The history and geography of human handedness

I. C. McManus

Summary

About 90% of people are right-handed and 10% are left-handed. Handedness is associated with functional lateralization for cerebral dominance, and may also be associated with various types of psychopathology. Broadly speaking, the vast majority of humans seem to have been right-handed since the emergence of the genus *Homo*, some three to four million years ago. Likewise, in all societies studied, there is a large excess of right-handers. However, there have been few studies exploring the detailed history and geography of handedness, not least because adequate pre-twentieth-century historical data are difficult to find, and very large sample sizes with consistent measurement methods are required for geographical studies. This chapter overviews the various sets of data that provide insight into handedness's history and geography.

It is probable that about 8% to 10% of the population has been left-handed for at least the past 200 000 years or so. Detailed data only began to become available for those born in the nineteenth century, and there is growing evidence that the rate of left-handedness fell precipitously during the Victorian period, reaching a nadir of about 3% in about 1895 or so, and then rising quite quickly until an asymptote is reached for those born after about 1945 to 1950, with 11% to 12% of men and 9% to 10% of women typically being left-handed in Western countries. The sex ratio seems to remain constant, not only during historical changes but also with geographical differences, and is presumably the result of a biological rather than a cultural process.

Geographical differences in handedness are clearly apparent both between continents (as in Singh & Bryden's, 1994, comparison of Canada and India) and within continents: rates in Europe seeming to be highest in Britain, Holland, and Belgium, and falling away towards the east and south, and within countries, seen well in Stier's (1911) study of the German Army, in Leask and Beaton's (2007) study of the United Kingdom, and between the various states of the USA, in the very large Gilbert and Wysocki (1992) database.

Ethnic differences in handedness are related to geographical differences, with left-handedness generally being more common in White, Asian and Hispanic populations – a difference seen both in the UK, and historically in the United States, where the difference between ethnic groups has grown smaller during the twentieth century, but was still present even for those born in the 1970s. Migration studies in the UK show that the lower rate of left-handedness in those from the Indian sub-continent is similar in those born in the UK and those born outside the UK, implying that genes rather than environment are the primary source of the difference.

Different rates of left-handedness can reflect either environmental or genetic differences between societies, and rates alone cannot distinguish the two processes. However, a mathematical model shows that effects of different social pressure or gene frequencies can be distinguished if family data on handedness are available. That model suggests not only that geographical differences but also historical differences primarily reflect changes in gene frequency rather than direct social pressure.

Introduction

The important discoveries of Dax and Broca in the nineteenth century showed that human brains are functionally asymmetric, most people processing language in their left hemisphere (Finger, 1994; Finger & Roe, 1999). However, it soon also became clear that a minority of people process language with their right hemisphere (Harris, 1991; Harris, 1993a), so that language processing can be seen as what geneticists call a

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polymorphism, there being two qualitatively different types, akin to human blood groups. Since at least the beginnings of recorded history, and probably long before, people have also noted that while most people are right-handed, a minority of individuals are the opposite way around, being left-handed. Handedness and language dominance also show a moderate correlation, although the pattern is somewhat counter-intuitive, about 5% to 6% of right-handers showing right hemisphere language dominance, compared with about 30% to 35% of left-handers.

Language dominance is not easy to assess reliably in large populations, with techniques such as functional Magnetic Resonance Imaging (fMRI) (Pujol *et al.*, 1999) or transcranial Doppler (Knecht *et al.*, 2000) requiring complex technology that is expensive and not particularly portable, while dichotic listening and tachistoscopic hemi-field studies are not particularly reliable within individuals. As a result, handedness, which is easily assessed by questionnaire or direct observation, has been studied both as an important lateralization in its own right, and also as a surrogate for language dominance. Handedness is thought by most researchers to be genetic in origin, although there are differences in the precise models (McManus & Bryden, 1992), and, perhaps crucially, most models also assume that the genes determining handedness also influence language dominance, making the study of handedness directly relevant to the study of language dominance. If left-handedness is under genetic control, as several theories suggest, then it is likely, as with other genetically determined biological characteristics, such as blood groups, that there will be geographical variation (or clines), because of some combination of genetic drift, founder effects, and selection, be it natural or artificial.

A simplifying assumption for many earlier studies of handedness, and here the present author is no exception (McManus, 2004), has been to regard either the rate of left-handedness itself, or the frequency of the underlying genes, as constant historically and geographically. However, neither proposition seems likely a priori, not least because almost all human polymorphisms vary geographically (see, e.g., Cavalli-Sforza, Menozzi & Piazza, 1994), and the frequency of some polymorphisms, such as that of sickle-cell anemia, also varies historically in relation to changing selection pressures (Cavalli-Sforza & Bodmer, 1971). It therefore seems probable that left-handedness, and perhaps the genes underlying it, will also vary both geographically and historically. If historical and geographical variation has been little studied by researchers, it is mainly because of the difficulty of obtaining adequate, large-scale databases. Attempts at meta-analysis of multiple small-scale studies have generally been unsuccessful, mainly because methods of measurement vary almost as much between studies as do rates of handedness (Raymond & Pontier, 2004; Seddon & McManus, unpublished manuscript, 1991).

Geographical and historical variation in handedness also raises the possibility that language dominance will also vary geographically and historically, as perhaps will other traits related to handedness and language dominance, and here one might think of dyslexia, stuttering, autism, schizophrenia, etc., in each of which atypical cerebral lateralization has been implicated. This chapter will concentrate on handedness, mainly because there is extensive data concerning it, but throughout the sub-text will be that similar conclusions might apply more broadly to cerebral dominance and its correlates.

Historical differences in the rate of left-handedness

The previous two centuries

Historical data on left-handedness are surprisingly rare, to the extent that a museum curator attempting to curate an exhibition on handedness referred to left-handers as being “a people without a history” (Sadler, 1997). Although estimating historical rates of left-handedness might seem easy, until recent years there has been very little systematic data. Modern work asking whether the historical rate of left-handedness might have changed systematically probably begins with that of Brackenridge (1981). However, quite the most important modern source on rates of left-handedness is the vast study by Gilbert and Wysocki (1992), which although never intended as a study of handedness has emerged as a key resource. In 1986, *National Geographic* magazine published a special issue on olfaction (Gibbons, 1986), which was accompanied by a "scratch and sniff" card, which readers were encouraged to scratch, report what, if anything, they could smell, and then, after completing a brief demographic questionnaire, return the card. Over 1.4 million people did so (Gilbert & Wysocki, 1987; Gilbert & Wysocki, 1992; Wysocki & Gilbert, 1989; Wysocki, Pierce & Gilbert, 1991). The authors of the original study felt it was possible that handedness and olfaction were linked (perhaps through cerebral dominance), and therefore Gilbert and Wysocki included two questions on handedness: one on writing hand and the other on throwing hand. Subsequent analyses have found no relationship between olfactory acuity and handedness, and it seems reasonable therefore to regard the survey as unbiased in relation to handedness (even if it is potentially biased in other ways, such as in sex, age, ethnicity, and olfactory ability). Respondents of course also reflect the typical readership of the magazine, which is likely to be more educated and middle-class than the population as a whole, but that is unlikely to be a source of bias in relation to handedness, since other large-scale studies have shown handedness to be unrelated to social class or education (McManus, 1981; Perelle & Ehrman, 1994).

The Gilbert and Wysocki data show two key findings. First, men are about 25% more likely to be left-handed than women; there being about five left-handed men for every four left-handed women, a finding that was also found in a large-scale meta-analysis (McManus, 1991), and helps cross-validate the data. More interestingly, there was also a strong relationship of handedness to year of birth, only about 3% to 4% of those born before about 1920 being left-handed, compared with about 11% to 12% of those born after 1950, a three fold difference. It should also be emphasized that the relative extent of the sex difference, expressed as an odds ratio, remained constant for those born in the early or late twentieth century.

