Research Journal of Biological Sciences 5 (1): 36-41, 2010
ISSN: 1815-8846

Evolutionary Back Grounds of Human Left Handedness

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Abstract: It has been reported the coexistence of both right and left-handed individuals at least since the Upper Paleolithic. There is still today a polymorphism of handedness in humans, in all populations. Left-handers are in the minority and left-handedness seems to be associated with several fitness costs, such as poorer health, lower height or reduced longevity. In this context, the persistence of the polymorphism is interesting and suggests that left-handedness must be associated with enhanced abilities. In humans, it has been proposed that the polymorphism of handedness is maintained by negative frequency-dependent selection (advantage being greater when the frequency of a trait is lower). The frequency-dependent advantage of left-handers in physical fights is strongly suggested by both the study of interactive sports in industrialized societies and a cross-cultural comparison of traditional societies. In western societies, left-handers are supposed to have a socio-economic status advantage. The differences between right and lefthanders 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.

Key words: Left-handedness, polymorphism, offspring, traditional socities, poorer health, Iran

INTRODUCTION

In western societies today, about 90% of the adult population is said to be right-handed with the remaining 10% consisting of persons variably identified as left-handed, ambidextrous and/or ambiguously handed (McManus, 2002; Soper *et al*., 1986).

A left handed person is a one who uses his left hand for major motor activities such as throwing a ball. However, these people can also use their right hand for fine motor activities such as writing, eating, etc. A pure lefty would be one that uses their left hand for all activities. Therefore, writing is not always the correct way to determine if one is left handed or right handed (Belth, 2008). For research purposes, handedness can be determined by asking people (usually by means of a questionnaire) which hand they use for a number of activities. In the general population, the scores on a handedness questionnaire result in a J-shaped distribution with a small peak of extremely left-handed individuals, ambidexter individuals in the middle and a large peak of extremely right-handed individuals (Van Strien *et al*., 2005). Genetic, biological and environmental models have been proposed to explain the population-level left-handedness. That genetic factors may play a role is supported by the observation that approximately 70% of individuals born to two left-handed parents are right-handed which is significantly lower than the proportion of right-handed individuals born to two right-handed parents (McGee, 1980; McManus and Bryden, 1992; Hopkins and Dahl, 2000). McManus (1991) claims that left-handedness is caused by a recessive allele which cancels out the pre-existing bias to the right. He believes that this recessive allele persists because it bestows left-handers with some cognitive advantages. Another model has been suggested by Annett (1985). She also believes that left-handedness is caused by a recessive allele. In this case, however, she believes that the allele persists because of a heterozygous advantage. Thus, individuals with a RS þ (right shift) and a RS-allele will have superior cognitive ability. Therefore, Annett's model would predict that lefthanders have no special advantage. In fact, because they are homozygous for the RS allele, they will be at a disadvantage (Faurie *et al*., 2008).

Some have suggested that prenatal sex hormones such as estrogen (Hines, 1982) and testosterone (Geschwind and Galaburda, 1985) can differentially affect the development of each cerebral hemisphere (Wisniewski, 1998; Hopkins and Dahl, 2000). The elevated levels of T *in utero* were hypothesised to slow down the growth of the left brain with a consequent compensatory growth of the right brain. This would in turn, decrease the degree of naturally occurring dominance of the left brain and increase the dominance of the right brain and would cause a weakening of

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right-handedness towards left-handedness (Tan and Tan, 2001). Delayed growth in the left hemisphere as a result of testosterone would account for the greater frequency of left-handedness in males (Geschwind and Behan, 1982). This theory does not exclude genetic hypotheses, as testosterone levels in utero have a genetic component (Llaurens *et al*., 2009). Here the researchers review the literature available regarding the eventual evolutionary mechanisms and consequences of left-handedness. In this study, the researchers report the information on fitness costs and benefits acting as selective forces on the proportion of left-handers. Further, the researchers try to determinate the evolutionary back grounds of human handedness included left-handedness as an adaptive character and explain the significance of negative frequency dependent selection as an important evolutionary mechanism involved in persistence of handedness polymorphism. Right and left-handers have coexisted at least since the Upper Palaeolithic (Faurie and Raymond, 2004) and left-handers are in the minority in all human populations (Raymond and Pontier, 2004). The persistence of the polymorphism of handedness requires an explanation because this trait is substantially heritable (Francks *et al*., 2002; McKeever, 2000; McManus, 1991; Sicotte *et al*., 1999) and several fitness costs are associated with left-handedness such as a lower height or a reduced longevity (Aggleton *et al*., 1993; Coren and Halpern, 1991; Gangestad and Yeo, 1997; McManus and Bryden, 1991; Faurie *et al*., 2005). Countervailing their costs the persistence of the polymorphism is interesting and suggests that left-handedness must be associated with some benefits (Faurie and Raymond, 2005).

