

Review

Why are some people left-handed? An evolutionary perspective

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Since prehistoric times, left-handed individuals have been ubiquitous in human populations, exhibiting geographical frequency variations. Evolutionary explanations have been proposed for the persistence of the handedness polymorphism. Left-handedness could be favoured by negative frequency-dependent selection. Data have suggested that left-handedness, as the rare hand preference, could represent an important strategic advantage in fighting interactions. However, the fact that left-handedness occurs at a low frequency indicates that some evolutionary costs could be associated with left-handedness. Overall, the evolutionary dynamics of this polymorphism are not fully understood. Here, we review the abundant literature available regarding the possible mechanisms and consequences of left-handedness. We point out that hand preference is heritable, and report how hand preference is influenced by genetic, hormonal, developmental and cultural factors. We review the available information on potential fitness costs and benefits acting as selective forces on the proportion of left-handers. Thus, evolutionary perspectives on the persistence of this polymorphism in humans are gathered for the first time, highlighting the necessity for an assessment of fitness differences between right- and left-handers.

Keywords: handedness; polymorphism; human

1. INTRODUCTION

The aim of this review is to identify the evolutionary forces involved in human handedness. Two main questions are critical to improve our understanding of the evolution of human handedness: (i) why is hand use asymmetric (i.e. why do individuals show a preference for one hand in most manual tasks)? and (ii) why is hand use asymmetry polymorphic (i.e. why do some individuals prefer the left hand and some the right for a similar task)? Most research on handedness has focused on the intersection of these two questions, namely, why are humans right-handed? As a consequence, the debate on the origin and understanding of handedness has been partially obscured, as left-handedness was historically considered as an anomalous or pathological case, thus ignoring the relatively high proportion of left-handers within human populations.

Previously, asymmetric hand use has been studied extensively. Corballis (2003) suggested that the evolution of human speech implied an association between speech and gesture, and thus brain lateralization for speech may be responsible for asymmetric hand use. This evolutionary explanation was further elaborated by Vallortigara & Rogers (2005) who evaluated

the costs and benefits of brain asymmetry. The aim of the present review is to clarify the question of the asymmetric hand use polymorphism in humans.

Many diverse studies on left-handedness have been conducted by researchers from various fields such as medicine, neurology and psychology. Although some data remain controversial, several hormonal, cultural and developmental factors have been found to be associated with handedness. Here, we attempt to review the information available on both proximal and ultimate aspects of handedness in humans to identify the evolutionary mechanism of the persistence of left-handers.

2. RIGHT AND LEFT HAND USE IN HUMAN POPULATIONS

To understand the evolutionary processes implied in handedness, it is first necessary to have a clear idea of the historical and geographical variation of this trait.

(a) *Hand preference assessment*

Handedness measures are based on hand use preference or hand performance (McManus 1996). However, there are no two clear categories such as left- and right-handers. For a given manual action, each individual shows a preference for the use of one hand, and it is not always the same hand for two different actions (Salmaso & Longoni 1985). This suggests that right- or left-handers are not general

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categories, but rather are defined as a function of the tasks. When the tasks considered are highly skilled and complex, and the individuals tested are specialized in these tasks, there is a very strong correlation between the different tasks (Bryden 1977; Wood & Aggleton 1989; Connolly & Bishop 1992; Marchant *et al.* 1995; Marchant & McGrew 1998). To study handedness variations in humans, it is important to choose tasks that are typical tasks among human populations from different cultures. Thus, some tasks commonly used in Western societies to measure handedness, such as writing or teeth brushing, are meaningless in other cultures. Hand preference for some tasks could also be modified by social or religious influence. For example, Teng *et al.* (1976) observed in China a strong social pressure for right-handed writing and eating, which has drastically decreased the proportion of left-handers for these tasks compared with other tasks.

Thus, the tasks chosen to measure handedness should be logically related to the biological hypothesis tested. For example, if one wants to assess handedness in the context of the hypothesis of a frequency-dependent advantage of left-handers in fights, tasks should be related to fighting actions. If the aim is to examine brain lateralization related to language, writing handedness is more relevant. Therefore, despite the complexity of the phenomenon, the biological causes for left- and right-handers still make sense under some circumstances.

(b) *Handedness in the past*

Handedness in ancient humans has been inferred by analysis of archaeological samples from skeletons, stone tools and various other artefacts (see Steele & Uomini (2005) for a review). By studying arm bone length, Trinkaus *et al.* (1994) observed a prevalence of right hand dominance in Neanderthal skeleton samples (dating from approx. 35 000 BP). For some tools, modern replication has shown that handedness conditioned the pattern of knapping scatters and that it is thus possible to infer the laterality of the tool maker by studying ancient tools (Rugg & Mullane 2001). A handedness polymorphism, with a majority of right-handers, has been inferred from tools dating from 300 000 to 400 000 BP. Data from tool shape or wear, which both reflect tool use, also allowed inferences on ancient human handedness. Phillipson (1997) reconstructed grip types on hand axes and cleavers dating from approximately 1 Myr ago, and also observed a majority of right users. However, it is a possibility that these estimations could have been modified by the use of these same tools by different individuals.

Dental marks have also been used to infer hand use for cutting food with a stone tool. These data suggest that the handedness polymorphism existed in Neanderthals (Bermúdez de Castro *et al.* 1988; Fox & Frayer 1997). Again, for this task, right-handers outnumbered left-handers. However, these could be biased by dietary or post-mortem marks.

