Chapter 9: Hypernotes

☞WWW☜ 9:1

Whether Ehud was actually a natural left-hander is very unclear, the original Hebrew having the sense of “a man with his right hand drawn up, contracted by accident or disease” (Moore, 1895 p.93), “of a kind that would seriously diminish the capability of a fighting man and make him seem to be harmless” (Soggin, 1987 p.50). Having said that, the same commentators also point out that the same term is used later for the 700 left-handers in the army who were said to be particularly skilled.

The date of 1200 BC is very approximate. The *Encyclopaedia Judaica* comments, “Insufficient chronological evidence makes it difficult for the historian to reconstruct the dates of the events recounted in Judges. ... No less vague is the background of the deliverance story of Ehud son of Gera and the period in which it took place” (Anonymous., 1971 8:583). The same source points out also that the events described later in *Judges* 20: 14-15, probably occurred earlier chronologically than those described in *Judges* 3: 15-22.

Sir Thomas Browne commented on the strangeness of “draw[ing] examples of the left from the sons of the right hand, as we read of seven thousand in the army of the Benjamites” (Wilkin, 1852 vol I, p.393). Cook (1914 p.262) says something similar. The comments arise from Benjamin, *Ben Yamin*, literally meaning “Son of the right hand”, although it also means “sons of the south”, and probably refers more to the geographical origin of the tribe than their handedness (Boling, 1975 p.86; 9599 /ft “ pp.247-8”}).

Cook (1914 p.243) pointed out that the passage does not say that the 700 are the only left-handers. It is also not clear whether the 700 are a part of the 26,000 or are in addition to them. The New English Bible which I quote in the main text abbreviates the episode. A fuller translation is “twenty six thousand men bearing arms, without including the inhabitants of Gibeah, and they amounted to seven hundred picked fighters. Of all this company, seven hundred were picked fighters, [left-handed]” (Soggin, 1987 p.291). When discussing the number seven hundred, Moore long ago suggested “[The] identity of number and phrase is suspicious” (Moore, 1895 p.429). To make matters worse, there are other versions of Judges that have 25,000 or 23,000 instead of 26,000 (Lias, 1902 p.196), and the Jewish historian Flavius Josephus in *The antiquities of the Jews*, written at the end of the first century AD, said, “The Benjamites' army was twenty five thousand and six hundred; *five hundred* of which were excellent at slinging stones with their left hands (my emphasis; Whiston, 1906 V.2.10(156)). The highest and lowest possible estimates then give 3.04% (700/23000) and 1.87% (500/26700). Probably not too much faith should be put in the precise percentage.

☞WWW☜ 9:2

Classical writing is replete with examples demonstrating that most people were right-handed. I'll restrict myself here to just two, taken from that early scientific treatise, *On the nature of the universe*, written in Latin about 80 BC by Lucretius (Latham & Godwin, 1994), who, in a description originating in Homer's *Odyssey*, describes an opulent household with "golden images of youths ... holding flaming torches in their right hands to illumine banquets" (p.38), and how, "The bronze statues by the city gates show their right hands worn thin by the touch of travellers who have greeted them in passing"(p.18). Clearly right-handedness is the norm.

Montaigne referred to the habit of cutting off the thumbs of prisoners, although he seems to refer to both thumbs: "Some person whose name I no longer remember, having won a battle at sea, ordered the thumbs of all his vanquished enemies to be cut off, to render them incapable of fighting or rowing" (Trechmann, 1935 I:140).

☞WWW☜ 9:3

Darwin corresponded with Ogle on the origins of handedness, receiving a letter from him on 25th Feb 1871, and replying to him on 25th Dec 1871, Christmas Day, when he sent him a copy of his notes on the handedness of his son William. Ogle was made Assistant Physician at St. George's Hospital in 1869 but resigned in 1872 on the grounds of ill-health. He subsequently went on and became Superintendent of Statistics, being responsible for the censuses of 1881 and 1891, and also translated some of the works of Aristotle. Despite his "ill-health" he died in 1912 at the age of 85 (Anonymous, 1912).

An exception to the belief that left-handedness was at about the same rate as in the book of *Judges* was Shaw (1878) who thought "the proportion of left-handed in the tribe of Benjamin seems to have been *greater* than at the present day" (my emphasis). He presumably had not read Ogle's paper since he also adds that "we have no reliable statistics ... either among ancients or moderns".

Harris (1990) provides a comprehensive review of early studies of the rate of left-handedness. An early review by Beeley (1918) of seven different studies found a median incidence of 4%, the same value as is cited in an article in Scientific American in March, 1910 (Huber, 1910 p.261).

☞WWW☜ 9:4

See also chapter 7 on sex differences. Although in the data of Gilbert and Wysocki (1992a) it looks as if the difference between the sexes increases over the years, that is not actually the case. Proportionately the excess of left-handed males remains the same over almost the entire range, as can be seen if the ordinate is plotted logarithmically. For the entire data, there are 29% more left-handed men than there are left-handed women, which is entirely compatible with other studies (McManus, 1991).

☞WWW☜ 9:7

For simplicity in the Euchiria, Lowgenia and Hipressia calculations I have merged together cases where one parent is right-handed and the other left-handed, with those few in which both are left-handed. It makes no difference to the conclusions.

The calculations are properly carried out using odds ratios rather than the risk ratios I have quoted here. However risk ratios are easier to describe, and I have therefore used them here (as in chapter 7). The rate of left-handed children when a parent is left-handed, 19.5%, is 2.5 times the rate when both parents are right-handed, 7.8%. However the odds of two right-handed parents having a left-handed child are 7.8%:92.2% = .0846, whereas the odds of a left-handed child when one parent is left-handed is 19.5%:80.5% = 2422. The odds ratio for a left-handed parent having a left-handed child in comparison with two right-handed parents is .2422/.0846 = 2.86 times. .

The mathematically convenient fact that the rate of the C allele is exactly twice the proportion of left-handers occurs because the genetic model is additive. It is not generally true of genetic models, and specifically is not the case when genes are recessive or dominant.

The reason for the apparently counter-intuitive result in Lowgenia, that a lower gene frequency results in a higher odds ratio, is because as the proportion of C alleles falls, so the likelihood that a right-handed parent will be carrying a *C* allele also falls. In the extreme case when *C* is close to zero, right-handers almost completely breed true, having hardly any left-handed offspring, whereas two left-handers still have to carry C alleles. The result is that as the frequency of *C* falls so the odds ratio gets higher and higher.

In the Hipressian calculations it is assumed that the left handers who change their handedness are a random 50% of all left-handers, irrespective of parental handedness, etc., and occurs in both the parents and the offspring.

