Journal of Human Evolution 57 (2009) 411–419

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

The prehistory of handedness: Archaeological data and comparative ethology☆

Natalie T. Uomini [a,b]

[a] *School of Archaeology, Classics and Egyptology, University of Liverpool, UK*
[b] *British Academy Centenary Research Project "Lucy to Language: the archaeology of the social brain", UK*

ARTICLE INFO

Article history:
Received 1 December 2007
Accepted 25 February 2009

Keywords:
Laterality
Hand preference
Manual laterality
Homo neanderthalensis
Australopithecus
Great apes
Chimpanzee
Gorilla
Hominin
Hominid

ABSTRACT

Homo sapiens sapiens displays a species wide lateralised hand preference, with 85% of individuals in all populations being right-handed for most manual actions. In contrast, no other great ape species shows such strong and consistent population level biases, indicating that extremes of both direction and strength of manual laterality (i.e., species-wide right-handedness) may have emerged after divergence from the last common ancestor. To reconstruct the hand use patterns of early hominins, laterality is assessed in prehistoric artefacts. Group right side biases are well established from the Neanderthals onward, while patchy evidence from older fossils and artefacts indicates a preponderance of right-handed individuals. Individual hand preferences and group level biases can occur in chimpanzees and other apes for skilled tool use and food processing. Comparing these findings with human ethological data on spontaneous hand use reveals that the great ape clade (including humans) probably has a common effect at the individual level, such that a person can vary from ambidextrous to completely lateralised depending on the action. However, there is currently no theoretical model to explain this result. The degree of task complexity and bimanual complementarity have been proposed as factors affecting lateralisation strength. When primatology meets palaeoanthropology, the evidence suggests species-level right-handedness may have emerged through the social transmission of increasingly complex, bimanually differentiated, tool using activities.

Introduction

Human hand use patterns can be characterised as complementary role differentiation (CRD). The CRD model of bimanual action derives from the Kinematic Chain model, which was proposed by Guiard (1987) and applied by Uomini (2006a) to the prehistoric activities that offer evidence for handedness (Steele and Uomini, 2009). In this model, one hand executes high frequency tasks (involving finer temporal and spatial resolution) while the other hand performs low frequency tasks (such as supporting an object). Rather than one hand being "dominant," the CRD model recognises that both hands have different but equally important roles (Corbetta and Thelen, 1996). "Right-handers" are thus defined as people who prefer to adopt the high frequency role with the right hand and the low frequency role with the left hand, as shown by experiments on humans for a complementary bimanual task requiring precision versus support (Hinckley, 1996; Hinckley et al., 1997). A hand role dichotomy appears to emerge between seven and thirteen months of age (Bresson et al., 1977; Ramsay et al., 1979; Michel et al., 1985; Kimmerle et al., 1995; Michel, 1998) and is well established by age three (Ingram, 1975; Gaillard, 1996), yet its genetic determinants are still unknown (Crow, 1998; Van Agtmael et al., 2001).

Beyond the individual, *Homo sapiens sapiens* displays lateralised hand preference at the species level. This means that a bias to the right-handed CRD pattern is found in all human populations around the world (reviewed in Llaurens et al., 2009), with the frequency of right handed persons in any given population varying between 74% and 96% (Hardyck and Petrinovich, 1977; Porac and Coren, 1981; McManus, 1991; Connolly and Bishop, 1992; Perelle and Ehrman, 1994; Annett, 2002; Raymond and Pontier, 2004; Faurie et al., 2005). There has never been any report of a human population in which left handed individuals predominate (Llaurens et al., 2009). In contrast to the human bias, it is clear from observations of experimental and spontaneous hand actions in captive and wild subjects that the non human primates do not show a species wide consistency in hand use patterns (Colell et al., 1995; Papademetriou et al., 2005). While group level biases can occur in some populations of chimpanzees (e.g., a rightward bias at Yerkes [Hopkins et al., 2007]) and for certain manual actions in some great apes (e.g., gorillas feeding on plants [Corp and Byrne, 2004]), there is no consistent pattern across populations at the

---

☆ This article is part of the 'Palaeoanthropology Meets Primatology' Special Issue.

0047-2484/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jhevol.2009.02.012

species level, since some populations are claimed to show a leftward bias (e.g., for termite fishing in Gombe's wild chimpanzees [Lonsdorf and Hopkins, 2005]).

Furthermore, these biases do not extend to all actions, nor do they reach the extreme degree of consistency seen in humans across all tasks including unimanual actions (McManus, 1985; Hopkins, 2006). As discussed below in more detail, the compilation of research led by various authors suggests that a species-wide group level manual preference across all tasks is not the norm in primates. Therefore, human handedness is unique in both its direction (rightward CRD pattern) and its strength (species wide preference), and remains to be explained in evolutionary terms.

The timing and context for the emergence of species handedness in hominins is therefore of much interest to palaeoanthropologists. Combining palaeoanthropology with primatology can help us decide whether human and nonhuman hand preference patterns are part of the same continuum, or are qualitatively different. A selection of archaeological and primatological findings for hand preference is discussed in a comparative framework, with a special focus on the population- versus species-level distinction.