Negative hands painted in caves during the Upper Palaeolithic in Western Europe, or more recently elsewhere in the world, could also be informative on the handedness of the painter. In all cases, both right and left hands are found, with a higher

prevalence of left hands, indicating a higher proportion of right-handers for this task (for a review see Steele & Uomini 2005).

Human representations in artistic samples were also used to track the handedness of artists, or the handedness of individuals depicted by artists. For the handedness of artists, Perello (1970) showed that representations differ between right- and left-handers and by studying painting from prehistoric caves (e.g. Altamira Cave, 14 000–18 500 BP), he inferred that handedness should be polymorphic. These methods could be reliable if the characteristic left-hander's marks on painting or engraving were formally tested on modern humans. Another approach consists of studying the handedness of the individual's depicted (e.g. Spennemann 1984). However, these methods are more problematic, as it has not been shown that handedness frequency in art reflects reality. In addition, there are known biases in the depiction of handedness, at the cultural, religious and aesthetic levels (Needham 1973; Faurie & Raymond 2004). Thus, the use of these data requires further study.

However, all the above-described studies clearly show a polymorphism of hand use in Hominid populations during prehistoric and historic times, with an overall dominance of right-handers. The polymorphism thus seems to have persisted over significant evolutionary time, suggesting that selection may play an important role in the persistence of this diversity. Another indication of selection pressures is provided by the study of the variation of the frequencies of right- and left-handers throughout the world.

(c) *Geographical variation*

The diversity of the tasks used to test handedness introduced complications in comparing hand preference across populations. When only one task is considered, there is still substantial geographical variation. Raymond & Pontier (2004) reviewed 81 studies on handedness that examined throwing or hammering in 14 countries in America, Africa, Europe, Asia and Australia and found a range of 5–25.9%, suggesting an important geographical variation in hand preference. Such geographical variations have also been observed for writing hand preference: in a survey of 12 000 subjects from 17 countries, 2.5–12.8% were left-handed for writing (Perelle & Ehrman 1994), and among seven ethnic groups based on 255 100 answers to a BBC internet study 7–11.8% were left-handed (Peters *et al.* 2006). Studies on traditional societies tend to show a similar range of variations. Faurie *et al.* (2005b) found a range of left-hander frequencies between 3.3 and 26.9% across eight societies.

The frequency of left-handedness thus seems to be variable among human populations, left-handers being always at a lower frequency than right-handers. Moreover, in most populations studied, the proportion of left-handers among women was lower than in men (reviewed in Raymond & Pontier 2004), suggesting an important influence of sex in the determinism of hand preference.

This polymorphism is thus present in every human population studied, suggesting that evolutionary mechanisms should be involved in its persistence.

However, for selection to take place, hand laterality should be a heritable trait. Thus, in the following sections, we review the determinism and transmission of hand preference in humans. The exact mechanisms have not yet been clearly characterized, but several influential factors have been identified.

3. GENETIC FACTORS

(a) *Handedness in families*

The study of handedness in families is a first attempt to characterize the mechanism involved, since it allows assessment of the transmission of this trait across generations. Tables 1 and 2 show a clear familial effect upon handedness. Two right-handed parents produce fewer left-handed offspring than parents with any other handedness combination and two left-handed parents produce the highest proportion of left-handed children, i.e. approximately 30–40% (McManus 1991; McKeever 2000). This suggests that hand preference could be transmitted by parents to their children, either at a genetic or learning level.

There is a higher prevalence of left-handedness in children of right-handed men and left-handed women (RxL mating) than left-handed men and right-handed women (LxR matings) (Annett 1973; Ashton 1982; Spiegler & Yeni-Komshian 1983; Risch & Pringle 1985; McManus 1991), thus suggesting stronger maternal effects on offspring handedness. Such a finding could result from a sex-linked genetic effect, or from a greater social influence likely to be exerted by the mother on the child. Note that McKeever (2000) observed this maternal effect only for sons, not daughters and also observed a paternal effect for daughters, but not sons. This would be consistent with an X-linked genetic determinism of handedness. Published heritability estimates for handedness range from 0.23 to 0.66 (Hicks & Kinsbourne 1976; Longstreth 1980; Porac & Coren 1981; Annett 1985; Risch & Pringle 1985; McManus & Bryden 1991; McKeever 2000; Warren *et al.* 2006). Some results of sex-specific heritability estimates are presented in table 3.

The fact that handedness runs in families is not convincing evidence of a genetic component, since parents also transmit a particular environment to their offspring. The transmission of genes can be distinguished from the transmission of environment by means of adoption studies. Unfortunately, there have been few such studies of handedness, where adoption had taken place early enough (before the age at which the direction of children's handedness is established). Carter-Saltzman (1980) showed that handedness of adopted children has no similarity with their adoptive parents, whereas the handedness of a control group showed a significant correlation with their biological parents. The same pattern was observed by Saudino & McManus (1998), although the sample size was again too small to distinguish properly between genetic and environmental components of variance.