It might seem surprising that left-handed parents in Hipressia are less likely to have left-handed children than in Lowgenia, particularly since left-handers in Hipressia are indeed exactly what they seem to be, left-handers. However Lowgenia is not the proper place to compare them with, because Lowgenia has a lower rate of C genes. The appropriate comparison is with Euchiria, and the 9.9% in Hipressia is comparable with Euchiria's 19.5% once it is taken into account that half of the genetic left-handers in Hipressia are forced to become right-handers.

☞WWW☜ 9:8

The data for Japan and the United Arab Emirates are in preparation at present. The data for Ivory Coast and Sudan can be found in De Agostini e*t al* (1997), although an analysis of them using the present methods is currently in preparation. Maharaj Singh has also recently published further data showing a much lower incidence of left-handedness in India compared with France (Singh, Manjary, & Dellatolas, 2001).

The method described here is only illustrative. In the full analysis it is possible to assess the extent to which any particular combination of incidence of left handedness and odds ratio of handedness in families results from the joint effects of social pressure and differences in gene frequency. In all the countries, including the West, there is always a small effect of social pressure, but it is of the same size everywhere (and might reflect measurement error). The differences between countries are however almost entirely accounted for by differences in gene frequency.

Another piece of evidence that supports the idea that differences in incidence of left-handedness between countries are genetic is that emigrants from Asia to the West continue to have low rates of left handedness after they have arrived in the West. For instance in the data of Gilbert and Wysocki, only 6.1% of the Asian respondents (about 10,500 in number) wrote with their left hand, compared with 9.5% of the White respondents. Since all were US residents that suggests that living in a society with a more relaxed attitude has not changed the incidence of left handedness. A similar result, with rather more control over the sample, is found in two large UK studies of applicants to medical school (McManus et al., 1995; McManus, Richards, & Maitlis, 1989). In a 1986 survey, of 355 UK nationals whose ethnic origin was from the Indian sub-continent, 8.7% were left-handed, compared with 12.0% of 1447 White applicants. Similarly, for a 1991 survey, of 1119 UK nationals whose ethnic origin was from the Indian sub-continent, 8.0% were left-handed, compared with 10.9% of 3455 White applicants. The effect is statistically significant, and there was no difference between the Indian group born in the UK and those born outside the UK. Likewise in a very large sample of 152,000 applicants to US medical schools, 13.1% of whites were left-handed, compared with 9.2% of Asian Indians, 6.3% of Vietnamese, 5.4% of Korean and 5.3% of Chinese (Halpern, Haviland, & Killian, 1998).

A recent review of handedness in Japan and the Far east can be found in Iwasaki (2000a) who cites several additional studies in Japanese which confirm the basic finding that the incidence of left-handedness is far lower in Japan. See also Ida e*t al* (Ida, Mandal, & Bryden, 2000).

☞WWW☜ 9:9

In the study of Chamberlain (1928) it is assumed that the students were eighteen when they entered university, and hence would have been born in 1909. Some would be somewhat older than that, perhaps by ten years or so. The siblings were as likely to be ten or more years older or younger, meaning that the majority of individuals would have been born between 1900 and 1920.

In the study of Gilbert and Wysocki study (1992a), the rate of left-handedn in those born before 1920 was 3.9%.

The family data for children born before 1939 are based on the studies of Ramaley (1913, Chamberlain (1928), Rife (1940), Merrell (1957), and the grandparental and parental data of McManus (1985); see McManus and Bryden (1992b). In some cases the data were published long after 1939, but refer to data from parents or grandparents who would have been born before 1939.

The full data for the risk ratios in the family studies are as follows. For those born before 1939, there were 13923 offspring, 7.27% of whom were left-handed. In the 12753 offspring of two right-handers, 6.1% were left-handed, compared with 20.1% of the 1170 offspring in which one parent was left-handed, giving a risk ratio of 3.29. For those born after 1955, there were 21085 offspring, 13.3% of whom were left-handed. In the 21085 offspring of two right-handers, 11.9% were left-handed, compared with 19.5% of the 3741 offspring in which one parent was left-handed, giving a risk ratio of 1.64. Those born between 1940 and 1954 were midway between the other two groups, both in their incidence of left handedness and odds ratio. There were 37592 offspring, 10.8% of whom were left-handed. In the 33153 offspring of two right-handers, 9.6% were left-handed, compared with 20.0% of the 4439 offspring in which one parent was left-handed, giving a risk ratio of 2.08.

☞WWW☜ 9:10

It has often been regarded as a problem that many family studies of handedness include all of the children in a family, not least because it means that the significance tests can be affected because the offspring are not independent. However it is an advantage from the present point of view as it means one can calculate the average number of children in a family. It should though be noted that one cannot calculate the standard deviation of the number of children, and therefore it is not straightforward to carry out significance tests on the differences..

☞WWW☜ 9:11

It is worth remembering that indirect social pressure requires the right-handed majority to be able to recognise which individuals in their society are left-handed. That means, therefore, that in Hipressia those left-handers who have changed to being right-handers, and can pass fully as right-handers, will *not* be under indirect social pressure and will continue to spread their genes for left-handedness. Direct and indirect social pressure can therefore work in entirely opposite directions, one requiring the absence of the other.

☞WWW☜ 9:12

Left-handers leave their mark in other ways as well. In the Geometric phase of early Greek pottery, from about 1000-700 BC, it was common to paint circles and semi-circles on to the pot. Right-handers prefer to draw and paint circles and semi-circles in a clockwise decoration (Alter, 1989; Van Sommers, 1984), whereas left-handers tend to go the other way. In the National Archaeological Museum and other museums in Athens I found twenty-eight such circles where one could tell if the circle were drawn clockwise or anticlockwise. Twenty-six were clockwise, and two anti-clockwise, suggesting that about seven percent of the craftsmen might have been left-handed.

Another possible indication of handedness is given in early pre-Dynastic pots from Egypt, which are often decorated with painted spirals, which start at the centre and spiralling outwards. So far in the 12 examples I have looked at in the Petrie Museum at University College London, all are clockwise. The numbers are as yet, however, too small to be able to draw any useful conclusions.

☞WWW☜ 9:13

The radiocarbon dating of Ötzi gives a figure of between 3350 and 3100 BC (Spindler, 1996).

It seems probable though unproven that Ötzi was right-handed. The pieces of cord he was carrying may well have been made by him himself, since they are such relatively trivial pieces of equipment requiring little skill to make. That is particularly true of the bowstring, made from twisted animal sinew, the raw materials of which were also found with Ötzi (Spindler, 1996 p.250).There is also evidence that Ötzi may have died because of the consequences of a serious injury, eight weeks or so before death, which damaged the right shoulder and broke several ribs on the right. He probably died lying on his left side, perhaps because of pain in the right shoulder. Damage to the right shoulder of a right hander would have been particularly disastrous in the dangerous conditions of the High Alps, and might have been responsible for his death (Zur Nedden et al., 1994). Recent work has also suggested that Ötzi has an arrow-head deep in his left shoulder, which almost certainly contributed to his death, showing evidence of heavy bleeding and possible damage to the brachial plexus (Holden, 2001).