Handedness in the past: Handedness in ancient humans has been inferred by analysis of archaeological samples from skeletons, stone tools and various other artifacts (Llaurens *et al*., 2009). Several studies indicate that the coexistence of both right and left-handed individuals has been maintained for a long time in hominids. The oldest undisputed evidence is from the middle (ca. 425,000-180,000 YBP) and early upper Pleistocene (upper Pleistocene was 180,000-10,000 YBP), where marking on incisors indicates the existence of *Homo neanderthalensis* individuals who were right or left handed for sharp tool manipulation while slicing meat held between the front teeth and the other hand (Bermudez de Castro *et al*., 1988; Lalueza and Frayer, 1997). In the *Homo sapiens* taxon, indications of handedness polymorphism come from studies of stone artefacts, holemaking rotation movements in wood and wear marks on spoons (e.g., Paleolithic: Keeley (1977) and Westergaard and Suomi (1996); Neolithic: (Faurie and Raymond, 2004). 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 (Steele and Uomini, 2005). 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 (Llaurens *et al*., 2009).

MATERIALS AND METHODS

Negative frequency selection as the most acceptable explanation for left-handedness maintenance: 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 (Llaurens *et al*., 2009). A polymorphism for a non-neutral trait can be observed in a population when there is a balance of selective forces. This can occur either if this trait is under frequency-dependent selection or if there is a spatial or temporal heterogeneity of selective pressures (Smith, 1989). If different values of the trait are associated to a frequency-dependent selective cost or advantage then stable coexistence will result. The most widespread and dramatic genetic polymorphism that of sexual dimorphism is certainly maintained by negative frequency-dependent selection (advantage being greater when the frequency of a trait is lower) (Vallortigara and Rogers, 2005; Ghirlanda and Vallortigara, 2004). Negative frequency-dependent selection is a potentially important process in the maintenance of genetic variation in fitness traits (Faurie *et al*., 2005).

Some costs associated with left handedness: In the absence of any cost, a frequency-dependent advantage would lead to a frequency of 50% at equilibrium. The fact that the frequency of left-handedness never reaches 50% in any human population investigated so far (Faurie *et al*., 2005; Raymond and 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 lefthanders (Aggleton *et al*., 1993). Longevity has been shown to be reduced in lefthanders, from a few months to a few years (Coren and Halpern, 1991; Aggleton *et al*., 1993). Left-handers may have more lethal accidents. However, the frequency of left-handers does not exceed 30% in any traditional society suggesting the existence of costs in non-industrialized environments as well (Faurie and Raymond, 2005).

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 and Balci, 2007), psychopathy, cleft palate syndrome, stuttering (Dellatolas *et al*., 1990) and schizophrenia (Yeo and Gangestad, 1993). 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 (Llaurens *et al*., 2009). There are studies that support the hypothesis that the fetal thymus controls development of lymphocytes which are responsible for recognition of self-antigens and thus, for prevention of autoimmunity. Suppression of thymic growth during fetal life might therefore favor the development of autoimmunity in later life (Geschwind and Behan, 1982). Ramadhani (2006) in a large prospective cohort study provide evidence for a substantially increased breast cancer risk among left-handed women. The connection between hand preference and breast cancer risk may lie in a common origin of intrauterine hormonal exposure.

Left-handedness as a beneficial trait: The frequency of left-handers is expected to be higher in societies where physical fights are frequent and violent. Indeed, the frequency of left-handers has been shown to be positively correlated with the rate of homicides in traditional societies (Faurie and Raymond, 2004). As lefthanders are less frequent, one is more likely to be confronted with a right-handed opponent in a physical fight. Left-handers would thus be more accustomed to right-handed competitors than vice versa. Therefore, they might enjoy a negatively frequency-dependent strategic advantage in fights when rare, relative to right-handers. This frequency-dependent superiority of left-handers in interactive contests would confer them fitness advantages, directly and indirectly. It could have historically influenced survival but also social status and reproductive success (Archer *et al*., 1995; Chagnon, 1988; Hill, 1984). The action of a negative frequency-dependent advantage of left-handers in physical fights is strongly suggested by the study of interactive sports which can be considered as a form of fighting interaction. The advantage in interactive sports could have some importance in western societies where it has been shown that student athletes have a higher number of sexual partners (Faurie and Raymond, 2004; Faurie *et al*., 2005). 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 and Wood, 1990; Goldstein and Young, 1996; Raymond *et al*., 1996; Grouios *et al*., 2000; Brooks *et al*., 2003; Laurens *et al*., 2009).