The study of twins could clarify the relative contribution of genetic and environmental factors. Monozygotic twin pairs are significantly more likely to be concordant for handedness than dizygotic pairs

Table 1. Frequency of left-handers in families, according to maternal/paternal handedness and the sex of the offspring. (Combined results, adapted from McManus (1991). Numbers in parentheses indicate sample sizes (total 64 582). L, left; R, right.)

| parental handedness | | left-handed offspring | |
|---------------------|--------|-----------------------|---------------|
| father | mother | sons | daughters |
| R | R | 10.4% (30 268) | 8.5% (26 020) |
| R | L | 22.1% (1815) | 21.7% (1688) |
| L | R | 18.2% (2308) | 15.3% (2100) |
| L | L | 27.0% (215) | 21.4% (168) |

Table 2. Frequency of left-handed writers in families, according to maternal/paternal handedness and the sex of the offspring. (Adapted from McKeever (2000). Numbers in parentheses indicate sample sizes (total 2632). L, left; R, right.)

| parental handedness | | left-handed offspring | |
|---------------------|--------|-----------------------|---------------|
| father | mother | sons | daughters |
| R | R | 16.97% (3329) | 16.39% (3666) |
| R | L | 25.29% (340) | 21.52% (395) |
| L | R | 15.45% (382) | 20.51% (429) |
| L | L | 37.14% (35) | 44.83% (29) |

(Sicotte *et al.* 1999). Table 4 shows that dizygotic twins do not differ from binomial expectations in their hand preference, whereas monozygotic twins show more concordance than would be expected by chance. These data therefore suggest that there is a genetic contribution to handedness. However, discordance of handedness among monozygotic twins also raises the question of cultural influence on hand preference. Even if the genetic and cultural contributions to transmission of hand preference are not fully determined, these results provide convincing evidence for a significant heritability, allowing the action of natural selection on this trait.

(b) *Genetic models of handedness*

Some authors have developed completely non-genetic theories for the determinism of side preferences (e.g. Morgan & Corballis 1978; Provins 1997). However, there is extensive evidence against these theories. These theories are beyond the scope of this review.

Several authors have tried to build genetic models to account for the transmission patterns observed. Three major problems have arisen for determining a genetic aetiology of handedness: (i) cultural biases influence the practice of hand usage, (ii) despite identical genotypes, approximately 18 per cent of monozygotic twins are discordant for handedness and (iii) only 30–40% of children from LxL couples are left-handed. Models of handedness generally assume a genetic basis to both laterality and hemispheric asymmetry (Levy & Nagylaki 1972; Annett 1985; McManus 1991). Conventional Mendelian genetic models fail to fit the data. An important and influential study modified the conception of asymmetrical development: by breeding inbred strains of mice, Layton (1976) showed

Table 3. Sex-specific estimates of handedness heritability in three studies on UK university students. (Hull University (studies 1 and 2) and Open University (study 3). Left-handedness criterion: writing hand (studies 1 and 3) left hand preference for any one out of the 12 items (study 2). Data from Annett (1973, 1978).)

| parent | father | | | mother | | | | | | | | |
|-----------|------------------|------|--------|------------------|------|--------|------|------|------|------|------|------|
| | sex of offspring | | female | sex of offspring | | female | | | | | | |
| study | 1 | 2 | 3 | 1 | 2 | 3 | | | | | | |
| h^2 (%) | 17.4 | 16.8 | — | 3.5 | 31.9 | — | 56.6 | 42.3 | 79.2 | 51.1 | 58.3 | 46.5 |

Table 4. Number of different handedness combinations in monozygotic and same sex dizygotic twins. (Combined results, adapted from McManus (1991). L, left; R, right.)

| handedness | monozygotic | dizygotic |
|--|-------------|-----------|
| R–R | 2184 | 1951 |
| R–L | 629 | 585 |
| L–L | 87 | 53 |
| observed/expected discordant pairs (%) | 90.1 | 99.3 |

that in mice carrying a recessive allele known as the *iv* mutation in homozygous form, exactly half of the mice presented *situs inversus*, i.e. a reverse disposal of organs within the body. The *iv* mutation was thus responsible for a random right–left disposal of organs. This random genetic factor had a strong influence on subsequent models of genetic determinism of handedness.

Causal models involving a single gene with major effects have been proposed, most influentially Annett's 'right shift theory' and McManus' model, which are based on a single hypothesized gene with two alleles. Such models have to include a significant role for chance factors during development, setting a 50 per cent threshold on the possible prevalence of left-handedness in any population, to explain the low rates of left-handedness in the children of two left-handed parents and to solve the problem of the occurrence of monozygotic twins discordant for handedness. A few other simple genetic models have been proposed such as the X-linked three alleles model (McKeever 2004) or the random-recessive model (Klar 2003). Nevertheless, there are a number of observed associations that are difficult to accommodate within any simple genetic model. Segregation analysis of hand preference and hand use on 1818 nuclear Hawaii families failed to fit any fully genetic model of handedness determinism and suggested that handedness phenotypic variation could be 10–20% explained by genetic causes and 80–90% environmental (Ashton 1980). The failure of these simple genetic models to fit the data indicates that the genetic determinism of handedness is not simple and may imply several genes or other unidentified factors.

(c) Molecular studies

Genome-wide approaches have identified a few regions that could possibly be implied in handedness. Using 14 markers distributed on the X chromosome in 180 pairs of left-handed brothers, Laval *et al.* (1998) suggested linkage between one marker on the X chromosome (Xq21) and relative hand skill measured by questionnaire and the Annett Peg board test (Annett 1994).