☞WWW☜ 9:14

The figure of 5% comes from the fact that of 13 boring implements studied by microwear analysis, the direction of turning was clockwise in 21, anticlockwise in 3, and could not be determined in 7 (Cahen, Keeley, & Van Noten, 1979 p. 681). However the three counter-clockwise implements all came from the same core, and were probably all made and used by the same person. There are therefore probably 1 left-hander and 21 right-handers in the sample, giving 4.54% left-handedness, or about 5%.

☞WWW☜ 9:15

It should be said that there is no shortage of studies claiming to estimate the proportion of right and left handers, some studies dating back to the last century (for a review see e.g. Cunningham, 1902). However many use methods which are, to say the least, dubious, and often rely on subjective assessments of the best hand in which a stone tool might be used (e.g. Posnansky, 1959). In other cases attempts have been made to assess handedness from skeletal remains, either of the skull or arm bones, but there is sufficient noise in the data to make any precise estimate of the incidence of left handedness difficult to interpret; see Steele (2000b) for a detailed review.

☞WWW☜ 9:17

There is evidence of earlier stone tools, made about two and a half million years ago (Roche et al., 1999; Semaw et al., 1997), although as yet there is no analysis of whether they are right or left handed.

☞WWW☜ 9:18

There actually seems to be no work on the inheritance of pawedness in cats, and so I have taken a little poetic license here. However there certainly is extensive work on pawedness in mice (Collins, 1968; Collins, 1969; Collins, 1977; Collins, 1985), and it seems extremely likely that the same conclusions apply in cats. I have therefore taken a chance in what I said.

In this book I make a strong claim that handedness, in the sense of a 90:10 mixture, is a peculiarly human phenomenon. Not all workers agree with that, and a recent strongly argued case has been made by Rogers (2000c), and while I accept that there are large numbers of motor and sensory asymmetries in other animals, I am yet to be convinced that these are phylogenetically related, being so diffuse in form and seemingly non-functional, that, *pace* Rogers, I am still willing to follow Corballis (1991a), as quoted by Rogers, that "right handedness and cerebral asymmetry are unique to humans".

☞WWW☜ 9:19

Annett (1991b) also found that almost exactly half of a group of captive gorillas were right handed. Amongst the New World monkeys there is also evidence that although individuals re highly lateralised, there is a 50:50 mixture of right and left handers on various tasks (Laska, 1998; Laska & Tutsch, 2000).

The estimate of sixty per cent of chimpanzees being right-handed is based on the unbiased task of Hopkins et al (2000d), in which of 169 chimpanzees, 97 out of 169 (57.4%) showed some shift towards the right hand.

The ultimate test of whether the laterality of chimpanzees is similar or different to that in humans will come with the identification of the relatively small percentage of genes which shows differences between humans and chimpanzees, a process that should soon be completed (Fujiyama et al., 2002).

An area of research related to that of handedness in the great apes, is that of brain asymmetry in the great apes, claims being made that, for instance, Broca's area shows the same anatomical asymmetries as it does in humans (Cantalupo & Hopkins, 2001). Although that may be so, it is also the case that ape and human brains are embedded in a body which has a myriad of ancient asymmetries, notably of the viscera. Anatomical asymmetries may therefore only reflect visceral *situs,* rather than being an indicator of functional brain asymmetry. That is supported by studies of humans with *situs inversus*, who show reversed anatomical asymmetry for the frontal and occipital petalias(Kennedy et al., 1999), but do *not* show reversed functional asymmetry, most individuals being right handed (Cockayne, 1938,Torgersen, 1950,Gordon, 1998), and having left language dominance as shown by dichotic listening (Tanaka et al., 1999) and by fMRI (Kennedy et al, 1999), the same direction of asymmetries as is found in humans with *situs solitus*, whose viscera are lateralised normally, with the heart on the left. In the absence of direct evidence of the great ape anatomical asymmetry being associated with functional asymmetries of cognitive or linguistic processing, the most parsimonious explanation for their asymmetry is that it reflects the location of the heart, which in humans and the great apes is on the left side[1].

☞WWW☜ 9:22[2]

The list of behavioural asymmetries could be extended far further. A recent one which attracted much attention is the asymmetric use of tapering leaves as tools by New Calendonian Crows (Hunt, Corballis, & Gray, 2001).

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[1] The contents of this paragraph were submitted to *Nature* as a letter immediately after the publication of the paper by Cantalupo and Hopkins. *Nature* however has a self-image of infallibility, and therefore almost never publishes criticism of any paper it has ever published. This was no exception. If it is infallible and beyond criticism in the judgements of its editors and referees then it is the only scientific journal in the world to be such.

[2] **☞WWW☜** was inadvertently omitted from the notes in the book.

As well as behavioural asymmetries, there are also occasional examples of anatomical asymmetries within the brain of non-human species, perhaps the most investigated being the habenular nucleus in the brain stem of a range of species, most notably the frog (Morgan, O'Donnell, & Oliver, 1973), which is typically double on the left and single on the right, although the pattern varies in other species, and the phylogeny is still somewhat obscure (Concha & Wilson, 2001). A finding of particular interest is that the asymmetry of the habenula is determined by the Nodal signalling pathway, and that if this is knocked out then the system does not become symmetric but instead becomes randomised, showing a 50:50 mixture of right and left (Concha et al., 2000). The functions of the habenulae are somewhat unclear, although they have been implicated in many functions (Sutherland, 1982), and in humans act as a major determinant of 5-HT levels in the brain (Morris et al., 1999)

☞WWW☜ 9:23

As well as in *The Origin of Species* Peckham, 1959 p.250-3, Darwin also mentions the flatfish in *The variation of animals and plants under domestication* (Darwin, 1905), where he comments that:

> "Many animals have the right and left sides of their body unequally developed: this is well known to be the case with the flatfish. In most flatfishes the left is the blind side but in some it is the right: though in both cases reversed or 'wrong' fishes are occasionally developed; and in *Platessa flesus* the right or left side is indifferenbtly the upper one."

☞WWW☜ 9:24[3]

Although there are many catalogues of the myriad of miscellaneous asymmetries found in animals, there are few serious attempts at putting them into order. A wise and thoughtful exception is that of Rich Palmer (1996).

☞WWW☜ 9:25

Termite fishing, as well as fishing for ants with sticks, are part of chimpanzee cultures, being found in some chimpanzee communities such as Gombe, where both are present, or sometimes only one is present, as in the Mahale K-group, who fish for termites but not for ants, or in other communities neither is present (Whiten & Boesch, 2001).