Figure 3.1 shows the Gilbert and Wysocki data in two versions. The original paper (Gilbert & Wysocki, 1992) contained only data from 1900 onwards (indicated by the vertical dashed line), and the solid line shows a constrained Weibull function, which has been fitted to the data (see McManus *et al.*, in press a). A reasonable account of just these data might be that the rate of left-handedness was low in the nineteenth century, and then rose through the twentieth century, reaching its current asymptote in about 1950. Interpreting the finding is, however, not so straightforward, mainly because the data are not proper historical series, but instead are cross-sectional, so that cohort effects must be inferred from individuals of different ages. The group born in 1900 in the Gilbert and Wysocki data were therefore aged 86 when the study was carried out in 1986. One possibility, extensively discussed in the handedness literature, is that left-handers die earlier, which results in a lower rate of left-handedness in older individuals (Coren & Halpern, 1991; Halpern & Coren, 1988; Halpern & Coren, 1991). Subsequent analyses of other data have convincingly shown that there is little evidence for differential mortality of left-handers (Ellis *et al.*, 1998; Halpern & Coren, 1993; Harris, 1993b; Harris, 1993c; Marks & Williamson, 1991; Wolf, D'Agostino & Cobb, 1991), although there is one study that compellingly suggests a higher mortality of young left-handed males in World War I, perhaps due to having to use right-handed equipment (Aggleton *et al.*, 1994). An alternative explanation of the lower rate of left-handedness suggests that the elderly are more likely, because of social pressure, either to have been forced to shift from writing with the left hand to writing with the right hand, or they prefer to call themselves right-handed, because of a taboo against left-handedness (Hugdahl *et al.*, 1993; Hugdahl, 1996). Both this and the differential mortality explanation become unlikely when one looks at the entire Gilbert and Wysocki database, which included unpublished data on individuals born between 1887 and 1899 (see McManus *et al.*, in press a). These data on these very oldest respondents are shown in Fig. 3.1, and the heavy dotted line shows the fit of a mixture of two constrained Weibull functions. Now it is clear that the very oldest respondents have a *higher* rate of left-handedness than those who are somewhat younger, an effect which is significant (McManus *et al.*, in press a), and is utterly at odds with explanations due either to differential mortality or greater social pressure to be right-handed. The best account of the Gilbert and Wysocki data is that it

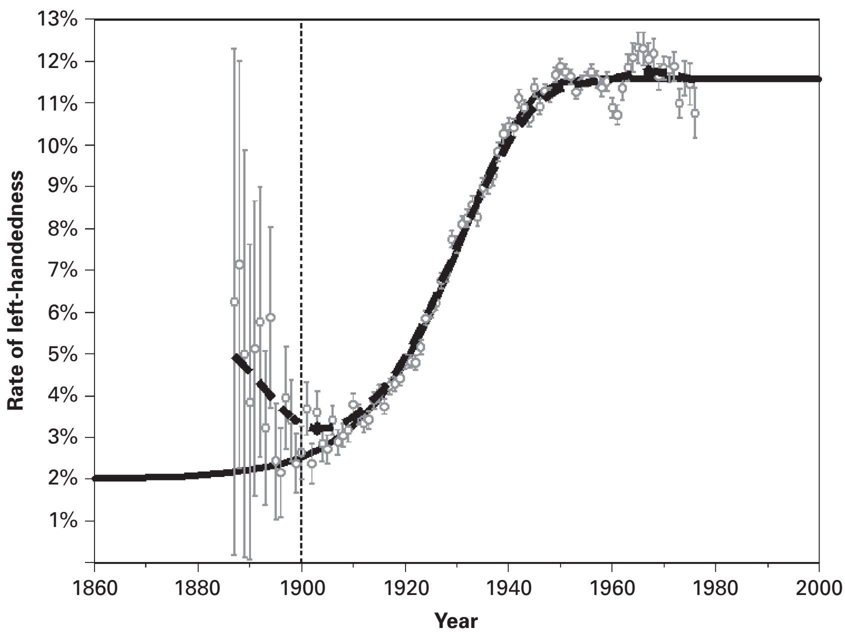

Figure 3.1 The overall rate of left-handedness in the data of Gilbert and Wysocki, 1992 (with permission), for those born from 1900 onwards (solid line); the fitted line is a constrained Weibull (for further details see McManus *et al.*, in press a). The data before 1900 (birth year 1887–99) are unpublished data from the Gilbert and Wysocki study, and are fitted by the dashed line, which is a mixture of two constrained Weibull functions.

directly reflects the actual rate of left-handedness in the population.

The additional Gilbert and Wysocki data implies that the rate of left-handedness might have been falling in those born in the last decade or so of the nineteenth century, and subsequently rose again in the twentieth century. Understanding the history of left-handedness in the nineteenth century therefore becomes important, although it is far from easy, adequate data sources being few and far between and not easy to interpret. The earliest scientific estimate of the rate of left-handedness is that of Ogle (1871), who asked 2000 consecutive patients at St George's Hospital whether they were right- or left-handed, 85 (4.25%) responded saying they were left-handed. Since these patients were adults in 1871, their mean year of birth was probably about 1835. Other somewhat later studies providing estimates of left-handedness rates for those born before 1900 include Lombroso (1884), Mayhew (see Crichton-Browne, 1907), Crichton-Browne (1907), Stier (1911), and Schäfer (1911), and in addition Parson (1924) and Burt (1937) provide early twentieth-century estimates, which help to validate the broad picture shown by Gilbert and Wysocki. Two other sources have also been analyzed recently. In 1953, the BBC broadcasted an early television science programme called *Right Hand, Left Hand*, to which over 6000 people returned postcards describing their handedness and basic demographics (McManus *et al.*, in press b). Although biased, with left-handers being substantially over-represented among the respondents, it is nevertheless possible to estimate the true rate of left-handedness, which is of particular interest for the respondents born before 1900. Finally, rates of left-handedness have also been estimated from the early documentary films made by Mitchell and Kenyon between 1900 and 1906, the oldest participants of which were born before about 1850 (McManus & Hartigan, 2007).

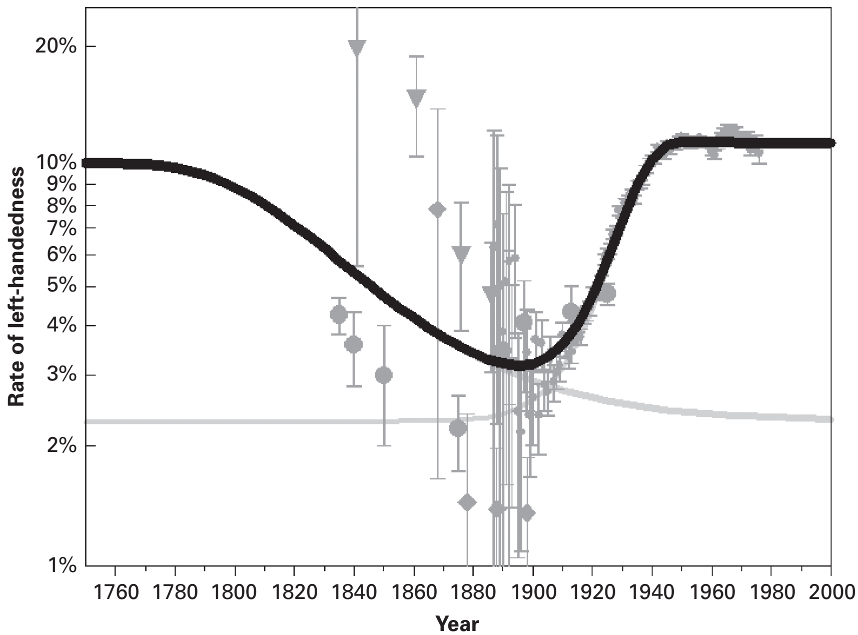

Figure 3.2 Summary of data from multiple studies on the rate of left-handedness during the nineteenth and twentieth centuries, from McManus *et al.* (McManus *et al.*, in press a). The solid black line is the fitted mixture of two constrained Weibull functions, which are shown separately as the two solid gray lines. Note that the ordinate is on a logarithmic scale.

The films showed large numbers of people waving at the camera, mostly with the right arm, and given modern data on the relationship between waving and hand preference, one can estimate the rate of left-handedness. Perhaps most striking is that left arm-waving is substantially more common among the *older* individuals, precisely the opposite pattern to that seen in the Gilbert and Wysocki data where left-handedness is most common in the *younger* individuals. The data from the Mitchell and Kenyon films are almost impossible to explain in terms of differential mortality or social pressure.