The first genome-wide screen was performed by Francks *et al.* (2002) who carried out a study on 195 reading-disabled sibling pairs by using 401 markers. They identified two putative quantitative trait loci (QTLs) for relative hand skill (Peg board test) on chromosome regions 2p11.2–12 and 17p11–q23. The QTL located at 2p12–q11 was further confirmed in a study of left-handed brothers (Francks *et al.* 2003a) and showed a parent-of-origin effect (Francks *et al.* 2003b). In a study of 25 Australian nuclear families, Van Agtmael *et al.* (2003) found genetic linkage for handedness on chromosome region 10q26 using a laterality quotient computed from questionnaires. In 584 Mexican-Americans, Warren *et al.* (2006) identified a linkage signal for drawing and writing handedness, assessed by questionnaire, within chromosome region 12q21–23. Genomic regions identified to be linked to handedness differed among studies, probably due to differences in the measurement of handedness. This suggests that several genes could influence handedness. Therefore, large studies with better genome coverage are needed to clearly identify the genes implied in relative hand skills and hand preferences.

Empirical studies, as well as family studies, have thus shown that hand preference has an important genetic component. To further identify the selection pressures involved in this trait, we have also focused on the environmental factors that have been shown to have a substantial influence on handedness.

4. DEVELOPMENTAL FACTORS

There are several developmental factors implied in handedness in humans. The existence of associations between left-handedness and various health problems have often led to a distinction being made between *pathological left-handedness*, which would arise from developmental stresses and *familial left-handedness*, which would be due to genotype (Harris & Carlson 1988). This hypothesis considered that some people are left-handed because they have suffered different types of pathology. The explanation of Satz *et al.* (1985) for the increased (often twofold) frequency of left-handers in clinical populations with central nervous system disorders (e.g. schizophrenia, epilepsy, mental retardation or learning disabilities) was based on the claim that early brain insult may cause the individual to switch to the opposite hand for unimanual activities. Thereby, markers of any stressor or pathological factor disrupting normal development and inducing a switch in hand preference, regardless of mechanism, would be

expected to show itself in a higher percentage of left-handedness (Coren & Halpern 1991).

(a) *In utero environment*

Lateralized behaviour seemed to be expressed in early developmental stage and could thus be influenced by the *in utero* environment. At 9–10 weeks, the foetus begins to exhibit single arm movements: a majority (75%, $n=72$) exhibited a greater number of right arm movements, 12.5 per cent a greater number of left arm movements, and 12.5 per cent an equal number of left and right arm movements (Hepper *et al.* 1998). Similar results were also observed for foetuses from 12 to 27 weeks (McCartney & Hepper 1999). From 15 weeks of gestation, the foetus exhibits a preference for sucking its right thumb (Hepper *et al.* 1991) and the sucking behaviour at foetal state is related to hand preference at a later age (10–12 years; Hepper *et al.* 2005). From 38 weeks of gestation, the foetus shows a preference for having its head turned to the right relative to its body (Ververs *et al.* 1994).

Hormonal factors associated with the intrauterine environment are a proposed source of development of left-handedness (Geschwind & Galaburda 1985*a–c*). This theory is based on the assumption that prenatal sex hormones exert powerful influences on the central nervous system of the developing foetus. Specifically, high levels of testosterone during foetal development or heightened sensitivity to these prenatal hormones will disrupt neural development, causing a number of physiological changes, and also result in an increased likelihood of anomalous dominance, i.e. left-handedness and/or weak lateralization (Geschwind & Behan 1982; McManus & Bryden 1991). It has been hypothesized that the left hemisphere matures later than the right, so that it is at risk for a longer period of time, and therefore more likely to be affected by an adverse environment. High levels of prenatal testosterone would slow neuronal growth in the left hemisphere, hence weakening its relative control. This theory does not exclude genetic hypotheses, as testosterone levels *in utero* have a genetic component (Manning *et al.* 2000*a*).

According to the Geschwind–Behan–Galaburda theory, dyslexia, immune disorders and left-handedness are thought to share a common underlying factor: an elevated level of prenatal testosterone, which acts independently on both the thymus and the brain in the embryo. It also favours compensatory mechanisms, which may explain specific high talents associated with left-handedness (McManus & Bryden 1991).

Testosterone retards the growth of structures involved in immunity, such as the *bursa of Fabricius* in the chick embryo and post-natally, the thymus gland in the rat (McManus & Bryden 1991). Retardation of the immune system increases susceptibility to immune disorders, such as atopic disorders of childhood (asthma, eczema, hay fever). Numerous case control studies were performed to test the association between handedness and immune disorders. Populations of patients affected by an immune disorder (such as immune thyroid or gastrointestinal tract disorder, type I diabetes, Crohn's disease, ulcerative colitis, allergy, etc.) were compared with a control population for their handedness, which was affected with a related disorder

of non-immune origin. High testosterone levels also seem to be associated with birth complications and birth stress (McManus & Bryden 1991). The correlations between left-handedness and various diseases are unclear, as positive (Searleman & Fugagli 1987; Smith 1987; Tonnessen *et al.* 1993) and negative (Pennington *et al.* 1987) results were both published. Studies in the general population also have led to contradictory results. The Geschwind and Galaburda model therefore remains controversial.

It is difficult to directly test for the effect of prenatal testosterone in humans. However, Manning *et al.* (1998) have shown that the ratio of the length of the second and fourth digits (2D and 4D) in right hands is negatively correlated with adult testosterone levels in men. As digit ratios are fixed *in utero* it may be that the 2D : 4D ratio is associated with prenatal testosterone. Manning *et al.* (2000*b*) also examined the relationship between relative hand skill (left hand skill–right hand skill) and the 2D : 4D ratio in children. The difference in 2D : 4D ratio between the two hands (left hand ratio–right hand ratio) showed a strong relationship with relative hand skill: a high ratio for the left hand together with a low ratio for the right hand correlated with a higher left hand performance. Furthermore, Medland *et al.* (2005) showed that the number of CAG repeats in an androgen receptor located on the X-chromosome explained 24 per cent of the genetic variance of handedness (i.e. 6 and 10% of the total variance for females and males, respectively). This suggested that sensitivity to androgen hormonal sensitivity to could be involved in handedness. The influence of the *in utero* environment could thus result from heritable factors such as maternal or foetal hormonal secretion or sensitivity.

