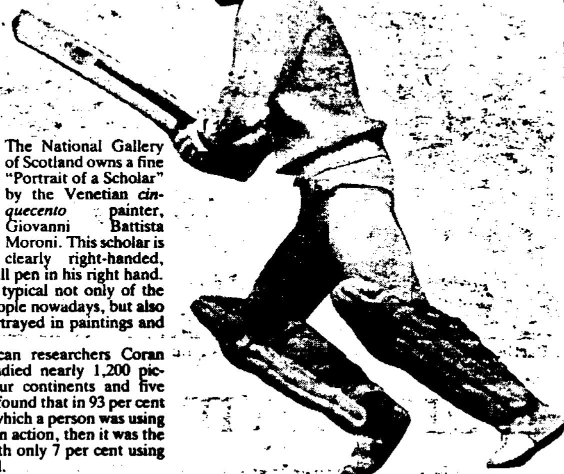
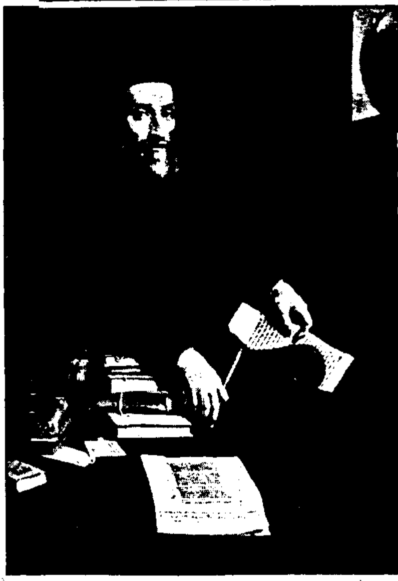
What makes us right- or left-handed? Is there any significance in it? Chris McManus looks at recent research which has attempted to unravel a centuries-old puzzle





Skilled hands: nothing sinister about Moroni's scholar (above); craftsmen on grass, cricketer David Gower and John McEnroe lean to the left.

Hands and feats

The National Gallery of Scotland owns a fine "Portrait of a Scholar" by the Venetian *cinquecento* painter, Giovanni Battista Moroni. This scholar is clearly right-handed, holding his quill pen in his right hand. As such he is typical not only of the majority of people nowadays, but also of persons portrayed in paintings and drawings.

The American researchers Coran and Porac studied nearly 1,200 pictures from four continents and five millennia and found that in 93 per cent of pictures in which a person was using one hand for an action, then it was the right hand, with only 7 per cent using their left hand.

Furthermore, the proportions of right and left-handers have been steady since the beginnings of recorded history, and are similar in all cultures. Why is a minority of the population left-handed, and how does left-handedness relate to other known asymmetries, such as of the heart, and of language dominance in the brain?

The modern literature on the subject has got itself into a confused mess over the best way of measuring handedness. If asked whether right or left-handed, the person on the Clapham omnibus will reply quickly and easily, describing the hand with which they hold a pen while writing.

If pressed they might also describe other activities for which they can use either hand, albeit more skilfully with one hand than the other.

And they might occasionally have activities for which they naturally use the opposite hand from their writing hand; indeed I remember well at the age of 13 discovering while at Scout camp that despite regarding myself as fully right-handed that I naturally and unconsciously used a felling axe in a typically left-handed manner.

Such considerations encourage researchers to produce handedness inventories in which subjects indicated the degree to which each hand was used for perhaps 30 or more items. A handedness score could then be calculated, which could be anywhere on a continuum between fully right-handed and fully left-handed.

Although some workers have argued that this means that the concept of two categories of handedness is inadequate, a deeper analysis shows that the distribution of handedness scores in the population is clearly bimodal, with two clear peaks corresponding to the conventional descriptions of right-handers and left-handers (the *direction* of handedness), and with the remaining variability best regarded as describing the extent or strength of commitment to one hand (the *degree* of handedness).

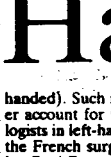
In general, we have little idea of why individuals differ in their degree of handedness, it not running in families, or having any obvious correlates, with the sole exception of age; children increase their degree of handedness during the first decade of life. The rest of this article will follow the commonsense description of the Clapham omnibus, that handedness is best assessed in terms of the hand used for writing, and will only consider questions about direction of handedness.