☞WWW☜ 9:26

Aristotle describes the hand as "an instrument that represents many instruments" in *De partibus animalium* (Peck, 1937 687.a), and Galen subsequently developed the theme in *De usu partium*:

> "[It is] of all instruments the most variously serviceable. So too it is spear and sword, and whatsoever other weapon or instrument you please; for all these can it be from its power of grasping and holding them all. For though the hand is no one particular instrument, it is the instrument for all instruments because it is formed by Nature to receive them all...". (Rowe, 1999 p.5).

[3] **☞WWW☜** was inadvertently omitted from the notes in the book.

☞WWW☜ 9:27

Sidney's shepherd tries to warn Man:

> "Deme it no gloire to swell in tyrannie.
> Thou are of blood; joy not to see things bleede:
> Thou fearest death; thinke they are loth to die."

The picture of the hands of primates (Schultz, 1969) also includes *Tupaia*, the tree shrew, which is nowadays not generally thought to be a primate (Fragaszy, 1998).

It is sometimes so easy to forget how important our hands are to us, for there is barely a thing we could do in our complex technological world without them. So deeply are we immersed in our use of them that we are like the old Chinese proverb, "The last person to notice the water is the fish". I was about to write about the events of yesterday, and to reflect on the amazing uses of these flesh-covered bony excrescences, derived ultimately from the fins of some prehistoric fish, when I realised that I couldn't even type those words into my word-processor, or use its touch-pad, or for that matter, write those words with a pen or pencil, without my hands to help me. With my word-processor I might just have got away with one finger, or even one toe, but some of the other activities I saw during that day would have been well beyond me. Perhaps most stunning was the evening in the local jazz club watching a quintet who were playing innovative free jazz. Watching those hands racing across the piano keyboard, playing complex chordal structures, watching the subtle rhythms of the percussionist, or the flying fingers of the clarinettist, saxophonist or double bassist, made it irresistible to speculate on why humans can do all of this and even animals such as the chimpanzee cannot. Part of the mistake is to look only at the hand itself. It is of course on the end of an arm of almost equal subtlety and important. The wide range of movement of the ball and socket joint of the shoulder, the hinge joint of the elbow, and the ability of the lower arm to rotate. And of course each of those players, be it the percussionist, the bass player, the pianist, or the clarinettist and saxophonist, were all doing *different* things with each hand. It is a remarkable ability. More remarkable still, at least from the perspective of an ape or a monkey, was that the bass player and wind players were each standing on their two legs, leaving the hands free to carry out these complex activities[4]. Earlier in the day we had watched our two daughters, then eleven-months old, crawling around, trying, only half successfully, also to carry a toy in one hand at the same time. They were also just realising that it was possible, if only for a few moments, to stand upright on their legs. So it is not only hands that are important, but also legs. Unless we are bipedal, there is little point in having sophisticated hands, as all they do is rest on the ground. Inevitably the evolution of tool using hands and a body that can stand on two legs are intimately connected.

☞WWW☜ 9:29

The symbol ☞WWW☜ was included in the book in error.

[4]Darwin (1874)is credited with being one of the first to notice that, "In throwing a stone or spear ... a man must stand firmly on his feet".

☞WWW☜ 9:29

Although it is tempting to see the hand of *Australopithecus* as a direct ancestor of the human hand, there are some problems in interpreting the wrist bones, which perhaps suggest knuckle-walking took place (Richmond & Strait, 2000).

Although it is not stated explicitly in the text another important aspect of being able to throw and being highly dextrous with the hands is that one needs to be bipedal. One cannot walk on four legs and throw at the same time. Manual dexterity and bipedalism must also, therefore, have co-evolved.

☞WWW☜ 9:30

It is possible that Neanderthal was somewhat less dextrous than *Homo sapiens* (Musgrave, 1971), although most modern authorities do not seem to support that position (Aiello & Dean, 1990 pp.392-4).

☞WWW☜ 9:33

The role of clock speed in determining what a computer can do and can do well is often neglected. A similar analogy probably applies also to brains. There is little doubt that human brains have increased in size dramatically, and presumably that is because increased computing power is needed for the new ecological niche in which the early hominids were living. It doesn't matter what that computing power was need for, and there have been many, many speculations, from language, through tool usage, throwing, and gossip.What does matter is that there are relatively few ways in which the brain computer can be made more powerful, given the biological equivalent of more mega-flops. How does one get a more powerful brain?

Our brains are exceedingly complicated neuronal machines which process information. Although in many ways the analogy of computers for our brains is overly strained and sometimes absurdly wrong, there are nevertheless many lessons that can be learned about the possible evolution of the brain by looking at the ways that computers have changed over the past half century. To the ordinary user of a computer they seem to look different every half decade or so. Where now people use a mouse to click and point at multicoloured displays in Windows, it was a decade ago that they were typing command lines into DOS with monochrome monitors. A decade before that they would take a pile of punched cards to a central computer facility and twenty-four hours later receive a pile of line-printer output with those oh so prestigious holes down the side. And a decade before that the computer was programmed either by flicking switches or feeding in paper tape with 5, 7 or 8 rows of holes. And ten years yet further back Alan Turing could only program one of the prototype computers in Manchester by typing in numbers to the base 32, using the numbers one to nine and then the letters A to V, a system he found perfectly natural and which he could never understand that other people found difficult. But these are all surface features. Deep down there is little that has really changed in the way computers work. My students always tell me that SPSS for Windows is so much better than the old DOS version and then are surprised when I show them that all the fancy coloured front end does is to generate a string of commands which are identical to the ones we used to type in the DOS version[5]. The languages we program in, be they FORTRAN, BASIC, C or whatever, are essentially all dialects of the very early languages such as ALGOL. They have a few more elegant features but there is nothing in them which would not be recognised by the people who developed the original languages. And the chips at the centre of the computer are still doing the same as they ever used to do, those things which Turing said any universal computing machine; taking numbers expressed in binary form, moving them from one place to another and performing operations such as addition and multiplication on them. They may now do it for 16, 32 , 64 or even 128 bits at a time, but again nothing deep down has really changed. So why have computers got so much more powerful over the last half century. There is really only one thing that accounts for it – speed. The early home computers were felt to go like the wind with their 1 MHz 6502 CPUs, whereas now the newspapers advertise Pentium computers which run at 1 Gigahertz – a thousand times faster. And why do computers go so much faster then they used to? Mainly because the people who designed firstly printed circuits with transistors, and then integrated circuits, managed to make them smaller and smaller, as they developed ever new photolithographic techniques for laying circuits in silicon, etching them with harder and harder UV light of ever shorter wave-length, and looking towards X-ray lithography for the next generation of chips[6]. Those same technologies also meant that memory could also grow and grow, so that now a word-processor program will take up more hard disk than the entire storage available thirty years ago on a university mainframe. The result of all that speed and all that memory is that the old programming methods can do things such as re-drawing the graphics on my screen at a speed that now makes it *feel* as if it instantaneous. The result is that I now can do things with my computer which I could not do before in real time. I could in principle have done them, but it would have been slow, and a video-game where one waits an hour for the screen to re-draw is not a game. How much of all this change is due to better programs, more elegant algorithms, new programming languages? Almost none. It is speed and ever smaller memory that makes computers work better and better[7].