(b) *Developmental instability in early foetal development*

Based on polygenetic inheritance of factors that influence development, another approach suggesting that developmental instability underlies variation in handedness has been considered. Yeo & Gangestad (1993) presented two studies in which they observed an increased incidence of minor physical anomalies and fluctuating asymmetries (classic markers of developmental instability) in both left-handers and extreme right-handers. They reported evidence that the minimum developmental instability is near the median of the distribution for relative hand skill. They also successfully predicted that extreme right-handers are more apt to have left-handed parents than moderate right-handers, because they possess genotypes predisposed to developmental instability (Gangestad & Yeo 1997). They suggested that deviation from moderate right-handedness reflects imprecise expression of the developmental design due to developmental instability. Consistent with this, Galaburda (1991) noted that left-handers show greater brain symmetry and more reversed asymmetry than right-handers. Yeo & Gangestad (1993) suggested that individuals vary only in the genes that determine the precision with which a design for moderate right-handedness is expressed. No brain damage is hypothesized, only regional variations in foetal growth rates. Moreover,

their observations suggest that polygenic homozygosity, some particular human leukocyte antigen alleles, and the lack of pathogen resistance may be important factors underlying developmental instability. This developmental instability could thus have a genetic basis.

Left-handedness has been reported to be common in a variety of disorders that presumably reflect developmental abnormality. These include neural tube defects, autism (Dane & Balci 2007), psychopathy, cleft palate syndrome, stuttering (Dellatolas *et al.* 1990) and schizophrenia (Yeo & Gangestad 1993). However, it should be noted that negative results have also been reported (Bishop 1990). Coren & Searleman (1987) suggested that if an individual has been subjected to a birth stressor or an atypical intrauterine environment, and if the stressor is mild enough, left-handedness might just be a behavioural marker linked to a syndrome caused by minor abnormalities in neurological development.

(c) *Birth stress*

According to Bakan (1971), left-handedness results from perinatal left hemisphere neurological damage, due to an oxygen deficiency induced by birth stress (e.g. premature birth, prolonged labour, Rhesus incompatibility, breech delivery, multiple birth, respiratory distress syndrome, primiparity, maternal age). He argues that the change in hand preference may be a residual effect of birth trauma. He presents evidence that hypoxia is more common in difficult births and that the left hemisphere is more vulnerable to the effects of hypoxia than the right (Bakan *et al.* 1973). Indeed, there is an excess of left-handers in babies with a history of birth stress (Schwartz 1988; Williams *et al.* 1992), and in individuals with neurological impairments of diverse kinds. However, several reports failed to support this hypothesis (Hicks & Beveridge 1978; Hicks *et al.* 1978, 1979; Annett & Ockwell 1980; Coren & Porac 1980; Dusek & Hicks 1980; McManus 1981; Ashton 1982; Searleman *et al.* 1989).

Coren & Porac (1980) found a higher average age for the mothers of left-handed children and Smart *et al.* (1980) observed more left-handed than right-handed children for primiparous mothers aged 39 years or older. However, negative findings were also reported concerning maternal age (McManus 1981; Ashton 1982; Peters & Perry 1991). Twins, regardless of zygosity, have an elevated rate of left-handedness compared with singletons (Sicotte *et al.* 1999; Williams *et al.* 1992). This could be due to particular *in utero* conditions encountered in multiple birth pregnancies.

(d) *Birth weight*

It has been proposed that birth weight and its consequences may be the unifying causal factor of 'pathological left-handedness' (D. Nettle 2003, unpublished data, Newcastle University). Low birth weight is associated with perinatal complications, neurological problems and a number of adult pathologies. There is evidence for an excess of left-handedness among extremely low birth weight babies (O'Callaghan *et al.* 1987; Powls *et al.* 1996).

Low birth weight could play a key role in the health problems associated with left-handedness. The

mechanism that has been proposed most frequently to explain an association between left-handedness and low birth weight involves early brain damage. Indeed low birth weight greatly increases the risk of early brain damage (Stewart *et al.* 1999). An alternative possibility is that foetal brain development is interrupted by birth (O'Callaghan *et al.* 1987). Thus, small or premature babies would have reached a different stage of cortical growth than heavier or full-term ones. Specifically, posterior left hemisphere structures such as the planum temporale tend to be larger than their counterparts on the right in right-handers, whereas in left-handers, these posterior asymmetries are more often absent (Habib *et al.* 1995). Structural asymmetries of the brain appear *in utero* (Chi *et al.* 1977), and are statistically related to hand preference (Beaton 1997), although this relationship between brain asymmetries and handedness is not strict.

If there really are two distinct groups of left-handers, one of pathological origin due to low birth weight, and another of familial origin, then there should be a tendency for bimodality in the birth weight distribution of left-handers. This predicts a lower overall birth weight for left-handers and a greater variance in birth weight for left-handed as opposed to right-handed individuals that should be investigated.