Figure 3.2 is a complex figure, taken from McManus *et al.* (in press a), which summarizes all of the historical data from the nineteenth and twentieth centuries. The solid black line consists of a mixture of two constrained Weibull functions, fitted using a maximum likelihood method, the two pale gray lines showing its components. The best statistical description of the recent history of handedness is that the rate was about 10% at the end of the eighteenth century, the rate then fell throughout the nineteenth century, until it reached its nadir in about 1890–5, and then rose during the twentieth century, reaching its asymptote in about 1950, after which rates seem to have been unchanged.

The historical reasons for the nineteenth- and twentieth-century changes are unclear at present, but the nineteenth century changes may reflect an increasing visibility and stigmatization of left-handers, resulting from the Industrial Revolution, with large numbers of individuals using complex machinery in mills and factories, coupled with increasing rates of education and literacy (Stephens, 1990; Stone, 1969; West, 1978). In an agricultural society, left-handers are relatively invisible (except perhaps, as Thomas Carlyle noted, when a group of men is scything a field, see Pye-Smith, 1871). However, both complex machines and education would not only have made left-handers more visible, but left-handers may also have appeared less capable and more clumsy, as left-handed adults worked on machines that were almost certainly designed with right-handers in mind, and left-handed children were taught to write with steel dip pens that needed to be dragged across the paper from left to right by right-handers, and were not capable of being pushed across by the left hand without digging into the paper and making blots and stains. Whatever the mechanism, it seems undoubted that there was a general stigmatization and discrimination against left-handers at the end of the nineteenth century, which Bertrand (2001, pp. 88 and 91) refers to as "La haute époque de l'intolérance", such that there was "La gaucherie persécutée".

The distant past

The history of handedness before 1800 consists almost entirely of a few isolated points, which often are illuminated only briefly through indirect evidence that has to be treated with great care. Claims that, for instance, left-handedness was much more common in medieval than modern Britain (Steele & Mays, 1995), must be treated with caution, because they are based on bone asymmetries, which even in modern samples are inaccurate indicators of handedness, Steele (2000) pointing out how, "perplexingly … left-handed subjects are equally likely to have a stronger grip in either hand" (p. 205). Likewise, although it is often hoped that cultural artifacts may provide insight into rates of handedness, interpretation is often difficult. For instance, although the twist of spun cotton or other fibers ("Z"- or "S"-twist) might at first seem to indicate handedness, the relationship of spinning direction to handedness seems to be weak (Minar, 2001), different fibers such as cotton and flax naturally twist in opposite directions (Batigne & Bellinger, 1953), there is evidence of communities of practice in different directions (Minar, 2001), and technological development can override pre-existing manual asymmetries (Crowfoot, Pritchard & Staniland, 2001).

No attempt will be made to be inclusive, although the broad picture that emerges, which is shown synoptically in Fig. 3.3, is fairly straightforward. Note in particular that the time axis for Fig. 3.3 is logarithmic, in terms of years before the present. The right-hand end of the figure shows the last two centuries, with a modern rate of left-handedness of about 11% (section a). The rate was similar, at perhaps 8% to 10% at the end of the eighteenth century, but then fell to 3% or so during the nineteenth century, rising again in the first half of the twentieth century (sections b and c).

For the past 5000 years the best historical data are the elegant study by Coren and Porac (1977), which looked at five millennia of artistic representations of unimanual activity (such as playing board games, throwing spears, writing, etc.). Overall about 8% of paintings, drawing, and sculptures show the left hand being used, with little variation over the entire period of recorded history (section d in Figure 3.3). Specific written references to left-handedness are rare, with the intriguing exception of a use for left-handed workers in Roman stone mines, where a left-hander and a right-hander worked cooperatively on removing blocks of stone in the very confined spaces of a mine (see Steele & Uomini, 2005, p. 229 for an account of the various work of Röder, Bedon, and Monthel).

Data on handedness from the prehistoric period and pre-literate societies are necessarily indirect, take many forms, and can be difficult to interpret; see Steele and Uomini (2005) for an overview. Frustratingly, some data, such as one of the two arrows carried by the "Ice Man", Ötzi, which had been fletched in the left-handed manner (Spindler, 1994), undoubtedly indicate the presence of left-handers, but do not allow an accurate estimate of the rate. However, the study of Spenneman (1984), looking at stone and bone tools from the Neolithic period of about 4000 BP (before present), found a rate of left-handedness of between 6% (of 597 tools at Twann in Switzerland) and 19% (of 51 tools at Bodman in Germany). The data of Cahen *et al.* (1979), from the Upper Paleolithic period of about 9000 BP found one likely left-handed toolmaker among 22 (5%), with left-handed knapping and counter-clockwise rotation marks. The study by Faurie and Raymond (2004) of silhouetted hand prints on the walls of Upper Paleolithic caves from about 30 000 to 10 000 BP also allows a proper estimate of the rate. About 77% of prints showed a left hand, a figure that the authors showed was almost identical to that provided by a modern group of 179 students carrying out

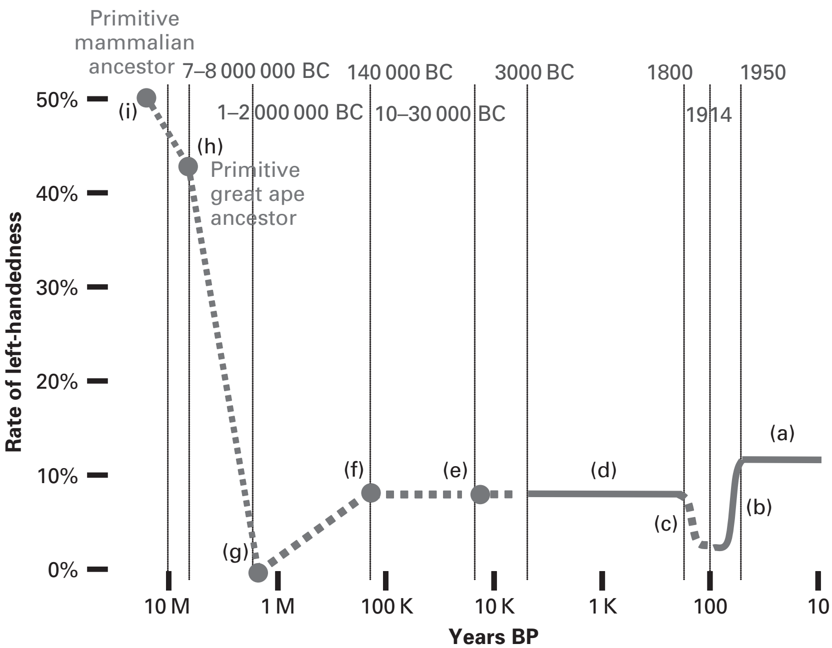

Figure 3.3 A synoptic map of the broad changes in the rate of left-handedness over the past ten million years. Note that the abscissa is logarithmic in terms of years before present.

the same task, 14 of whom were left-handed, implying a similar Upper Paleolithic rate of left-handedness to that of the modern period (point e in Fig. 3.3).

A study of a much earlier population by Fox and Frayer (1997), looked at tooth striations on Neanderthal teeth from about 130 000 BP (see also de Castro, Bromage & Jalvo, 1988). These striations probably come either from techniques for eating meat, or from the use of animal tendons or plant matter as primitive "dental floss" to remove interdental detritus. In the 20 specimens, the direction was compatible with right-handed use in 18 cases and left-handed use in 2 cases, giving an estimated rate, albeit not a particularly accurate one, of about 10% (point f in Fig. 3.3). Earlier than this, there is once again clear but isolated evidence of the presence of a left-hander who was knapping stone tools at the Boxgrove Site of about 500 000 BP (Roberts & Parfitt, 1999). Phillipson (1997) also looked at edge modification in 54 stone tools from the Lower Paleolithic period of about 500 000 to 1 000 000 years BP at Kariandusi in Kenya, and suggested that 6 (11%) were compatible with left-hand use.