It is considered that left-handers are more intelligent than right-handers because of different abilities which naturally exist in them. Although, some studies proved that the average intelligence of left handers is fractionally lower than that of right handers, at the top end of the intellectual spectrum they do better (McManus, 1997). Typically, left handed people are seen to be more creative, more likely to notice the size, shape and form of things, more likely to see the whole picture or concept. All these in amalgamated form show that left-handers have more power of perception as compared to right-handers (Ghayas and Adil, 2007). Some studies point to better interhemispheric transfer and a larger corpus callosum in non-right-handers. 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 larger corpus callosum has also been reported to be associated with superior verbal fluency or to confer advantages in some forms of memory; two advantages from which left-handers could benefit (Llaurens *et al*., 2009).

Faurie *et al*. (2008) reveal a complex association between handedness and socioeconomic status. They found that left-handedness frequency is significantly higher among women of higher educational level, among categories of higher income and among individuals who have a higher position in the company. An association between handedness and socio-economic status could be due to possible differences in cognitive abilities. Another possibility is that socio-economic status and hand preference may be related through cultural influences. Left-handers have higher average incomes and their incidence has been found to be very high in some social categories as artists and musicians (Quinan, 1922), mathematicians (Annett and Manning, 1990; Peters, 1991) and sport competitors (Raymond *et al*., 1996).

The extent to which the reproductive advantage of these categories (Faurie and Raymond, 2004) contributes to persistence of the polymorphism remains to be formally investigated.

RESULTS AND DISCUSSION

Handedness considered as an adaptive character: In the theory presented by Corballis, handedness is described as a neutral character. Right-handedness is regarded as a direct consequence of the left-hemisphere dominance for vocalization.

Corballis seems to have not considered two points: the importance of direct selection pressures for the evolution of handedness, the evolutionary significance of the polymorphism of handedness. It is however, difficult to consider handedness as a neutral character. For most manual tasks, especially those tasks involved in competitive activities, increasing performance by the specialization of one hand is certainly adaptive. Aggressive interactions are responsible for fundamental selection pressures acting during primate and human evolution. The higher prevalence of right-handedness might well be due to a previously existing cerebral bias. But the specialization of one forelimb leading to right or left-handedness is better viewed as the result of natural selection.

The second problem that is not tackled by Corvallis's theory is the existence of a polymorphism of handedness. Left handedness is associated with several fitness costs but the persistence of an apparently stable proportion of left-handers implies the balancing of these costs by some advantage. One of the observed costs is the smaller size and weight of lefthanders (O'Callaghan *et al*., 1987). Size is a component of the reproductive value, at least in males (Mueller and Mazur, 2001; Pawlowski *et al*., 2000). However, smaller size and weight is probably not a disadvantage in weapon fights. When weapons were prevalent in hominids, the weight (and probably height) disadvantage of left-handers in fights was considerably reduced.

The persistence of the polymorphism of handedness might well be partly explained by an advantage of left-handers in weapon manipulation and fights. This polymorphism, as well as handedness itself, needs to be understood in the view of adaptation and natural selection (Faurie and Raymond, 2003).

REFERENCES

Aggleton, J.P. and C.J. Wood, 1990. Is there a left-handed advantage in ballistic sports. Int. J. Psychol., 21: 46-57.

Aggleton, J.P., R.W. Kentridge and N.J. Neave, 1993. Evidence for longevity differences between left handed and right handed men: An archival study of cricketers. J. Epidemiol. Commun. Health, 47: 206-209.

Annett, M. and M. Manning, 1990. Arithmetic and laterality. Neuropsychologia, 28: 61-69.

Annett, M., 1985. Left, Right, Hand and Brain: The Right Shift Theory. LEA Publishers, London.

Archer, J., R. Holloway and K. McLoughlin, 1995. Self-reported physical aggression among young men. Aggress. Behav., 21: 325-342.

Beaton, A.A., 1997. The relation of planum temporal asymmetry and morphology of the corpus callosum to handedness, gender and dyslexia: A review of the evidence. Brain Lang., 60: 255-322.