Does this tell us anything about the ways that the brain might have evolved? Probably, yes, a lot. Some things about brains and nervous systems have hardly changed since nerve cells were invented. All nerves have myelin sheaths and sodium-potassium pumps to keep high levels of potassium inside the cell so that electrical impulses can be conducted, and all chemical transmission at synapses is much the same in principle from worm to man. Of course the details might be slightly different, a novel neurotransmitter here, an inhibitor there, but there is as much novelty as in the central processor of most computers. Brains also are pretty much the same. Networks of cells, the neurones, in layers, interconnected with short, medium and long-range connections to one another, and with occasional large bundles of fibres, nerves, sending the output to some other part of the brain. Look for a single big idea in the way the neurones are connected and there is only one in the game, lateral inhibition. But it was discovered in *Limulus*, the horse-shoe crab, an invertebrate that seems hardly to have changed in a hundred million years and yet is a perfectly adequate model for the process in human brains. Of course I exaggerate a little for rhetorical effect, but there are few really big

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[5]These can be seen in the syntax window in SPSS for Windows.

[6]For a brief history of integrated circuits, and a graphic illustration of Moore's Law see Mullins (2000e).

[7]And it has been argued that one of the great tragedies of the memory and processing revolution is that it has been squandered in massively inefficient software which proliferates to fill whatever space can be provided for it.

new ideas out there in brain evolution. Except for a couple of exceptions, and they are little to do with how nerves work and even less to do with what the nerves are actually doing. They are the same as in computers. Build them big, build them fast, and miniaturise as much as possible. Make neurones smaller, and allow them to be more interconnected, that is how the richness of the networks increases, and then allow the brain to be even larger, so that even more neurones can be fitted in, and then the same old programs, the same old methods of nervous transmission, the same old synapses, the same old programs if one likes, may well be able to do things which are interestingly new, radically new, like walking or talking of fantasising.

If one wants a very practical example of how speed and memory can do things which are fundamentally different, one only has to look at an article in *New Scientist* in which a radically new wheelchair was being designed for the disabled (Daviss, 2000). Most wheelchairs have four wheels because that means they are stable and can sit still on the ground. The trouble is they are not very good at doing much else, such as going up kerbs or stairs. Re-arrange the four wheels so that in effect the wheel-chair is standing upright on just two of them, put in some powerful motors and some position sensors which are connected to three powerful Pentium computers and then, like balancing a broomstick on one's palm by continually moving it around, suddenly, almost miraculously, the wheelchair is stable on two wheels, it can climb kerbs, go up stairs and even go across deep sand without falling over. None of the technology is really new except the powerful computers which are running it; and what is new about them is that they are fast. But it couldn't be done without them. And suddenly it is liberating, novel, exciting. There is no reason why a bigger, faster brain with more memory couldn't account for many of the changes that have occurred in the evolution of the human brain.

As a view of brain evolution, the emphasis on size and speed has all sorts of advantages, of which the main one is that evolution can only work by changing genes, and genes can only produce proteins, and those proteins can only produce cells that are slightly differently shaped, or are connected in different ways or are packed in somewhat different fashions. They cannot possibly work at high conceptual levels. It seems almost impossible that a gene could in any serious way be responsible for syntax or counting or reading or any of the high level mental skills that so concern psychologists. Those things are going to have to emerge, somehow, as epiphenomena from altering the tiny details of the way that neurones are connected. Some forms of connection, some forms of inhibition, some recurrent networks, some forms of mutual inhibition may be better for certain mental tasks, just as some forms of memory organisation are better for processing music files or images or acting as servers on computers. But changing the basic design is as unlikely as the computer industry deciding to use ultraviolet photolithography to produce silicon chips with little nano-balls on nano-wires that work in the same way as an ultra-miniaturised abacus[8]. It ain't possible. Evolution can only build on what it has, not what might be desirable. And what it has are neurones, with chemical transmitters which are connected in particular ways during a few months of fetal life. That is what genes can alter and is the raw material on which evolution of the brain has to depend.

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[8]The exception could well be quantum computers, although that seems a long way off as yet.

☞WWW☜ 9:35

Calvin points out that timing can be increased also by having arrays of timing processors which work in parallel. The result can be a far greater increase in accuracy than the ten to fifteen per cent difference which seems to apply to the left hemisphere in the Nicholls task. Calvin (1982) cites the nice example of how on its 1831 voyage the *Beagle* had 22 chronometers to make the measurement of longitude more precise than any single chronometer would allow.

☞WWW☜ 9:39

I have simplified the story here somewhat. In a more detailed account elsewhere (McManus, 1999) I have suggested, following Maynard-Smith and Szathmáry (Maynard Smith & Szathmáry, 1995), that the genes underlying language evolved in two separate stages, and so the *C** gene mutated into a *D** gene, which allowed only proto-language, which would still have benefited proto-humans over their competitors. Subsequently the *D** gene mutated into the modern *D* gene which allowed full syntax, and which may, following Bickerton (Bickerton, 1996a; Bickerton, 1996b), have evolved from the development of a novel piece of neurological circuitry, the fronto-cerebellar circuitry. That has also sorts of explanatory advantages, not least the fact that the cerebellum is being more and more realised to be intimately involved in precise timing, one of the quintessential aspects of language and in particular spoken language, and it also accounts for the otherwise mystifying neurological patients with cerebellar lesions and an impairment of syntax (Silveri, Leggio, & Molinari, 1994). The modern *C* gene is then proposed to have evolved out of the modern *D* gene, making the evolutionary sequence $C^* \rightarrow D^* \rightarrow D \rightarrow C$.

Recent work (Howard, 2001; Rao & Wu, 2001) has suggested the possibility that the human brain has evolved some novel circuitry which is not found in the chimpanzee brain, involving a pathway from the telencephalon to the dorsal thalamus. Such pathways must be controlled by genes, which have not yet been found, and may well be responsible for some aspects of language and the other cognitive abilities which differentiate humans and apes.

Nichols (1999; Adler, 2000) in her controversial analysis of grammatical structures in languages suggests that "there is no evidence that human language in general has changed since the earliest stage recoverable by the method used here. There is simply diversity, distributed geographically" (p.277). Since her methods typically seem to date this diversity from between 50,000 years ago (when the Australasian languages separated; p.228) and about 100,000 years ago (p.27), that might suggest the *D* gene mutated at about that time, humans having only proto-language during the long period of cultural stasis before that.