Undoubtedly the oldest data on human handedness are those of Toth (1985) (see also Ambrose, 2001) who looked at the flakes left by the stone tool making of *Homo habilis* at the site of Koobi Fora in the African Rift Valley, which is from about 1.5 million years BP. There was a modest excess of flakes typical of those produced by right-handers, which was entirely compatible with the rate of such flakes found in modern knappers who are known to be right-handed. The implication, albeit not a strong one, is that perhaps *all* humans at that time were right-handed (indicated as point g in Fig. 3.3). Without repeating the theoretical arguments again here, elsewhere (McManus, 1999) I have argued that handedness in humans is likely to have evolved in two stages, in the first of which was the evolution from an ancient *C** gene to what I call the *D* gene, when the majority of humans became right-handed, and a second, subsequent stage, with the evolution of the modern *C* gene, when a substantial minority of humans became left-handed, the polymorphism of *D* and *C* genes presumably being maintained by heterozygote advantage or some other mechanism.

Modern humans evolved from a primitive great ape ancestor, perhaps about 7 to 8 million years ago, and that primitive great ape ancestor must itself have derived from a primitive mammalian ancestor. The handedness of modern great apes is controversial, with some researchers believing that great apes do not show population level handedness (i.e., 50% are right-handed and 50% are left-handed (Annett & Annett, 1991; Marchant & McGrew, 1991; Marchant & McGrew, 1996). However, a meta-analysis by Hopkins (2006) suggested that perhaps 60% of bonobos and maybe 55% of chimpanzees and gorillas show right-handedness, although there are concerns that some of the difference from 50% may result from imitation learning in captive animals.

Geographical differences in the rate of left-handedness

People everywhere are mostly right-handed, as was recognized as long ago as 1837 by the English physician, Sir Thomas Watson, who wrote:

> The employment of the right hand in preference to the left is universal throughout all nations and countries. I believe no people or tribe of left-handed persons has ever been known to exist. ... Among the isolated tribes of North America which have the most recently become known to the civilized world, no exception to the general rule has been met with. Captain Back has informed me that the wandering families of Esquimaux, whom he encountered in his several expeditions towards the North Pole, all threw their spears with the right hand, and grasped their bows with the left. (Watson, 1836)

Watson's strong theoretical position is still acceptable today, as also is Back's perception of the right-handedness of the "Esquimaux", Delacato (1963) reporting that in photographs of 46 Canadian and Greenland Inuit using "an arm for one purpose or another", 43 were using the right hand and only 3 (6.5%) were using the left hand. Likewise data from New Guinea (Connolly & Bishop, 1992), Amazonia (Bryden, Ardila & Ardila, 1993) and Tristan da Cunha (McManus & Bryden, 1993) all support the universal predominance of right-handedness, but their small sample sizes usually preclude any other detailed comparison of rates and the drawing of any strong conclusions on mechanism and process.

Although Watson was correct that right-handers predominate in all human societies, the related question of whether *rates* of left-handedness vary between countries is much more open to contention. Despite there being many papers in the literature with titles such as "The rate of left-handedness in ....", such studies usually say little about whether countries differ because they typically use different methods to measure handedness, making it unclear whether differences are due to the method of measurement or a difference in the true rate of left-handedness. Indeed Raymond and Pontier (2004), after their long meta-analysis, could still only entitle their paper, "Is there geographical variation in human handedness?" The problem of finding geographical differences is compounded by the fact that sample sizes are typically small (and although several hundred individuals may seem reasonable, it is not). Detecting differences in small proportions of individuals between populations requires surprisingly large samples, as can be seen even with the seemingly straightforward question of sex differences in the rate of left-handedness. We now believe that there about five left-handed males for every four left-handed females, male to females ratios of 1.238, 1.211, 1.207, 1.343, and 1.273 being found in the very large studies of Gilbert and Wysocki (Ross *et al.* 1992), Halpern *et al.* (1998), Peters *et al.* (2006), Carrothers (1947), and the meta-analysis of Seddon and McManus (unpublished manuscript, 1991). However, to have an 80% chance of finding such a difference with a one-tailed test at the 5% significance level requires about 2500 males and 2500 females, a number that is far larger than in most of the studies that had looked at sex differences (and therefore, for instance, the conclusion of Erlenmeyer-Kimling *et al.* (2005), that 517 children of schizophrenic parents did not show the standard sex difference in rates of left-handedness, is very unsafe). Using a similar calculation, when the rate of left-handedness is 10% in one population, then to find a significant difference with 80% power at the 5% level when the true rate in a second population is 5%, 6%, 7%, 8%, or 9% requires samples in each population of 350, 600, 1100, 2500, and 11 000, making it unlikely that most studies will reliably be able even to find quite largish differences.

One of the clearest studies to look systematically for differences in handedness between countries was that of Singh and Bryden (1994), which used large samples of students in Canada and India, two countries expected to be very different in their rate of handedness, and it used the identical questionnaire in both countries. The rate of left-handedness was 9.8% in Canada compared with only 5.2% in India, a nearly twofold difference, with factor structure being very similar (see also Singh *et al.* 2001). A parallel study comparing Canada and Japan found an even larger difference, the rate of left-handedness in Japan being only 4.7% (Ida & Bryden, 1996). Another study finding clear differences between countries in the rate of left-handedness is the important study of Perelle and Ehrman (1994), which benefited both from a large sample size and a single consistent questionnaire translated for use in all the countries.

The very large sample sizes needed for proper geographical studies of handedness, which allow some form of mapping, are often only available when the data have been collected for some other purpose, with handedness being tagged on as an additional question (as for instance in the *National Geographic* study, described earlier). A similar situation exists in the case of a recent internet-based study of sexual behavior and attitudes, which was carried out under the auspices of the BBC (Reimers, 2007). The survey was live from February 2005 to May 2005, during which time more than half a million people provided some data and 255 116 individuals completed all six sections of the study. One of the questions asked, "Which is your natural writing hand?" (Peters *et al.* 2006). Overall there were sufficient respondents from Europe to allow a map to be drawn, although for the map shown in Fig. 3.4 it has been necessary to group together some countries as sample sizes were otherwise too small. However, a trend surface analysis, which is weighted by the sample size in each country, has no such problems, and from that it is clear that the highest rates of left-handedness in Europe are in Britain, the Netherlands, and Belgium. To a first approximation the rate of left-handedness then declines as one moves away from those countries, be it west to Ireland, south-west to France and then the Iberian peninsula, north-east to Scandinavia, or east to Germany, Poland, the Baltic, and Russia, or south-east to the Balkans, Greece, Bulgaria, and Romania. The reasons for such geographical differences are not clear, although Medland *et al.* (2004) have suggested that countries with a more formal education system have lower rates of left-handedness than those with a more informal education system.

Somewhat surprisingly, it is sometimes easier to find evidence for geographical trends *within* countries rather than *between* them, in part because in national surveys the same survey methods are used in the same language for subjects. One of the biggest, and still one of the best, such studies is that of Ewald Stier (1911), who in 1909 surveyed the soldiers of the German Army. As expected the overall rate was much lower than in modern Europe, at about 3.9%, but the real interest comes in the details of his study, as in the map shown in Fig. 3.5, which shows how the rate of left-handedness was lowest for those from Eastern Prussia, and highest for those from southern Germany, around Stuttgart, where there were over twice as many left-handers as in the East. Comparing Fig. 3.5 with Fig. 3.4 suggests that many of the same trends can still be found today, with higher rates in Germany than in Poland and the Baltic States, and higher rates still towards the Swiss border. Other studies finding differences within countries are rare, but mention should be made of the study of Olivier (1978) in France, left-handedness being most frequent in the north, and of lowest frequency in Brittany and the Massif central, in Italy of Viggiano *et al.* (2001), where left-handedness was more frequent in the north of the country than the south (see also Salmaso & Longoni, 1983), and in Britain, where Leask and Beaton (2007) showed that within mainland Britain, left-handedness is less common in Scotland and Wales than in England (a trend that perhaps is hinted at in Fig. 3.4, where Ireland has a lower rate of left-handedness than the United Kingdom).