Belth, A., 2008. Causes of Left-Handedness. Edward A. Sherman Publishing Co. Inc., Island.

Bermudez de Castro, J.M., T.G. Bromage and Y.F. Jalvo, 1988. Buccal striations on fossil human anterior teeth: Evidence of handedness in the middle and early Upper Pleistocene. J. Hum. Evol., 17: 403-412.

Brooks, R., L.F. Bussiere, M.D. Jennions and J. Hunt, 2003. Sinister strategies succeed at the cricket World Cup. Cup. Proc. R. Soc. B., 271: S64-S66.

Chagnon, N.A., 1988. Life histories, blood revenge and warfare in a tribal population. Science, 239: 985-992.

Coren, S. and D.F. Halpern, 1991. Left-handedness: A marker for decreased survival fitness. Psychol. Bull., 109: 90-106.

Dane, S. and N. Balci, 2007. Handedness, eyedness and nasal cycle in children with autism. Int. J. Dev. Neurosci., 25: 223-226.

Dellatolas, G., I. Annesi, P. Jallon, M. Chavance and J. Lellouch, 1990. An epidemiological reconsideration of the Geschwind–galaburda theory of cerebral lateralization. Arch. Neurol., 47: 778-782.

Faurie, C. and M. Raymond, 2003. Handedness: Neutral or adaptive. Behav. Brain Sci., 26: 220-220.

Faurie, C. and M. Raymond, 2004. Handedness frequency over more than 10,000 years. Proc. Biol. Sci., 271: S43-S45.

Faurie, C. and M. Raymond, 2005. Handedness, homicide and negative frequency-dependent selection. Proc. R. Soc. London B, 272: 25-28.

Faurie, C., S. Billiard and M. Raymond, 2005. Maintenance of handedness polymorphism in humans: A frequency-dependent selection model. J. Theor. Biol., 23: 85-93.

Faurie, C., S. Bonenfant, M. Goldberg, S. Hercberg, M. Zins and M. Raymond, 2008. Socio-economic status and handedness in two large cohorts of French adults. Br. J. Psychol., 99: 533-554.

Francks, C., S.E. Fisher, I.L. MacPhie, A.J. Richardson, A.J. Marlow, J.F. Stein and A.P. Monaco, 2002. A genomewide linkage screen for relative hand skill in sibling pairs. Am. J. Hum. Genet., 70: 800-805.

Gangestad, S.W. and R.A. Yeo, 1997. Behavioral genetic variation, adaptation and maladaptation: An evolutionary perspective. Trends Cogn. Sci., 1: 103-108.

Geschwind, N. and A.M. Galaburda, 1985. Cerebral lateralization: Biological mechanisms, associations and pathology: I. A hypothesis and a program for research. Arch. Neurol., 42: 428-459.

Geschwind, N. and P.O. Behan, 1982. Left-handedness: Association with immune disease, migraine and development learning disorder. Proc. Natl. Acad. Sci. USA., 79: 5091-5100.

Ghayas, S. and A. Adil, 2007. Effect of handedness on intelligence level of students. J. Indian Acad. Applied Psychol., 33: 85-91.

Ghirlanda, S. and G. Vallortigara, 2004. The evolution of brain lateralization: A game theoretical analysis of population s tructure. Proc. R. Soc. London B., 271: 853-857.

Goldstein, S.R. and C.A. Young, 1996. Evolutionary stable strategy of handedness in major league baseball. J. Comp. Psychol., 110: 164-169.

Grouios, G., H. Tsorbatzoudis, K. Alexandris and V. Barkoukis, 2000. Do left-handed competitors have an innate superiority in sports. Percept. Mot. Skills, 90: 1273-1282.

Hill, J., 1984. Prestige and reproductive success in man. Ethol. Sociobiol., 5: 77-95.

Hines, M., 1982. Prenatal hormones and sex differences in human behavior. Psychol. Bull., 92: 56-80.

Hopkins, W.D. and G.F. Dahl, 2000. Birth order and hand preference in chimpanzees (*Pan troglodytes*): Implications for pathological models of handedness in humans. J. Comp. Psychol., 114: 302-306.

Keeley, L.H., 1977. The functions of paleolithic flint tools. Sci. Am., 237: 108-126.

Lalueza, C. and D.W. Frayer, 1997. Non-dietary marks in the anterior dentition of the Krapina neanderthals. Int. J. Osteoarchaeol., 7: 133-149.