Lateralised ancestors

Markers of hand preference in prehistory are found in material culture from the actions of lateralised tool manufacture and use that leave traces on objects, and in fossil skeletal asymmetries resulting from asymmetric use of the upper limb muscles over an individual's lifetime. These data have been extensively reviewed by Steele (2000), Weaver et al. (2001), Steele and Uomini (2005, 2009), Auerbach and Ruff (2006), Cashmore et al. (2008), and Uomini (2008, 2009). Examining a selection of these data sets reveals that, due to the nature of prehistoric remains, it is especially important to establish the level of study gained by the data (individual, population, or species), which is often misunderstood.

Most archaeological material usually pertains to undefined populations, whereas fossils can be individually discriminated. Archaeological methods that rely on overall proportions in an assemblage cannot statistically analyse handedness frequencies in terms of individual preferences as in living subjects. While statistical treatment of prehistoric data sets can reveal tendencies at the species level, neither tools nor flakes can be taken to represent individual hominins. Since one knapper can produce many flakes, and indeed can produce and use many tools, it is not appropriate to treat each flake or each biface as one data point. Awareness of the non independence of elements in an assemblage is therefore crucial to our understanding of laterality data. (McGrew and Marchant, 1997a).

For example, Toth's (1985) seminal study of Oldowan and Acheulean flakes from Koobi Fora, Kenya rests on the preferential direction of flaking along the perimeter of the platform during single-platform flaking for the production of Karari scrapers (a type of core scraper). Toth's (1982) replication experiments with his own right-handed knapping led to the premise that right handers prefer to flake to the right of previous removals and left handers prefer to flake to the left of previous removals.[1] However, if each flake is determined by the previous, this would mean all the flakes knapped from a single platform core should constitute one single data point. At Koobi Fora, there was no option but to count each flake as one. In fact it is almost never possible to identify an individual's flakes in archaeology (in situ knapping scatters may be one exception [cf. Fischer, 1990; Roberts et al., 1997; Wenban-Smith, 1997]).

One avenue to approaching the individual from flakes could be the Cone of Percussion method. Rugg and Mullane's (2001) experiment with four left-handed knappers and four right-handers found strong correlations between the direction of skew in a flake's cone of percussion and its knapper's hand preference. Applying this method to 647 Lower Palaeolithic flakes from Swanscombe and Purfleet, UK, Uomini (2001) found a weak bias ($p = 0.02$) towards right skewed flakes. However, 67% of flakes were unscorable and the method was difficult to implement without an objective measuring tool. Nonetheless, if cone skew does reveal knapping hand, this method will be extremely valuable as a universally applicable tool for determining the ratio of right- to left-handed knappers in all industries that contain flakes, including the earliest knapped stone.

The lateralised resharpening flakes studied by Cornford (1986) at the Neanderthal site of La Cotte de St. Brelade, Jersey, Channel Islands (240–122 ka) are independent of each other because they each represent an isolated knapping event. These flakes result from applying a *coup du tranchet*, in order to rejuvenate the cutting edge, to the left or right corner of a scraper whose morphology demands a specific holding position to successfully remove the flake. Cornford (1986) found statistically significant proportions of flakes struck by right handed knappers, showing a strong bias in the population. Despite their validity as independent data points, these flakes are still not directly linked to individual persons.

The frequency of left and right hand stencils ("negatives") in Upper Palaeolithic cave art has often been cited as evidence for handedness. Making a stencil involves pressing one hand against the cave wall while finely spraying pigment (e.g., powdered ochre in a liquid base) over it. The pigment can be sprayed either directly from the mouth or by finely manipulating a pair of blowing tubes held in a container (Barry Lewis, pers. comm.). Experiments suggest that right handers prefer to hold a blowing "pen" in the right hand, which produces similar proportions of left hand stencils (Faurie and Raymond, 2005) as found in prehistoric cave paintings. Worldwide there is a constant preponderance ($p < 0.001$) of left hand stencils, which spans the time range of known rock art (Kirchner, 1959; Delluc and Delluc, 1993; Steele and Uomini, 2009). Here again, hands are usually counted individually, even though clusters of hand stencils at a given site may be the work of one artist. However, even if individuals can be identified from their hand stencils (Gunn, 2006), it may not be possible to distinguish a connected series of stencils made in one bout of stencilling from those made on separate occasions.

An archaeological assemblage that is well-constrained in space and time is probably the least useful for finding species level handedness due to the likelihood of overlap in one population. By reconstructing grips and examining use-wear damage on 54 handaxes and cleavers aged about 1 Ma from Kariandusi, Phillipson (1997) found a statistically significant right hand bias according to the binomial test (two-tailed $p < 0.01$). In another vein, according to White's (1998) proposed method for producing twisted bifaces (thinning the biface using a sequence of eight alternating holding positions), a right handed holding configuration produces the "twisted" Z-shaped profile that is characteristic of many Lower Palaeolithic twisted bifaces in Britain, France, and Ethiopia (Evans, 1897; White, 1998; Galloti and Piperno, 2003). The surface-collected context of the Kariandusi artefacts reduces the possibility of overlap, making them likely independent data points. Similarly, the reported high frequency of Z-twists can also be considered a species bias considering the wide spatiotemporal range of the data. An equally wide range is in Semenov's (1964) estimate of an 80% frequency of right sided use-wear on Mousterian and Upper Palaeolithic end scrapers from Europe and the former USSR.

Fossils provide independent data points when individuals are clearly-defined. As Cashmore et al. (2008) describe, fossil skeletal

---

[1] Thus a right-hander produces slightly more rightward flakes alongside his leftward flakes (this is Toth's [1982] widely-cited 56: 44 ratio, often wrongly cited as a ratio of right- to left-handed people).