Although developmental and perinatal problems can be partly due to environmental conditions, they are significantly heritable (e.g. Cai *et al.* (2007) for birth weight or Moller & Thornhill (1997) for developmental instability), indicating a genetic contribution. Their link with left-handedness therefore represents a negative selection pressure.

5. CULTURAL INFLUENCE

Environmental factors could also exert selection forces on left-handers. Laland *et al.* (1995) criticized the fact that none of the most often cited models of handedness incorporate cultural influences on handedness, despite widespread evidence of their importance. Attitudes towards left-handedness vary from one culture to another (Needham 1973; Teng *et al.* 1976; Harris 1992; Bryden *et al.* 1993; Mandal *et al.* 1999). Cultural and environmental factors could change hand preference in three ways, which correspond to different degrees and types of pressure by: (i) changing the hand used for some activities (e.g. writing, eating), with no change for other unimanual activities, (ii) reducing the degree of hand preference, when weak pressure applies to all hand actions, or (iii) changing the overall preferred hand, when strong pressure applies to all hand actions.

- (i) Dellatolas *et al.* (1988) observed an increase in the frequency of left hand use for writing in France ('generation' effect), showing clearly that the educational attitude towards left hand writing has significantly changed in France during the second half of the twentieth century. The same phenomenon has been observed in other countries (e.g. Italy: Salmaso & Longoni 1985; Brazil: Berdel Martin & Barbosa Freitas 2003). Studies of school children in China and

Taiwan have found that only 3.5 and 0.7% used their left hand for writing (Teng *et al.* 1976). This contrasts with a 6.5 per cent figure for Asian school children living in the United States, where cultural pressures have been reduced (Hardyck *et al.* 1976). In two African countries (Ivory Coast and Sudan), the target activity against left hand use was eating and there remains strong cultural pressure for this activity (De Agostini *et al.* 1997). In Japan, the proportion using the left hand for writing and eating are only 0.7 and 1.7%, respectively (Shimizu & Endo 1983), again suggesting strong cultural pressures. Coren (1992) reported a reduction of the degree of hand preference as a consequence of environmental influences: subjects who reported attempts to change handedness (by parents, teachers) could switch their hand preference for the targeted tasks. However, he also noted that this cultural influence on one particular task (e.g. writing or eating) did not condition hand preference for other tasks.

- (ii) De Agostini *et al.* (1997) showed that the proportion of subjects with weak handedness is higher among those who reported earlier injuries causing a temporary shift of hand use. Bryden *et al.* (1993) also observed that positive reinforcement for right hand use can modify patterns of handedness, and alter the relationships among different handedness tasks.
- (iii) Bryden *et al.* (1993) suggested that the Tucano of Amazonia successfully modify preference at an early age through positive reinforcement, and that this switched preference is manifested in all unimanual activities.

Mikheev *et al.* (2002) have found that highly qualified right-handed judo wrestlers more frequently preferred to perform certain judo movements with the left hand than right-handed controls. They suggest that during motor skill acquisitions (long-term judo training), lateral preferences are modified through neuroplastic development. However, an alternative hypothesis to consider is that less asymmetry is advantageous in judo and so that individuals with low asymmetry are more likely to become qualified judo wrestlers.

Genetic, developmental and environmental components have been identified to be involved in hand preference determinism. Hand preference has been shown to be heritable and variable across populations, suggesting that evolutionary processes are acting on this trait.

6. EVOLUTIONARY FORCES ACTING ON THE POLYMORPHISM OF HANDEDNESS

The variation in morph frequencies for a given trait is essential to characterize the selective forces involved. A polymorphism maintained in all populations of a given species is a rare case. It can happen for a neutral trait, but is easily lost by genetic drift, so that at least some populations lose the polymorphism. The fact that the polymorphism of handedness is maintained in all

human populations suggests that handedness is not a neutral trait, and that some selective forces are maintaining this diversity. Directional selection, if acting alone, would lead to the fixation of the advantageous morph, and eliminate the polymorphism. The ancient and ubiquitous polymorphism observed for handedness is thus a signal of balancing selection acting on this trait. This balancing selection could result from a situation-dependent benefit. Hence, we tried to identify, in the existing publications, the deleterious and advantageous traits associated with left-handedness, as they could, respectively, represent fitness costs and benefits playing a relevant evolutionary role.

(a) *Left-handedness as a costly trait*

The frequency of left-handers has been reported to vary according to age classes (Porac *et al.* 1980; Gilbert & Wysocki 1992). This could be interpreted as due to changing patterns of social norms (Hugdahl *et al.* 1993): for example, writing handedness was submitted to more social pressures in the past than in the present (Dellatolas *et al.* 1988). As a consequence, studies using hand preference for writing as the marker of handedness will find that mean age at death is lower for left-handers, even if the longevity of left- and right-handers was actually the same. Nevertheless, even when hand preference assessment was based on other tasks, longevity has been shown to be reduced in left-handers, from a few months to a few years (Halpern & Coren 1988, 1991; Coren & Halpern 1991; Aggleton *et al.* 1993), but some contradictory evidence also exists (Wood 1988; Anderson 1989; Harris 1993; Hicks *et al.* 1994; Berdel Martin & Barbosa Freitas 2003).

Three factors may explain the reduced longevity of left-handers: (i) prenatal and perinatal birth stressors, more probable in left-handers, (ii) genetic effects and intrauterine hormones may have reduced the effectiveness of the immune system of left-handers, and (iii) left-handers may have more lethal accidents. However, fitness costs have not been directly measured yet, so we are still unable to properly evaluate its evolutionary significance.