☞WWW☜ 9:40

The dynamics of the fixing of one gene when there are two in the gene pool with identical fitness is well shown by Cavalli-Sforza and Bodmer (Cavalli-Sforza & Bodmer, 1971). It occurs because any population is necessarily finite in size (and in practice is usually small in terms of the effective population size), with the result that binomial sampling fluctuations occur, meaning that slowly one gene begins to predominate over the other in its proportion in the population. That would be a random walk except that the walk is occurring between two absorbing barriers at 0% and 100%. Once the proportion reaches either of those values, which it must do given sufficient time, then there is no way back, and one gene is fixed, whereas the other is eliminated from the gene pool.

☞WWW☜ 9:41

A real problem for genetics is that the advantage of a heterozygote need have nothing to do with the ostensible function of the gene, since genes often have multiple functions, and the balance can occur due to two seemingly unrelated processes. It is therefore possible that people with the *DC* genotype can also run faster, can metabolise food more efficiently, or any of a host of factors which might mean that the have more offspring and hence are fitter. In the absence of any evidence for such processes I have chosen in this book to ask the question which is neuropsychologically most interesting, of what might be an advantage resulting from the effects of the *DC* genotype upon neural organisation itself. As a possible example, it seems to be the case that left-handers overall are somewhat less likely to suffer from left-handers or ulcers. Whether it is handedness *per se* which is the cause of that association, or the association is more specifically with the DC or CC genotype, is still not clear.

☞WWW☜ 9:42

Theories that some people have different brains from others typically invoke pathological factors, as in Satz's theory of pathological left-handedness (Satz, 1972; Satz, Baymur, & Van der Vlugt, 1979; Soper & Satz, 1984), or in Coren and Searleman's rare-trait marker model (Coren & Searleman, 1990). In each of these cases some factor, either unilateral trauma, or a process akin to fluctuating asymmetry, pushes modules from one hemisphere to another. In effect that can 'randomise' a complex system, and it can be seen as being akin to a phenocopy of the effects produced by the DC or CC genotype.

Finch and Kirkwood (2000f) have summarised the neglected role of randomness in biology: "Chance is omnipresent in living systems, being at once the source both of creative novelty in evolution and of corruption and decay" (p.4). The positive advantages of randomness are seen well in the benefits that are brought to sensory systems by the introduction of noise, so-called 'stochastic resonance' (Ferster, 1996; Wiesenfeld & Moss, 1995).

A rare example of randomness being expressed in organisms at the biochemical level is seen in the worm *Caenorhabditis elegans*, which has two structurally and functionally identical AWC neurons involved in olfaction, but there is a receptor, STR-2, which is randomly expressed in either the right or the left neuron but never in both. The asymmetry seems to be essential for the proper working of the system since mutants which are symmetric have defects (Wes & Bargmann, 2001). The formal analogy to the CC genotype proposed for handedness is also a close one in several ways, not least the fact that a neural substrate can be expressed randomly on one side or the other but not both.

☞WWW☜ 9:43

The same principles of organisation and randomness can be seen in large social organisations, particularly where a slight rearrangement of an otherwise well functioning system can sometimes benefit the overall workings of the system. A large organisation in which everyone does the same job in perpetuity is doomed to die through stasis. But equally, continual and massive reorganisations are unlikely to be beneficial. A little change though might shift an organisation from being good to being extremely good, and hence becoming very successful at a particular task, as a new alignment of individuals and skills becomes a powerful problem-solving force.

☞WWW☜ 9:45

The precise numbers of anomalous individuals given that there are a dozen modules can readily be calculated from the binomial distribution, as shown below:

Number of anomalous modules	*DD*	*DC*	*CC*
0	100%	3.17%	0.02%
1	0%	12.67%	.29%
2	0%	23.23%	1.61%
3	0%	25.81%	5.37%
4	0%	19.36%	12.08%
5	0%	10.32%	19.34%
6	0%	4.01%	22.56%
7	0%	1.15%	19.34%
8	0%	0.24%	12.08%
9	0%	0.04%	5.37%
10	0%	0.0035%	1.61%
11	0%	0.0002%	0.29%
12	0%	0.000006%	0.02%

In DC individuals with twelve modules and a 0.25 probability of any one being lateralised atypically, then 26% of individuals will have three atypical modules, 23% will have two atypical modules, 13% will have only one atypical module, and 3% will have no atypical modules. Overall then 65% will have three or less atypical modules. Only 5% of DC individuals will have six or more atypically located modules, compared with 61% of CC individuals.

References

Adler, R. 2000, "Voices from the past", *New Scientist*, **26th Feb 2000**, 36-40.

Aiello, L. & Dean, C. 1990, *An introduction to Human Evolutionary Anatomy,* London: Academic Press.

Alter, I. 1989, "A cerebral origin for "directionality."", *Neuropsychologia*, **27**, 563-573.

Annett, M. & Annett, J. 1991b, "Handedness for eating in gorillas", *Cortex*, **27**, 269-275.

Anonymous 1912, "William Ogle [Obituary]", *British Medical Journal*, **i**, 929-930.

Anonymous. 1971, *Encyclopaedia Judaica,* Jerusalem: Keter.

Beeley, A. L. 1918, *An experimental study in left-handedness,* Chicago: University of Chicago Press.

Bickerton, D. 1996b, "Catastrophic evolution: the case for a single step from protolanguage to full human language," in *Evolution of language: Social and cognitive bases for the emergence of phonology and syntax*, J. Hurford, M. Studdert-Kennedy, & C. Krugar, eds., Cambridge: Cambridge University Press.

Bickerton, D. 1996a, *Language and human behaviour,* London: UCL Press.

Boling, R. G. 1975, *Judges: Introduction, translation and commentary,* New York: Doubleday.

Cahen, D., Keeley, L. H., & Van Noten, F. L. 1979, "Stone tools, toolkits, and human behavior in prehistory", *Current Anthropology*, **20**, 661-683.

Calvin, W. H. 1982, "Did throwing stones shape hominid brain evolution?", *Ethology and Sociobiology*, **3**, 115-124.

Cantalupo, C. & Hopkins, W. D. 2001, "Asymmetric Broca's area in great apes", *Nature*, **414**, 505-505.

Cavalli-Sforza, L. L. & Bodmer, W. F. 1971, *The genetics of human populations,* San Francisco: W.H.Freeman.

Chamberlain, H. D. 1928, "The inheritance of left-handedness", *Journal of Heredity*, **19**, 557-559.

Cockayne, E. A. 1938, "The genetics of transposition of the viscera", *Quarterly Journal of Medicine*, **31**, 479-493.