Another example of a large national survey finding geographical differences is the Gilbert and Wysocki

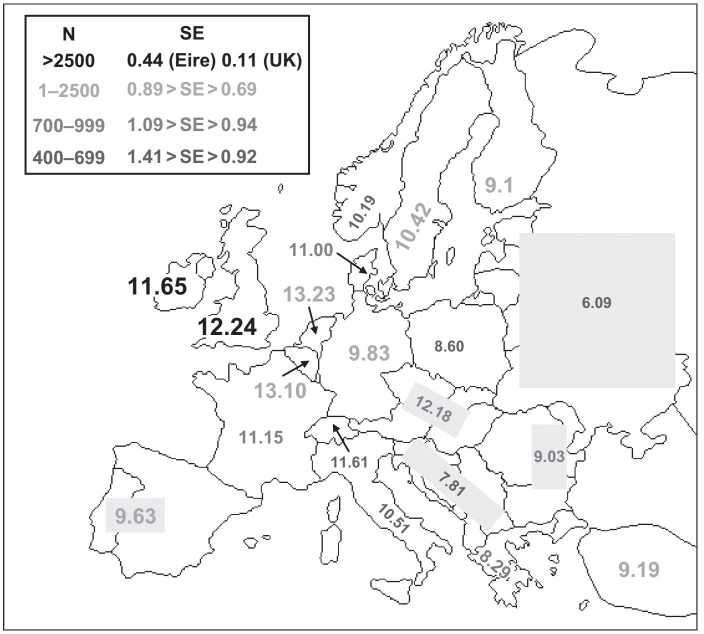

Figure 3.4 Rates of left-handedness in different European countries, based on data in the BBC internet survey (McManus & Peters, in press). Where sample sizes of contiguous countries are relatively low the countries are merged together, indicated by the gray boxes overlapping borders (e.g., Spain and Portugal were grouped together). The rate of left-handedness is shown as a percentage. The sample size and the approximate standard errors are shown by different sizes of numbers, the key being provided at the top left.

(1992) study, where the zip code for each US respondent was recorded in the database, but no further analyses were ever carried out on those data. However the Gilbert and Wysocki data reveal some fascinating trends, which are both geographical and historical (McManus & Wysocki, in press). Zip codes for each respondent can readily be translated into latitudes and longitudes, and handedness can then be mapped. Figure 3.6 shows the percentage of left-handers in White Americans born in 1950 and afterwards in each of the contiguous states of mainland United States. Even at this level of spatial resolution it can be seen that the highest rates of left-handedness are in the north-east, in Maine, Vermont, Massachusetts, and Connecticut, whereas the lowest rates are in the mid-West, in Wyoming and North Dakota. More detailed mapping suggests that left-handers are also more frequent in the north-east of the USA, as well as in Florida, and around the west coast cities of San Francisco, Portland, and Seattle. The causes of these differences are complex, but of particular interest is that as one looks at those born a generation and then two generations earlier, the geographical patterns shift, with left-handers then being more common in the agricultural areas of the United States, such as the mid-west and the south. The implication is that there may be differential migration of left-handers.

Finally, it should be mentioned that there must always be a worry about whether there are response biases in surveys, particularly those carried out using magazine readers or internet browsers. To respond to the BBC internet survey a respondent must have a computer, must understand English well, and must be aware of the survey, all of which may make biases possible. Having said that, similar trends are apparent to those in Stier's (1911) study, which used a conscripted sample, and was entirely in the subjects' native language, thereby providing a validation in principle of the method.

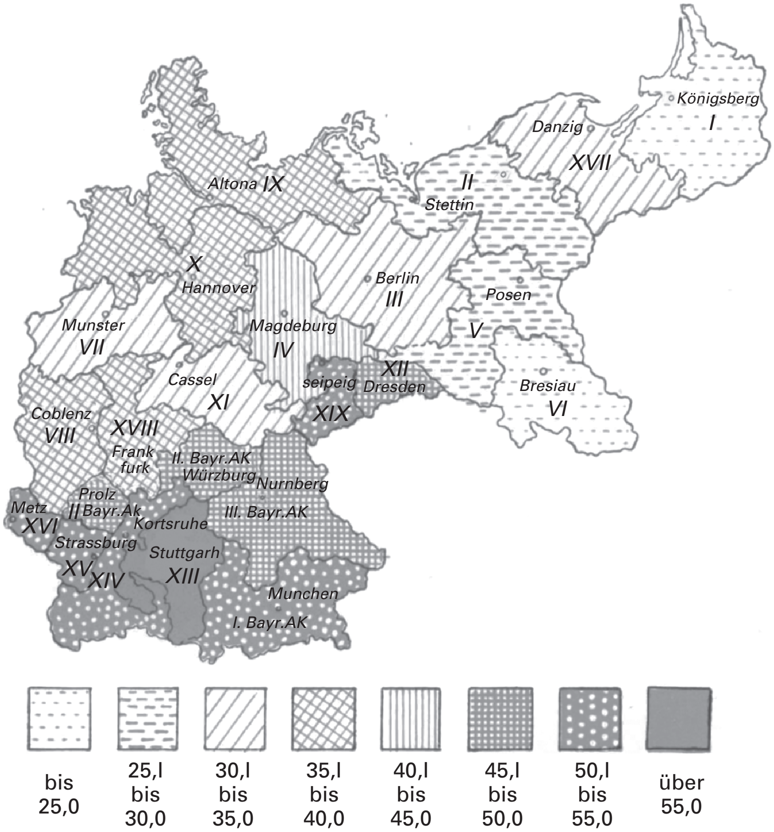

Figure 3.5 The rate of left-handedness in German soldiers in 1909 (plotted as left-handers per thousand) in relation to the area in which they were recruited (Stier, 1911).

Ethnicity and handedness

Analysis of handedness by ethnicity has been left until last, since in the modern world, ethnicity, which in some sense expresses the distant geographical origin of individuals, perhaps many generations previously, inevitably incorporates a historical component according to when an individual's family or ancestors migrated from one geographical region to another. Few studies have assessed ethnic differences in handedness, and the two sets of data presented here, one from the UK and the other from the USA, have both been prepared specially for this chapter.

Singh and Bryden (1994) showed that the rate of left-handedness was lower in the Indian sub-continent than in the West. A classic epidemiological method for distinguishing the effects of genes and culture is to observe migrants between two countries which differ in some characteristic. If migrants become like the society to which they have migrated then socio-cultural factors are probably responsible for the difference, whereas if the difference remains in the migrants then genes are probably responsible. The method can be used to look at handedness in applicants for medical education in the UK, considering only those who are either White or from the Indian sub-continent (Table 3.1; for further details of these studies see McManus *et al.*, 1995; McManus, Richards & Maitlis, 1989). The odds ratio for the difference between White and Asian (Indian sub-continent) applicants is

Table 3.1 Handedness of 4902 applicants to UK medical schools for admission in 1986 and 1991, comparing self-classified Indian sub-continent applicants with White applicants, with non-White applicants divided into those born in the UK and those not born in the UK. Logistic regression showed an overall effect of being male (OR = 1.387, $p < 0.001$), and a highly significant effect of being White (OR = 1.513, $p < 0.001$), but no significant effect of being born in the UK (OR = 1.218, $p = 0.117$). Restricting the analysis to those of Asian origin, there was still a significant effect of being male (OR = 1.558, $p = 0.017$), but no effect of being born in the UK (OR = 1.273, $p = 0.182$). Analyses comparing the 1986 and 1991 cohorts (not shown here) showed no significant differences.