Concerning the accidental mortality, a higher risk of accidents for left-handers has been observed in Western societies (Halpern & Coren 1991; Daniel & Yeo 1994), probably due to the industrialized environment designed for a right-handed majority (Porac & Coren 1981; Coren & Halpern 1991). As shown by Aggleton *et al.* (1993), an important part of the difference in lifespan between left- and right-handers is due to accidental death and death in warfare. According to Aggleton *et al.* (1993), the most likely explanation for the increase in accidental death among left-handed men concerns their need to cope in a world full of right-handed tools, machines and instruments. The fact that a difference still remained, after removal from the sample of the known cases of accidental death, suggests, however, that some other factor may produce a left-handed disadvantage. However, it is also possible that the sources used did not mention all the cases of unnatural death. Interestingly, De Agostini *et al.* (1997) suggested that injury on upper limbs that made a person unable to use the preferred hand could lead to

mixed handedness and create an association between accident frequency and mixed handedness. In a study on 556 dead Brazilians, Berdel Martin & Barbosa Freitas (2003) pointed out that dextral and not sinistral individuals manifested an increased vulnerability to accidental death. Further investigations on these aspects are thus needed with reliable information on death causes and birth cohort. The importance of survival before and during the reproductive period of life for the fitness of an individual is clear. Moreover, there is now clear evidence that survival beyond menopause is of great importance for women's reproductive value (Lahdenperä *et al.* 2004). Unfortunately, the link between life expectancy and handedness has as yet only been reliably investigated for men. The impact of longevity on human fitness is not fully characterized. The importance of reduced longevity in left-handedness evolution is thus still unclear.

Another cost for left-handers resides in the lower body size observed for left-handers (Coren 1989b; Fudin *et al.* 1994). This could have fitness consequences as body size is an important component of selective value in humans (Guégan *et al.* 2000; Nettle 2002b; Silventoinen *et al.* 2003). For males, it is clearly established that height is correlated with reproductive success (Pawlowski *et al.* 2000; Mueller & Mazur 2001; Nettle 2002a). Coren *et al.* (1986) also showed that an association between delay in physical maturation (based on the onset of secondary sexual characteristic, age of menarche and relative body size) and left-handedness (see Eaton *et al.* (1996) for contradictory results). A delay in sexual maturity could also have an influence on reproductive success and thus lead to some fitness cost for left-handers. Further investigations are needed to quantify the influence of this factor.

The frequency of left-handers among homosexual men seemed to be higher than in the general population: in their meta-analysis, Lalumiere *et al.* (2000) reported 39 per cent greater chance of being non-right-handed. As reproductive success has been shown to be lower for homosexual men, this could introduce some fitness bias (Berman 2003). However, the association between handedness and sexual orientation is still being discussed (Bogaert *et al.* 2007), and the proportion of homosexual men in the general population is low: from 2 to 6 per cent of males in the general population, depending on the study (Kinsey *et al.* 1948; Sandfort 1998; Berman 2003). Therefore, the effect of this association has probably a low influence on the evolution of handedness frequencies.

Some potential fitness costs are thus suggested by the literature, but proper estimation of the actual consequences on fitness are not yet identified, limiting the evolutionary significance of these results.

(b) *Left-handedness as a beneficial trait*

It was shown that left-handers could have greater intermanual coordination (Gorynia & Egenter 2000; Judge & Stirling 2003). Left-handers have indeed smaller asymmetries in hand skills than right-handers (Peters 1989; Curt *et al.* 1992; Judge & Stirling 2003) and are less lateralized in language dominance (Steinmetz *et al.* 1991). Smaller right-left differences as well as higher intermanual coordination in left-handers

may be due to greater control of both hemispheres. There are contradictory results but some studies point to better interhemispheric transfer in non-right-handers (Gorynia & Egenter 2000; Christman & Propper 2001). A larger *corpus callosum* has been detected in non-right-handers (Witelson 1985), but the precise implications for interhemispheric interaction are unclear. Moreover, there is considerable controversy about the relation to handedness: the degree of hand lateralization rather than its direction may be related to callosal morphology (Beaton 1997). This is supported by the finding that left-handers, who are less lateralized show significantly higher values than right-handers in intermanual coordination, a performance thought to be more demanding in terms of bihemispheric control, and that may be due to a more efficient exchange of information transmitted by callosal pathways (Gorynia & Egenter 2000). A larger *corpus callosum* has also been reported to be associated with superior verbal fluency (Hines *et al.* 1992) or to confer advantages in some forms of memory (Christman & Propper 2001); two advantages from which left-handers could benefit.

Creativity has also been reported to be linked with left-handedness (Newland 1981), more specifically in men (Coren 1995). The proportion of left-handers also appeared to be greater in gifted children (IQ > 131) than in non-gifted children (Hicks & Dusek 1980), but the importance of this effect at the population level remains to be quantified, owing to the low proportion of gifted children. A few studies have considered that left-handers could have special talents that could lead to benefits, such as enhanced musical (Aggleton *et al.* 1994; Kopiez *et al.* 2006) or mathematical capacities (Casey *et al.* 1992; Crow *et al.* 1998), although this last fact seems controversial (Peters 1991). All these advantages may play a significant role in the social status of left-handers.