Collins, R. L. 1968, "On the inheritance of handedness. I: Laterality in inbred mice", *Journal of Heredity*, **59**, 9-12.

Collins, R. L. 1969, "On the inheritance of handedness. II: Selection for sinistrality in mice", *Journal of Heredity*, **60**, 117-119.

Collins, R. L. 1977, "Toward an admissible genetic model for the inheritance of the degree and direction of asymmetry," pp. 137-150 in *Lateralization in the Nervous System*, S. Harnad et al., eds., New York: Academic Press.

Collins, R. L. 1985, "On the inheritance of direction and degree of asymmetry," pp. 41-71 in *Cerebral lateralization in non-human species,* S. D. Glick, ed., New York: Academic Press.

Concha, M. L., Burdine, R. D., Russell, C., Schier, A. F., & Wilson, S. W. 2000, "A Nodal signalling pathway regulates the laterality of neuroanatomical asymmetries in the zebrafish forebrain", *Neuron*, **28**, 399-409.

Concha, M. L. & Wilson, S. W. 2001, "Asymmetry in the epithalamus of vertebrates", *Journal of Anatomy*, **199**, 63-84.

Cook, T. A. 1914, *The curves of life,* Constable (Reprinted in Dover Books, 1979): London.

Corballis, M. C. 1991a, *The lop-sided ape: evolution of the generative mind,* New York: Oxford University Press.

Coren, S. & Searleman, A. 1990, "Birth stress and left-handedness: the rare trait marker model," pp. 3-32 in *Left-handedness: Behavioral implications and anomalies*, S. Coren, ed., Amsterdam: North-Holland.

Cunningham, D. J. 1902, "Right-handedness and left-brainedness", *Journal of the Anthropological Institute of Great Britain and Ireland*, **32**, 273-296.

Darwin, C. 1874, *The descent of man and selection in relation to sex,* 2 edn, London:

Darwin, C. 1905, *The variation of animals and plants under domestication,* Popular edn, London: John Murray.

Daviss, B. 2000, "Access all areas", *New Scientist*, **26th August**, 28-31.

De Agostini, M., Khamis, A. H., Ahui, A. M., & Dellatolas, G. 1997, "Environmental influences in hand preference: An African point of view", *Brain and Cognition*, **35**, 151-167.

Ferster, D. 1996, "Is Neural Noise Just a Nuisance?", *Science*, **273**, 1812-1812.

Finch, C. E. & Kirkwood, T. B. L. 2000f, *Chance, development and Aging,* Oxford: Oxford University Press.

Fragaszy, D. M. 1998, "How non-human primates use their hands," pp. 77-96 in *The psychobiology of the hand*, K. J. Connolly, ed., London: MacKeith Press.

Fujiyama, A., Watanable, H., Toyoda, A., & et al 2002, "Construction and analysis of a human-chimpanzee comparative clone map", *Science*, **295**, 131-134.

Gilbert, A. N. & Wysocki, C. J. 1992a, "Hand preference and age in the United States", *Neuropsychologia*, **30**, 601-608.

Gordon, A. G. 1998, "Handedness and laterality of the viscera revisited [letter]", *Neurology*, **51**, 1515.

Halpern, D. F., Haviland, M. G., & Killian, C. D. 1998, "Handedness and sex differences in intelligence: Evidence from the Medical College Admission Test", *Brain and Cognition*, **38**, 87-101.

Harris, L. J. 1990, "Cultural influences on handedness: historical and contemporary theory and evidence," pp. 195-258 in *Left-handedness: Behavioral implications and anomalies*, S. Coren, ed., Amsterdam: North-Holland.

Holden, C. 2001, "Ötzi death riddle solved", *Science*, **293**, 795-795.

Hopkins, W. D. & Fernández-Carriba, S. 2000d, "The effect of situational factors on hand preferences for feeding in 177 captive chimpanzees (*Pan troglodytes*)", *Neuropsychologia*, **38**, 403-409.

Howard, P. 2001, "Neanderthal revolutionary or Cro-Magnon fascist, on your head be it", *The Times*, **2oth July**, 20-20.

Huber, J. B. 1910, "Why are we right-handed?", *Scientific American*, **102**, 260-269.

Hunt, G. R., Corballis, M. C., & Gray, R. D. 2001, "Laterality in tool manufacture in crows", *Nature*, **414**, 707-707.

Ida, Y., Mandal, M. K., & Bryden, M. P. 2000, "Factor structures of hand preference questionnaires: A 'skilled' and 'unskilled' factors artifacts?," pp. 175-190 in *Side bias: A neuropsychological perspective*, M. K. Mandal, M. B. Bulman-Fleming, & G. Tiwari, eds., Dordrecht: Kluwer.

Iwasaki, S. 2000a, "Age and generation trends in handedness: An Eastern perspective," pp. 83-100 in *Side bias: A neuropsychological perspective*, M. K. Mandal, M. B. Bulman-Fleming, & G. Tiwari, eds., Dordrecht: Kluwer.

Kennedy, D. N., O'Craven, K. M., Ticho, B. S., Goldstein, A. M., Makris, N., & Henson, J. W. 1999, "Structural and functional brain asymmetries in human situs inversus totalis", *Neurology*, **53**, 1260-1265.

Laska, M. 1998, "Laterality in the use of the prehensile tail in the spider monkey (*Ateles geoffroyi*)", *Cortex*, **34**, 123-130.

Laska, M. & Tutsch, M. 2000, "Laterality of tail resting posture in three species of New World primates", *Neuropsychologia*, **38**, 1040-1046.

Latham, R. E. & Godwin, J. 1994, *Lucretius: On the nature of the universe,* Harmondsworth: Penguin.

Lias, J. J. 1902, *The Book of Judges,* Cambridge: Cambridge University Press.

Maynard Smith, J. & Szathmáry, E. 1995, *The major transitions in evolution,* Oxford: W.H.Freeman.

McManus, I. C. 1985, *Handedness, language dominance and aphasia: a genetic model. Psychological Medicine, Monograph Supplement No.8,*

McManus, I. C. 1991, "The inheritance of left-handedness," pp. 251-281 in *Biological asymmetry and handedness (Ciba foundation symposium 162)*, G. R. Bock & J. Marsh, eds., Chichester: Wiley.

McManus, I. C. 1999, "Handedness, cerebral lateralization and the evolution of language," pp. 194-217 in *The descent of mind: Psychological perspectives on hominid evolution*, M. C. Corballis & S. E. G. Lea, eds., Oxford: Oxford University Press.

McManus, I. C. & Bryden, M. P. 1992b, "The genetics of handedness, cerebral dominance and lateralization," pp. 115-144 in *Handbook of Neuropsychology, Volume 6, Section 10: Child neuropsychology (Part 1)* , I. Rapin & S. J. Segalowitz, eds., Amsterdam: Elsevier.