Llaurens, V., C. Faurie and M. Raymond, 2009. Why are some people left-handed: An evolutioanry perspective. Phil. Trans. R. Soc. London B., 364: 881-894.

McGee, M.G., 1980. Population genetic analysis of human hand preference: Evidence for generation differences, familial resemblance and maternal effects. Behav. Genet., 10: 263-275.

McKeever, W.F., 2000. A new family handedness sample with findings consistent with X-linked transmission. Br. J. Psychol., 91: 21-40.

McManus, I.C. and M.P. Bryden, 1992. The genetics of handedness, cerebral dominance and lateralization. Handbook Neuropsychol., 6: 115-144.

McManus, I.C. and M.P. Bryden, 1991. Geschwind's theory of cerebral lateralization: Developing a formal, causal model. Psychol. Bull., 110: 237-253.

McManus, I.C., 1991. The inheritance of left-handedness. Ciba Found. Symp., 162: 251-281.

McManus, I.C., 1997. Psychology in the Perspective. 2nd Edn., Addison Wesley Longman Inc., New York.

McManus, I.C., 2002. Right Hand Left Hand: The Origins of Asymmetry in Brains, Bodies, Atoms and Cultures. Harvard University Press, Cambridge, MA.

Mueller, U. and A. Mazur, 2001. Evidence of unconstrained directional selection for male tallness. Behav. Ecol. Sociobiol., 50: 302-311.

O'Callaghan, M.J., D.I. Tudehope, A.E. Dugdale, H. Mohay, Y. Burns and F. Cook, 1987. Handedness in children with birth weights below 1000 g. Lancet, 1: 1155-1155.

Pawlowski, B., R.I.M. Dunbar and A. Lipowicz, 2000. Tall men have more reproductive success. Nature, 403: 156-156.

Peters, M., 1991. Sex, handedness, mathematical ability and biological causation. Can. J. Psychol., 45: 415-419.

Quinan, C., 1922. A study of sinistrality and muscle coordination in musicians, iron-workers and others. Arch. Neurol. Psychiatry, 7: 352-360.

Ramadhani, M.K., 2006. Pathological Left-handedness Revisited: Origins and Later Life Health Outcorigins Outcomes. Proefschrift Universiteit Utrecht, Utrecht, Netherlands.

Raymond, M. and D. Pontier, 2004. Is there geographical variation in human handedness?. Laterality, 9: 35-52.

Raymond, M., D. Pontier, A.B. Dufour and A.P. Moller, 1996. Frequency-dependent maintenance of left handedness in humans. Proc. R. Soc. London B., 263: 1627-1633.

Sicotte, N.L., R.P. Woods and J.P. Mazziotta, 1999. Handedness in twins: A meta-analysis. Laterality, 4: 265-286.

Smith, J.M., 1989. Evolutionary Genetics. Oxford University Press, New York.

Soper, H.V., P. Satz, D.L. Orsini, R.R.Henry, J.C. Zvi and M. Schulman, 1986. Handedness patterns in autism suggest subtypes. J. Autism Dev. Disord., 16: 155-167.

Steele, J. and N. Uomini, 2005. Humans, Tools and Handedness. In: Knapping: The Necessary Conditions for a Unique Hominin Behaviour, Roux, V. and B. Bril (Eds.). McDonald Institute for Archaelogical Research, Cambridge, UK., pp: 217–239.

Tan, U. and M. Tan, 2001. Testosterone and grasp-reflex differences in human neonates. Laterality, 6: 181-192.

Vallortigara, G. and L.J. Rogers, 2005. Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. Behav. Brain Sci., 28: 575-589.

Van Strien, J.W., G.C.L. van Haselen, J.M. van Hagen, I.F.M. de Coo, M.A. Frens and J.N. van der Geest, 2005. Increased prevalence of left-handedness and left-eye sighting dominance in individuals with Williams-beuren syndrome. J. Clin. Exp. Neuropsychol., 27: 967-976.

Westergaard, G.C. and S.J. Suomi, 1996. Hand preference for stone artefact production and tool-use by monkeys: Possible implications for the evolution of right-handedness in hominids. J. Hum. Evol., 30: 291-298.

Wisniewski, A.B., 1998. Sexually-dimorphic patterns of cortical asymmetry and the role of sex steroid hormones in determining cortical patterns of lateralization. Psychoneuroendocrinology, 23: 519-547.

Yeo, R.A. and S.W. Gangestad, 1993. Developmental origins of variation in human preference. Genetica, 89: 281-296.