Ethnic origin	Males	Females	Total
White	13.0% (302/2331)	9.6% (248/2581)	11.2% (550/4902)
Indian sub-continent	9.2% (92/995)	6.1% (47/769)	7.9% (139/1764)
Born in the UK	10.7% (57/534)	6.0% (26/430)	8.6% (83/964)
Not born in the UK	7.6% (35/461)	6.2% (21/339)	7.0% (56/800)

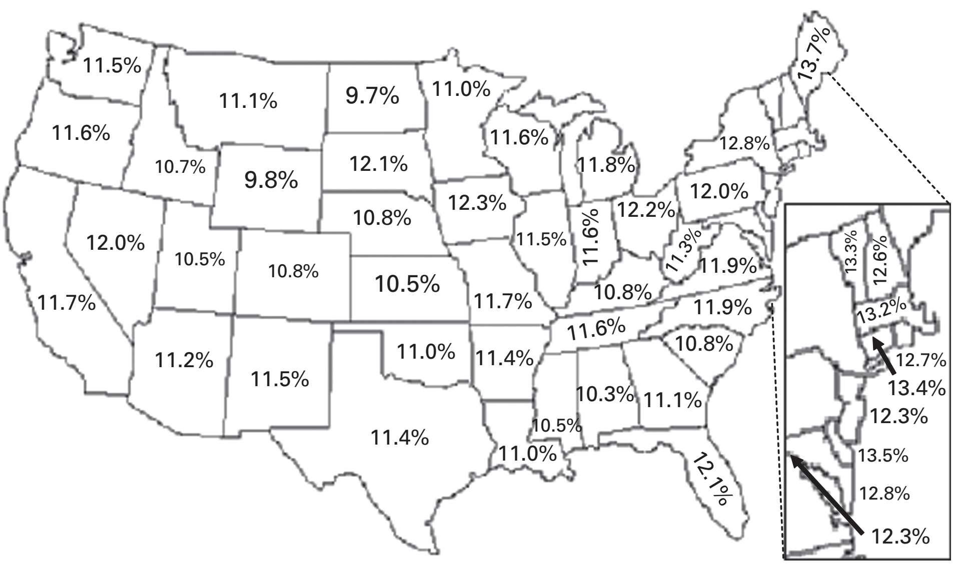

Figure 3.6 Rate of left-handedness of White respondents, born from 1950 onwards, in each of the contiguous states of the USA, based on the data of Gilbert and Wysocki (1992); for further details see McManus and Wysocki (in press). Sample sizes vary from 1197 for the District of Columbia to 52 081 for California, with a mean of 8427, median of 5267, and inter-quartile range of 2879–11 939. The standard error for a state of median size is about 0.4%.

1.513×, which is broadly similar to that observed in Singh and Bryden's (1994) comparison of Canada and India. Most importantly, though, there is no difference between the Asian applicants born in the UK and those born in the Indian sub-continent (and presumably reared outside of the UK for at least their early childhood), which suggests that socio-cultural factors are relatively unimportant in the origin of ethnic differences in handedness, and implies instead that genes may be more important in determining differences.

Ethnicity can also be looked at in the very large Gilbert and Wysocki (1992) study. Although 97% of

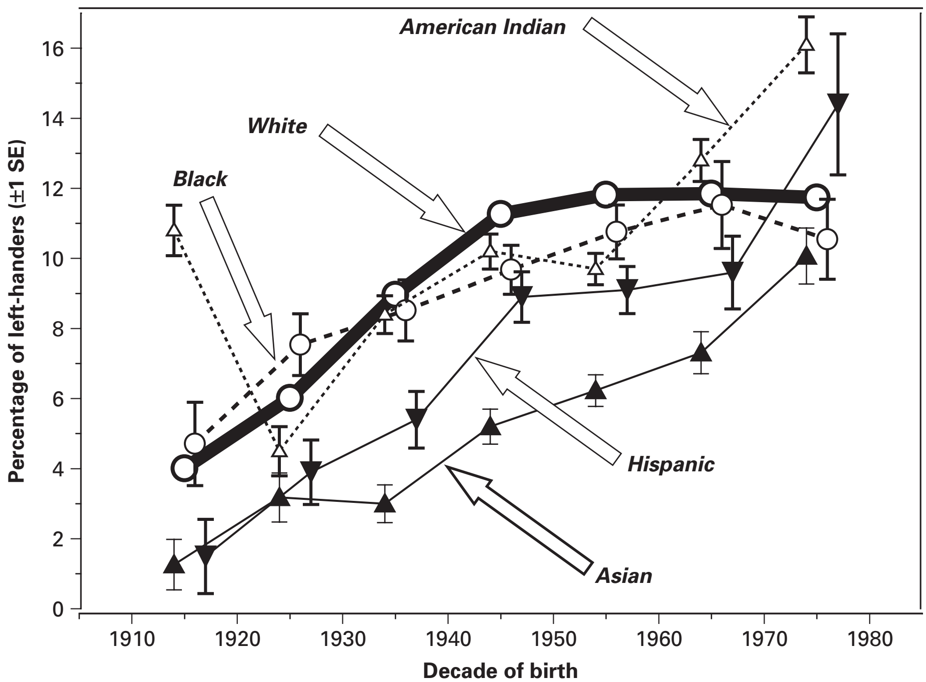

Figure 3.7 Left-handedness rates (± 1 SE) in US respondents from different ethnic groups in the Gilbert and Wysocki study, averaged across sex. Groups are broken down by birth decade (1910–19, 1920–29, etc.) and plotted at the decadal mid-points, with some groups moved slightly to the left or right to prevent standard error bars overlapping. The solid black line with open circles is for White respondents, and standard errors are smaller than the size of the symbol. Ethnic groups are shown as Black (○– – – ○), American Indian (Δ– – – Δ), Hispanic (▾– – – ▾), and Asian (▴– – – ▴). Statistical analysis used hierarchical logistic regression. At the first step, effects of year of birth and sex were entered, the non-linear age trend being taken into account by a quintic polynomial. At the next step, ethnicity showed a highly significant effect (Wald chi-square = 374.7, 4 d.f., $p < 0.001$), with only Asians and Hispanics showing significantly lower rates of handedness from the White reference group ($p < 0.001$ in each case). Ethnicity by sex interactions were tested at the next step, but were not significant (Wald chi-square = 3.508, 4 d.f., $p = 0.477$). Finally, the interaction of linear trend of year of birth by ethnicity was tested, and was highly significant (Wald chi-square = 53.43, 4 d.f., $p < 0.001$), with only the Asian and Hispanic sub-groups showing a significantly lower slope than in the White reference group ($p < 0.001$ in each case).

the US respondents in the Gilbert and Wysocki survey were White, the vast sample size meant there were still sufficient non-White respondents in the USA to allow an analysis by ethnicity and year of birth. Considering only those born from 1910 onwards, numbers being very small before that, there were 8387 respondents describing themselves as Black, 10 080 as Asian (presumably mostly from the Far East), 2513 as American Indian, and 12 049 as Hispanic, numbers that are larger than even most of the largest other studies of handedness.

Figure 3.7 shows the rate of left-handedness in the five ethnic groups in relation to year of birth. The Black and American Indian groups show similar historical changes to the White group, whereas both the Asian and Hispanic groups show lower rates of left-handedness overall, and also a lower rate of increase in the rate of left-handedness than do the other groups. The lower rate of left-handedness in the Asian groups is compatible with other studies suggesting lower rates of left-handedness in China, Japan, and the Indian sub-continent (Iwasaki, 2000; Teng *et al.* 1976), and the lower rate of left-handedness in the Hispanics is similar to that found in the Iberian peninsula in the European data (see Fig. 3.3), and the effects are also similar to those of the large study of Halpern *et al.* (1998), where among US medical school applicants, left-handedness was reported in 13.1% of 92 523 Whites, 10.7% of 11 778 Blacks, 10.5% of 6171 Hispanics, 9.2% of 9055 Indian sub-continent applicants, 6.3% of 3533 Vietnamese, 5.4% of 4087 Koreans, and 5.3% of 7413 Chinese applicants. A striking feature also of Fig. 3.7 is the excess left-handedness in males being similar in all ethnic groups, again suggesting some stable and constant mechanism maintaining sex differences (and hence probably not cultural or social pressures against women, as has sometimes been implied).

Explaining geographical and historical differences in the rate of left-handedness

The analyses of this paper have so far been mainly descriptive, but provide a clear demonstration that rates of left-handedness vary between different countries. Singh and Bryden's (1994) comparisons of India and Canada provide compelling evidence of differences between countries in two different continents, and other studies have shown differences across the continent of Europe and across the states of the USA. There are differences between ethnic groups within the USA, Asians and Hispanics having lower rates of left-handedness, and there are also large historical shifts in the rate of left-handedness across the twentieth century, those historical shifts being paralleled within the separate ethnic groups that comprise the USA. The challenge is to explain the origin of these differences: differences that are present in both space and time.

Explaining geographical differences

Most explanations in biology distinguish nature and nurture, which to a large extent can be conceptualized as genes and environment. When populations differ in their rates of left-handedness then the most important question concerns whether the differences are genetic or environmental in origin. Distinguishing such explanations were key questions for Phil Bryden during the final years of his life, particularly after he had collected his data showing large and clear differences between Canada and India. However, the obvious theoretical problem is that a low rate of left-handedness in India can result either from social pressure, which results in left-handers being forced, overtly or covertly, to behave as right-handers, or from differences in gene frequency between Canada and India, *and prevalence data alone cannot distinguish between genetic and social causes*. The key insight, however, which Phil Bryden and I developed together in what as it happened were the last months of his life, is that the effects of genes and social pressure can be distinguished if each is modeled separately, and family data are available.