McManus, I. C., Richards, P., & Maitlis, S. L. 1989, "Prospective study of the disadvantage of people from ethnic minority groups applying to medical schools in the United Kingdom", *British Medical Journal*, **298**, 723-726.

McManus, I. C., Richards, P., Winder, B. C., Sproston, K. A., & Styles, V. 1995, "Medical school applicants from ethnic minorities: identifying if and when they are disadvantaged", *British Medical Journal* , **310**, 496-500.

Merrell, D. J. 1957, "Dominance of hand and eye", *Human Biology*, **29**, 314-328.

Moore, G. F. 1895, *A critical and exegetical commentary on Judges,* Edinburgh: T&T Clark.

Morgan, M. J., O'Donnell, J. M., & Oliver, R. F. 1973, "Development of left-right asymmetry in the habenular nuclei of *Rana temporaria*", *Journal of Comparative Neurology*, **149**, 203-214.

Morris, J. S., Smith, K. A., Cowen, P. J., Friston, K. J., & Dolan, R. J. 1999, "Covariation of activity in habenula and dorsal raphe nuclei following tryptophan depletion", *NeuroImage*, **10**, 163-172.

Mullins, J. 2000e, "Integrated circuits (Inside Science No. 136)", *New Scientist*, **9th December**, 1-4.

Musgrave, J. H. 1971, "How dextrous was Neanderthal man?", *Nature*, **233**, 538-541.

Nichols, J. 1999, *Linguistic diversity in space and time,* Chicago: University of Chicago Press.

Palmer, A. R. 1996, "From symmetry to asymmetry: Phylogenetic patterns of asymmetry variation in animals and their evolutionary significance", *Proceedings of the National Academy of Sciences of the USA*, **93**, 14279-14286.

Peck, A. L. 1937, *Aristotle: Parts of animals,* London: Heinemann.

Peckham, M. 1959, *The Origin of Species by Charles Darwin: A variorum text,* Philadelphia: University of Pennsylvania Press.

Posnansky, M. 1959, "Some functional considerations on the handaxe", *Man*, **59**, 42-44.

Ramaley, F. 1913, "Inheritance of left-handedness", *American Naturalist*, **47**, 730-739.

Rao, Y. & Wu, J. 2001, "Neuronal migration and the evolution of the human brain", *Nature Neuroscience*, **4**, 860-862.

Richmond, B. G. & Strait, D. S. 2000, "Evidence that humans evolved from a knuckle-walking ancestor", *Nature*, **404**, 382-385.

Rife, D. C. 1940, "Handedness, with special reference to twins", *Genetics*, **25**, 178-186.

Roche, H., Delagnes, A., Brugal, J. P., Feibel, C., Kibunjia, M., Mourre, V., & Texier, P. J. 1999, "Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya", *Nature*, **399**, 57-62.

Rogers, L. J. 2000c, "Evolution of side biases: Motor versus sensory lateralization," pp. 3-40 in *Side bias: A neuropsychological perspective*, M. K. Mandal, M. B. Bulman-Fleming, & G. Tiwari, eds., Dordrecht: Kluwer.

Rowe, K. 1999, *Dead hands: Fictions of agency, renaissance to modern,* Stanford, CA: Stanford University Press.

Satz, P. 1972, "Pathological left-handedness: An explanatory model", *Cortex*, **8**, 121-135.

Satz, P., Baymur, L., & Van der Vlugt, H. 1979, "Pathological left-handedness: cross-cultural tests of a model", *Neuropsychologia*, **17**, 77-81.

Schultz, A. H. 1969, *The life of primates,* London: Weidenfeld and Nicolson.

Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., & Mowbray, K. 1997, "2.5-million-year-old stone tools from Gona, Ethiopia", *Nature*, **385**, 333-336.

Shaw, Mr. 1878, "On righthandedness", *Journal of the Anthropological Institute of Great Britain and Ireland*, **7**, 94-96.

Silveri, M. C., Leggio, M. G., & Molinari, M. 1994, "The cerebellum contributes to linguistic production: a case of agrammatic speech following a right cerebellar lesion", *Neurology*, **44**, 2047-2050.

Singh, M., Manjary, M., & Dellatolas, G. 2001, "Lateral preferences among Indian school children", *Cortex*, **37**, 231-241.

Soggin, J. A. 1987, *Judges: A commentary,* 2 edn, London: SCM Press.

Soper, H. V. & Satz, P. 1984, "Pathological left-handedness and ambiguous handedness: a new explanatory model", *Neuropsychologia*, **22**, 511-515.

Spindler, K. 1996, "Iceman's last weeks," pp. 249-263 in *Human mummies: A global survey of their status and the techniques of conservation*, K. Spindler et al., eds., Wien: Springer-Verlag.

Steele, J. 2000b, "Handedness in past human populations: Skeletal markers", *Laterality*, **5**, 193-220.

Sutherland, R. J. 1982, "The dorsal diencephalic conduction system: a review of the anatomy and functions of the habenular complex", *Neurosci.Biobehav.Rev.*, **6**, 1-13.

Tanaka, S., Kanzaki, R., Yoshibayashi, M., Kamiya, T., & Sugishita, M. 1999, "Dichotic listening in patients with situs inversus: brain asymmetry and situs asymmetry", *Neuropsychologia*, **37**, 869-874.

Torgersen, J. 1950, "Situs inversus, asymmetry and twinning", *American Journal of Human Genetics*, **2**, 361-370.

Trechmann, E. J. 1935, *The essays of Montaigne,* London: Oxford University Press.

Van Sommers, P. 1984, *Drawing and cognition: descriptive and experimental studies of graphic production processes,* Cambridge: Cambridge University Press.

Wes, P. D. & Bargmann, C. I. 2001, "*C. elegans* odour discrimination requires asymmetric diversity in olfactory neurons", *Nature*, **410**, 698-701.

Whiston, W. 1906, *The works of Flavius Josephus,* London: Routledge.

Whiten, A. & Boesch, C. 2001, "The culture of chimpanzees", *Scientific American*, **January**, 48-55.

Wiesenfeld, K. & Moss, F. 1995, "Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDS", *Nature*, **373**, 33-36.

Wilkin, S. 1852, *The works of Sir Thomas Browne (revised version of 1836 edition),* London: Henry Bohn.

Zur Nedden, D., Wicke, K., Knapp, R., Seidler, H., Wilfing, H., Weber, G., Spindler, K., Murphy, W. A., Hauser, G., & Platzer, W. 1994, "New findings on the Tyrolean 'Ice Man': Archaeological and CT-body analysis suggest personal disaster before death", *Journal of Archaeological Science*, **21**, 809-818.