Some studies concerning socio-economic status and cognitive abilities have tried to estimate differences in social status between right- and left-handers (see Faurie *et al.* (2008) for a review). Left-handers are supposed to have particular cognitive capacities that could lead them to particular kinds of professional activities. Faurie *et al.* (2008) highlighted that left-handers could have some particular socio-economic positions, which could lead to a socio-economic advantage. A few studies have compared the earnings of right- and left-handers. Denny & O'Sullivan (2007) revealed that the hourly earning of left-handed men was greater (approx. 4%) and observed an opposite result for right-handed women. Ruebeck *et al.* (2007) also found a significant increase of wage for left-handed men in the group with high levels of education and did not observe any effect of handedness on wages for women. The differences between right- and left-handers socio-economic statuses could be related to their reproductive success, though the importance of socio-economic status in human mate choice directly benefits the offspring.

Another important benefit of left-handedness could be represented by a strategic advantage of left-handers in sports: a number of studies have noted an excess of left-handers at the top levels of sports such as tennis,

baseball and fencing (Annett 1985; Voracek et al. 2006). The left-handed advantage in many sports can be explained tactically without any hypothetical additional neurological advantage (Wood & Aggleton 1989). As right-handers are more frequent, an individual is always more likely to be confronted by a right-handed opponent, so right-handers are not used to the different gestures of left-handers, whereas left-handers are used to the right-handers way of playing. Thus, left-handers have a surprise advantage, which increases when their frequency is lower (Raymond et al. 1996). Left-handedness frequencies in interactive sports (such as fencing, boxing, tennis, baseball, cricket), offering a strategic advantage to the rarer left-hander, appear to be very high, when compared with non-interactive sports (gymnastics, swimming, bowling), where the frequencies are no different from those of the general population (Aggleton & Wood 1990; Goldstein & Young 1996; Raymond et al. 1996; Grouios et al. 2000; Brooks et al. 2003). This strategic advantage of left-handers in interactive sports could be a marker of a strong selective advantage during fights. This advantage in fights could indeed lead to direct benefit through increased survival during fighting interaction or indirect benefit through acquisition of higher social status, facilitating access of partners. It is negatively frequency dependent because it is higher when the left-handers are rarer. Theoretical approaches have confirmed that the maintenance of two opposite asymmetrical morphs by frequency-dependent selection could be an evolutionary stable strategy (Ghirlanda & Vallortigara 2004; Faurie et al. 2005a). The frequency-dependent strategic advantage of left-handers in fights could be the source of balancing selection involved in the persistence of the handedness polymorphism in the general population.

7. DISCUSSION

The existence of frequency-dependent selection acting on handedness has been suggested by the correlation observed between the frequency of left-handers and the rate of homicide, indicating a frequency-dependent advantage of left-handers in violent interactions (Faurie & Raymond 2005). However, in the absence of any cost, a frequency-dependent advantage would lead to a frequency of 50 per cent at equilibrium. The fact that the frequency of left-handedness never reaches 50 per cent in any human population investigated so far (Faurie et al. 2005b; Raymond & Pontier 2004) indicates that some costs associated with left-handedness must exist.

The costs associated with left-handedness have mainly been studied in Western societies, and have often been attributed to the technological environment with asymmetrical artefacts being dangerous for left-handers (Coren 1989a; Aggleton et al. 1993; Daniel & Yeo 1994). However, the frequency of left-handers does not exceed 30 per cent in any traditional society, suggesting the existence of costs in non-industrialized environments as well (Faurie & Raymond 2005).

There seem to be increased health risks and problems among left-handers. It still remains to be established whether these are characteristic of all left-handers, or of a subgroup whose left-handedness is of the pathological

type. The problem is that 'pathological' and 'familial' left-handers, if these two categories exist, cannot in fact be distinguished, since no gene of major effect has been identified, whose presence could be tested for. The alleles in single-gene models are postulated from an *ad hoc* assumption, rather than on the basis of empirical genetic data. An indication of the probable heterogeneity of left-handers is the lateralization of language. Although 97 per cent of right-handers demonstrate predominant left hemisphere language localization, only 60 per cent of left-handers demonstrate left hemisphere language dominance, 30 per cent show bihemispheric language and approximately 10 per cent show right hemisphere language (Geschwind 1970; Annett 1985). Precise characterization of categories of left-hander should help the understanding of the evolution of handedness.

To be able to identify the evolutionary forces acting on handedness, data on left-handedness frequency dynamics over time are critical. Writing handedness has been shown to vary during the twentieth century, due to cultural influences. For hand preference in other tasks, there are surprisingly few studies addressing this question. Comparison of arm waving in Victorian England films (1897 and 1913) and in a modern population, from Google images, suggested that left-handers frequency has increased in England during the last century (McManus & Hartigan 2007). However, the reliability of these data are questionable, especially because arm waving is not a complex task needing hand specialization. Further investigation of left-handedness frequency across generations is needed to establish if the left-handed polymorphism is variable or at equilibrium.

If the polymorphism of handedness is nearly stable, it would be very unlikely to empirically detect variations of fitness estimates because differences between left- and right fitness are expected to be low near the equilibrium value. In fact, at the equilibrium value, the fitness of right- and left-handers is equal (although this does not mean that all fitness components are necessarily equal). In such a case, some advantages for one trait could be found for one handedness category, and other advantages for other traits for another handedness category. This could explain many discrepancies in handedness studies.

What is currently lacking is a way to clearly identify the left-hander categories in order to better estimate fitness costs and benefits associated with each category. It is also pivotal to further investigate the possible current evolution of left-handedness frequencies, and to examine, in different environments, the type of selection, particularly frequency dependent, acting on handedness.

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