About 8 per cent of the population are left-handed, although many surveys have found somewhat differing results: in the 1930s it was not popular to be left-handed, and lower incidences were reported, whereas now it is often felt fashionable to be left-handed, particularly given that popular sporting personalities such as David Gower and John McEnroe are conspicuously left-handed.

In addition, left-handers are more interested in why they are a minority group, and hence are more likely to respond to questionnaires about handedness (and perhaps to read articles about it, or, as I found recently, to attend lectures on the subject, 30 per cent or so of my audience at a lunchtime public lecture being left-handed). Such reasons cannot however account for the interest of psychologists in left-handedness. In the 1860s the French surgeon and anthropologist, Paul Broca, reported the remarkable finding that in eight patients who were aphasic (that is, had lost their powers of speech) as the result of a stroke, all also had a paralysis (a hemiplegia) of the right half of their body.

Since the left half of the brain controls the right half of the body, and vice-versa, the implication was that the brain damage must have been on the left side, and hence that their linguistic abilities must have also been in the left half of the brain. This functional asymmetry has been repeatedly demonstrated, although a few caveats must now be added.

In right-handers, probably 95 per cent or so have their language on the left side, the remaining 5 per cent having right-sided language. Left-handers, contrary to popular expectation (and indeed to late 19th-century neurological theorizing) do not show the reverse pattern (that is right hemisphere language), but instead a majority also have their language in the *left* hemisphere, but a more sizeable minority (about 30 per cent or so) have right hemisphere language.



Psychologists regard language as one of the most important characteristics of the human mind, and its relationship to the lateral organization of the brain is of particular interest. However, it is not easy to assess language dominance (except in cases where a patient has had a stroke and become aphasic), and therefore the reasons why some individuals have right-hemisphere language dominance are not easily studied.

Left-handedness, therefore, can act as a surrogate for the more interesting questions about language dominance, particularly given that there is a correlation between hand dominance and language dominance. If we had an adequate understanding of the causes of left-handedness then we should be able to extend that knowledge to language dominance, and perhaps also to that miscellany of conditions such as dyslexia, stuttering and schizophrenia which have been linked to atypical lateralization.

Left-handedness, like other biological traits, has two possible origins. It could be inherited, or else it could be due to environmental events, either in the form of learning, or of traumatic insults to the brain which reverse its typical organization.

That there is almost certainly a genetic or inherited component to handedness is suggested by many studies in which left-handedness has been shown to run in families.

That the familial influence is genetic (and not due to, say, intra-familial learning) is shown by adoption studies, in which children's handedness is closer to that of their biological parents than that of their adoptive parents.

Despite the enthusiastic attempts of some workers to find environmental influences upon handedness, none has yet been shown convincingly.

The much publicized theory that we are all naturally right-handed, but that some people have suffered minor degrees of damage to the left half of their brain during childbirth, as a result of obstetric complications, is convincingly refuted by an analysis I carried out of the 12,000 children in the National Child Development Study, who had their handedness assessed at the age of 11, and had had the details of their birth recorded at the time by an obstetrician or midwife; no relationship was apparent between left-handedness and birth complications.

Similarly, there is no evidence that head injury in childhood causes left-handedness, nor that left-handedness is learnt from parents.

The problem then is to explain familial trends in left-handedness. This, however, is not straightforward as handedness does not follow any of the traditional simple patterns expected of single Mendelian genes. Thus, two right-handers do not breed true (about 6 per cent of their offspring being left-handed), and neither do two left-handers breed true (only about 35–40 per cent of their offspring being left-handed); one right and one left-handed parent have about 15 to 20 per cent of left-handed offspring.

More problematic still is that identical (monozygotic) twins, who have identical genes, are frequently not identical for handedness, about 15 per cent of pairs having one left-handed and the other right-handed.

It should be noted that this phenomenon is not due to any process of "mirror imaging" due to identical twins coming from separate halves of a single egg; there is no biological evidence for that process (and logically it would be unsound – what after all would be the handedness of identical triplets, in the case where one twin splits again?).

The key to understanding handedness is to place it in the context of other biological asymmetries, of which the most important is that the heart is usually on the left side. In the typical vertebrate the heart, stomach and spleen are on the left, and the liver and appendix on the right (*situs solitus*). In about one in 20,000 people this situation is reversed completely (*situs inversus*), so that heart, stomach and spleen are on the right, and so on.