Euchiria, Hipressia, and Lowgenia

In a popular book on handedness (McManus, 2002), I illustrated the separate effects of genes and culture by describing three mythical countries, which I named Euchiria, Hipressia, and Lowgenia. The model is based around the McManus genetic model of handedness (McManus, 1985; McManus & Bryden, 1992), which needs to be briefly described, although it seems likely that any broadly similar genetic model will show similar effects.[1] The model suggests that at a single genetic locus there are two alleles, named *D* (for dextral) and *C* (for chance). One hundred percent of *DD* homozygotes are right-handed, whereas *CC* homozygotes have a 50:50 chance of being right- or left-handed. The alleles are additive in the heterozygote, so that 25% of *DC* individuals are left-handed, and the remaining 75% are right-handed. The model explains not only how handedness runs in families, but also why as a result of the random effects of the *C* allele about one in five monozygotic twin pairs is discordant for handedness. Finally, by assuming that the same alleles determine handedness and language dominance, the

[1] An exception may be the Annett model, which as well as a parameters to describe the frequency of the RS-gene, also has a threshold parameter that can be adjusted separately in each population, and which therefore is confounded with rate of handedness.

Table 3.2 Familial patterns of handedness in the mythical countries of Euchiria, Lowgenia, and Hipressia (see text for details). Note that *p(L|DD)* indicates the conditional probability of being left-handed, given that an individual has the *DD* genotype, etc.). L_{par} refers to families in which at least one parent is left-handed.

	Euchiria	Lowgenia	Hipressia
$p(C)$	0.2	0.1	0.2
$p(L\|DD)$	0	0	0
$p(L\|DC)$	0.25	0.25	0.125
$p(L\|CC)$	0.50	0.50	0.250
$p(L)$	*0.100*	*0.050*	*0.050*
$p(L\|R \times R)$	0.078	0.038	0.045
$p(L\|L_{par})$	0.195	0.160	0.099
Odds ratio	2.87×	4.79×	2.34×

model readily explains why about 5% of right-handers and 35% of left-handers are right hemisphere dominant for language.

Euchiria is a country in which only genes determine handedness, and because the rate of left-handedness, *p(L)*, is set at exactly 10%, the calculations of the McManus model are particularly easy, because the frequency of the *C* allele, *p(C)* is double that of *p(L)*, and hence is 20%. The top of the first column of Table 3.2 shows the frequency of the *C* allele, the probability of each of the three genotypes being left-handed, and the resulting rate of left-handedness, which is 10%. For convenience, and because two left-handed parents is a relatively rare combination, families are divided into those for whom both parents are right-handed ($R \times R$) and those in whom at least one parent is left-handed (L_{par}). When at least one parent is left-handed, the proportion of left-handers in the offspring, $p(L|L_{par})$, is 19.5%, compared with only 7.8% when both parents are right-handed, $p(L|R \times R)$. Calculating a conventional odds ratio, as $19.5 \times (100 - 7.8)/(7.8 \times (100 - 19.5)$, shows a child with at least one left-handed parent is about 2.87 times more likely to be left-handed itself.

Lowgenia is similar in many ways to Euchiria, except that the frequency of the *C* allele is lower, being exactly half that found in Euchiria, so that *p(C)* is 10%, and the unsurprising consequence is that the rate of left-handedness is also half that found in Euchiria, *p(L)* being 5%. What is rather more counter-intuitive, at least for those not used to genetic calculations, is that the odds ratio for the effect of having at least one left-handed parent is *higher* in Lowgenia than in Euchiria, being 4.79× in Lowgenia, rather than the 2.87× found in Euchiria. A reduction in gene frequency therefore *increases* the odds ratio of the child of a left-handed parent being left-handed.

Hipressia is more complicated, because not only genes but also social pressure affect the rate of left-handedness, both of which need to be modeled. Hipressians do not like left-handers and do their best to make them indistinguishable from right-handers, but human resilience being what it is, they are only successful in half the cases. The gene frequency in Hipressia, *p(C)*, is the same as in Euchiria, but instead of a half of *CC* individuals and a quarter of *DC* individuals becoming left-handed as they would in Euchiria, social pressure against left-handers in Hipressia means that only a quarter of *CC* individuals and an eighth of *DC* individuals become left-handed (or putting it more precisely, a quarter of *CC* individuals and an eighth of *DC* individuals, who would have become left-handed in Euchiria, instead become right-handed in Hipressia because of social pressure, making them what geneticists call "phenocopy right-handers"). The unsurprising result, once again, is that the overall rate of left-handedness in Hipressia is exactly half that found in Euchiria, being 5%. That rate of 5% is exactly the same as the rate found in Lowgenia, showing how two entirely different causal mechanisms result in the same overall rate of left-handedness. However, and it is a key point, the pattern of left-handedness in Hipressian families is very different from that found in Lowgenia, the odds of a Hipressian being left-handed when they have a left-handed parent being 2.34× higher than if both parents are right-handed, compared with 4.79× in Lowgenia. The Hipressian odds ratio is therefore *lower* than in Lowgenia (and indeed is also lower than in Euchiria). The key theoretical conclusion is that gene frequency differences and social pressure can be distinguished by looking at odds ratios in families.

The model that Phil Bryden and I had developed was quickly tested, because Bryden not only had data on the rate of left-handedness in Canada and India, but had already carried out a preliminary analysis of how handedness ran in families in the two countries (Bryden *et al.* 1995). In Canada, where the rate of left-handedness was 9.8%, the odds ratio was 2.09×, whereas in India, where the rate of left-handedness was 5.2%, the odds ratio was 3.07×. The implication was clear: the majority of the difference between Canada and India must be due to differences in gene frequency rather than due to differences in social pressure. Subsequently, Bryden and I collaborated with Taha Amir in the United Arab Emirates (UAE), and Yokahida Ida in Japan, and we also put together larger Western samples (mainly Canada and the UK), and Indian samples. Of 17 850, 14 924, 4485, and 656 offspring in the West, UAE, India, and Japan, for whom *p(L)* was 11.5%, 7.5%, 5.8%, and 4.0% respectively, the odds ratios for the effect of having a left-handed parent were 2.11×, 2.23×, 3.18× and 3.57× respectively, which is the pattern expected from gene frequency differences. Geographical differences in the modern world seem therefore to be primarily genetic in origin, rather than due to differences in social pressure (or what I will refer to subsequently as "direct social pressure").

Explaining historical differences

If geographical differences in rates of left-handedness can be explained in terms of differences in gene frequency, what about historical differences? "The past is a foreign country", as L. P. Hartley said at the beginning of *The Go-Between* (albeit often being misquoted as "the past is another country"). If so, then the same methods that distinguish the causes of geographical differences should also distinguish the causes of historical differences. Fortunately, a number of family studies of handedness in Western countries have been published over the past century, the earliest being that of Ramaley (1913), who described data collected in a group of undergraduate students (the probands), who therefore would have been born in about 1888. In 1992, Phil Bryden and I (McManus & Bryden, 1992) had already reviewed 25 such studies, and had broken them down into three groups, those for whom the probands were born between 1880 and 1939, 1940 and 1954, and 1955 and 1979, the rates of left-handedness in the offspring being 7.28%, 10.83%, and 13.25% (whereas, the parents, being born a generation earlier, had rates of left-handedness of 4.44%, 6.11%, and 9.34%). The odds ratios for the effect of having a left-handed parent were 3.29×, 2.08×, and 1.64× in the three groups respectively. Just as with the geographical data, when the rate of left-handedness is lower, so the odds ratio is higher, implying that the historical differences also reflect differences in gene frequency. That suggestion was also strongly supported by a reanalysis of data from the huge study of the German Army by Stier (1911), the conscripts for whom would have been born in about 1890, and of whom 3.87% were left-handed, a lower value than any of the family studies we had analyzed. Stier reported the number of left- and right-handers with left-handed relatives, and by making some reasonable assumptions, one can estimate the odds ratio for the effect of having a left-handed parent as being about 5.2×, a higher value than any of the odds ratios in the other familial studies. Once again, Stier's data suggest that historical differences reflect genetic differences rather than effects of social pressure.