Incidentally, these individuals have the same incidence of left-handedness as normal individuals, indicating the existence of at least two primary asymmetries.

Occasionally rats, mice, fish and birds have been found with *situs inversus*, and in one case, the *iv* mutation in mice, selective breeding has resulted in a strain in which a high proportion of offspring have *situs inversus*, showing the genetic control of *situs*.

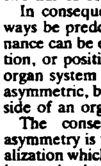
Nevertheless, even when two mice homozygous for the *iv* gene produce offspring, they do not produce 100 per cent offspring with *situs inversus*, but instead produce exactly 50 per cent of offspring with *situs inversus* and 50 per cent with *situs solitus*.

Geneticists should note that this is not the phenomenon of partial penetrance, but instead represents a different mechanism. What is seen in the *iv* mouse is an example of *fluctuating asymmetry*, the biological base line from which all other asymmetries must deviate.

As a result of biological noise during the development of an individual, it is statistically highly improbable that the billions of cells in individuals will be arranged precisely identically in the two halves of the body.

In consequence, one half must always be predominant, and this dominance can be exacerbated by canalization, or positive feedback, so that an organ system can become completely asymmetric, being present only on one side of an organism.

The consequence of fluctuating asymmetry is that the particular lateralization which an individual will show is completely out of biological (or any other) control; it is as if a metaphorical coin were tossed *in utero* during the organism's development. Strictly, therefore, the *iv* gene does not produce *situs inversus*; rather it removes the normal control of lateralization and substitutes a chance process.



I have proposed that a similar mechanism controls handedness in humans. There are two genes, *D* (for Dextral) and *C* (for Chance). Individuals with the *DD* genotype are all right-handed, whereas those with the *CC* genotype have no control over handedness, and instead a notional coin is tossed during development to decide whether the individual is right or left-handed (and 50 per cent will become left-handed). Heterozygotes (the *DC* genotype) are mid-way between the homozygotes, 25 per cent becoming left-handed and 75 per cent becoming right-handed.

This model, which gives a good fit to published data, explains why right-handers do not breed true (since many right-handers are either *DC* or *CC* genotypes), and why left-handers do not breed true (since there is no sinistral gene to produce pure left-handedness).

Indeed, the model makes the strong prediction that there is no population (selected independently of handedness or cerebral lateralization) in which there are more than 50 per cent of left-handers.

If such a population were found then this genetic model must fail. The model also explains why identical twins do not also have identical handedness. If the twins are of the *CC* genotype then for each twin a coin will be tossed to decide whether they are right or left-handed. But since they are two separate individuals with separate developments, there will be two separate coins which may come down differently, resulting in twins discordant for handedness.

The model can readily be extended so that the same gene controls both handedness and cerebral dominance for language, but that separate coins are tossed for deciding on the lateralization of motor control and language; the result is to predict similar proportions of right language dominance in right and left-handers as are actually found.

We have now seen why some people are left-handed; they probably do not have a gene which is carried by most humans. That gene has probably been in the human gene-pool since at least 1 million BC, but is not apparently found in other apes and monkeys, since none of these show population right-handedness (being like other animals such as dogs, cats, and mice in which each individual shows a preference for right or left paw, but 50 per cent prefer the left paw and 50 per cent the right – fluctuating asymmetry once more).

Two questions need to be answered. The first, of why we are mostly right-handed rather than left-handed, can probably never be answered; it could merely be that the dextral gene got there first. The second concerns the origin of the gene for right-handedness.

One possible evolutionary sequence is that at some time in the very remote past, during the early evolution of the vertebrates, a gene emerged which produced an asymmetric circulatory system, resulting in our present left sided heart.

At a subsequent time, perhaps one to two million years ago a copy of this gene was transposed onto another chromosome and subsequently mutated, so that instead of causing an asymmetry in the circulatory system it resulted in cerebral asymmetry (and perhaps indirectly resulted in speech).

Subsequently, other copies might also have arisen and resulted in genes for the other primary asymmetries (such as those for hand-clasping, arm-folding, and eye-dominance).

Such a hypothesis is testable in principle, as is the genetic model outlined above, since molecular biology can now look not only for genes responsible for particular characteristics, but also for related gene sequences with the human genome, or in other species. That is a suitable challenge for the modern successors to Moroni's scholar.

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