Social pressure can take many forms, and it is useful to distinguish between *direct* and *indirect* social pressure. Direct social pressure involves left-handed individuals being made to write with their right hand, as seems to have happened in some Victorian schools (see, e.g., Ireland, 1880), and has occurred in many other forms around the world to prevent left-handers using their left hands (see McManus, 2002). However, direct social pressure of this sort only alters the phenotype, not the genotype, and the individuals still carry the genes that made them originally left-handed, and if transmitted those genes would allow those individuals' offspring to become left-handed. Indirect social pressure is much more subtle, and does not directly alter the phenotype of the left-hander, but instead acts to make left-handers stigmatized, ostracized, and taboo, so that they find it harder to have offspring. The result is that their genes are less likely to be passed on, and hence the frequency of the genes responsible for left-handedness falls, and left-handedness becomes less common in the next generation. To see how this might happen one must consider the very different social world of relatively small nineteenth-century communities, where most people knew one another, transport was less good, most people married people living less than 30 kilometers away, marriage was relatively early, as also was first childbirth, so that families were large, often with eight or ten children, child-bearing only ceasing at menopause. In such a world, any subtle denigration, mockery, or stigmatization of the left-handed, perhaps for clumsiness or awkwardness at writing or technical skills, or indeed for mere difference itself, might result in marriage and hence childbirth being delayed by five or ten years, so that the number of offspring would be reduced. The consequence would be a fall in the number of *C* alleles and hence in the rate of left-handedness. Indirect social pressure, although less brutal than direct social pressure, could be of far greater consequence in its eventual effects.

If the theory of indirect social pressure is correct, then there is a clear prediction: left-handers at the end of the nineteenth century should have had fewer children than right-handers. Fortunately that prediction can not only be readily tested, but the data has already been presented in our review of the genetics of handedness (McManus & Bryden, 1992). Family studies typically include all children, and hence if the number of parents is known as well as the number of offspring, then the mean number of offspring can be calculated. Table 3.3 shows that while at the end of the twentieth century, right- and left-handed parents had similar numbers of children, despite parents around the turn of the century in general having more children than modern parents, left-handers had relatively fewer children, two left-handed parents having only 2.32 children, compared with 2.69 children when one parent was left-handed, and 3.10 children when both parents were right-handed. Two right-handed parents therefore had 34% more children than two left-handed parents. It is therefore at least possible that historical shifts in the rate of left-handedness are driven by differences in fertility (and the ultimate test of any evolutionary theories concerns whether groups of individuals differ in the numbers of offspring).

Table 3.3 The average number of offspring in relation to parental handedness, in familial studies of handedness carried out in different periods, classified by the birth year of probands (from McManus & Bryden, 1992).

Birth year of probands	Number of studies	Number of parental pairs	Parental handedness R × R	R × L	L × L
1880–1939	5	4180	3.10	2.69	2.32
1940–54	5	3800	3.17	3.05	3.00
1955–80	6	7323	2.49	2.60	2.57

The consequences of historical and geographical differences in left-handedness

Were the rate of left-handedness to vary, either historically or geographically, and particularly if that variation is due to differences in gene frequency, what consequences does that have for neuropsychology and neuropsychiatry? The answer depends in part on the nature of the genetic system underlying handedness and cerebral dominance, and for obvious reasons I will consider the McManus model, which suggests that 25% of *DC* individuals and 50% of *CC* individuals are left-handed. More generally (McManus, 1984; McManus, 1985) the model says that 25% of *DC* individuals and 50% of *CC* individuals, but no *DD* individuals, will have atypically directed lateralization for any character controlled by the gene. A crucial corollary is that the chance processes for each character will be statistically independent.

If there is a probability p_G that any individual modular character will be atypically organized (such as, left-handedness or right-sided language) in a particular genotype, *G*, and if we consider two modular traits, such as handedness and language, then $(1 - p_G)^2$ will have the typical phenotype (the one described in neuropsychology textbooks, which for handedness and language is right-handedness and left-sided language), $2.p_G.(1 - p_G)$ will have one atypical trait, and p_G^2 will have both traits anomalously organized (in this case, left-handers with right-sided language). For *DD*, *DC*, and *CC* individuals, p_G is 0, 0.25, and 0.5 respectively. However, *DD* individuals are far more frequent in the population than *DC* who are more frequent than *CC* individuals. Combining all the numbers, then it is easy to show that if the rate of left-handedness is 10%, then 7.8% of right-handers and 30.0% of left-handers will have language in the right hemisphere, which corresponds broadly with the data.

There may, however, be multiple modular traits controlled by the *D* and *C* alleles, with perhaps several separate modular traits for aspects of spoken and written language, several modular traits for aspects of visuo spatial and facial processing, and so on. If there are *n* modular traits, then $(1 - p_G)^n$ individuals will have the textbook pattern with no anomalies, and $1 - (1 - p_G)^n$ will have at least one anomaly (such as a right-sided component of language, or a left-sided component of visuo spatial processing). The number of modules is not at present known, but Table 3.4 calculates the percentage of individuals with anomalous organization in relation to the number of modules and the rate of left-handedness in the population. The basic finding is very simple: irrespective of the number of modular traits controlled by the *C* allele, the proportion of anomalous traits rises approximately linearly with the rate of left-handedness. If it is the case that dyslexia, stuttering, autism, schizophrenia, or other conditions are related to atypical cerebral lateralization, and hence to the presence of a *C* allele, then the rate of those conditions should change geographically or historically in parallel with the rate of left-handedness.[2] In particular, in the West there may well have been a three- or fourfold increase in the rate of those conditions since Victorian times, and in other cultures the rate might well be rising as left-handedness increases in frequency. That may help to explain how conditions that we now think of as common, were rare and difficult to describe and characterize in the nineteenth century. However, and it is relevant in the context of current speculations about a rising rate of autism, the rate of cerebral dominance related anomalies should be relatively constant for those born in the West after about 1950. Whether or not there are historical and geographical variations in neuropsychiatric conditions remains to be seen; collecting adequate evidence to assess the idea will not be easy, but the hypotheses relating their rate to handedness and cerebral dominance differences are testable, and have interesting implications for interpreting differences in neuropsychiatric disease prevalence.

Table 3.4 The effect of the rate of left-handedness on the percentage of individuals with atypical cerebral organization (e.g., crossed cerebral dominance, "anomalous" dominance).

	Number of modular traits					
Rate of left-handedness	1	2	3	5	10	"Very large"
2.5%	2.5%	4.3%	5.7%	7.5%	9.2%	9.8%
5%	5.0%	8.6%	11.3%	14.7%	18.0%	19.0%
7.5%	7.5%	12.8%	16.7%	21.6%	26.3%	27.8%
10%	10.0%	17.0%	22.0%	28.3%	34.2%	36.0%
12.5%	12.5%	21.1%	27.1%	34.7%	41.6%	43.8%

Note: when the number of modular traits is very large (and is effectively infinite), then all *DC* and *CC* individuals will show at least one anomalous trait. If the rate of left-handedness is *p(L)*, then the frequency of the *C* allele is 2.*p(L)*, the frequency of the *D* allele is 1 – 2.*p(L)*, the frequency of *DD* individuals is $[1 - 2.p(L)]^2$, and hence the combined frequency of *DC* and *CC* individuals, which is the proportion of individuals with anomalies, is $1 - [1 - 2.p(L)]^2$.

ACKNOWLEDGMENTS

I am very grateful to Chuck Wysocki and Avery Gilbert for providing me with raw data from their large study of handedness, and to Michael Peters and Stian Reimers for their collaboration in studying the data from the BBC internet study.

[2] It should also be said that small numbers of anomalies may well be beneficial, while large numbers of anomalies are deleterious. Elsewhere in my "theory of random cerebral variation" (McManus, 2002) I have argued that *DC* individuals in particular are more likely to have single anomalies that might result in beneficial consequences, perhaps in the form of special talents for particular tasks that involve unusual interactions between modules.

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