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journal homepage: [www.elsevier.com/locate/jhevol](http://www.elsevier.com/locate/jhevol)The prehistory of handedness: Archaeological data and comparative ethology<sup>☆</sup>Natalie T. Uomini<sup>a,b</sup><sup>a</sup> School of Archaeology, Classics and Egyptology, University of Liverpool, UK<sup>b</sup> British Academy Centenary Research Project "Lucy to Language: the archaeology of the social brain", UK

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## 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.

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## 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

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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 non human 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, in press). 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<sup>1</sup>. 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]).

<sup>1</sup> 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).

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

asymmetries show that a greater right arm robusticity was well established in Neanderthals, possibly from hunting with spears (Schmitt et al., 2003). Furthermore, the lateralised dental striations on 29 *Homo heidelbergensis* and Neanderthal teeth, interpreted as caused by cutting food held with the teeth (Martin, 1923; Semenov, 1964; Trinkaus, 1983; Bermúdez de Castro et al., 1988; Lozano et al., 2008), yield a statistically significant bias toward right handed striations (binomial two-tailed  $p < 0.01$ ). When combining the available dental data with endocast and humerus asymmetries for Neanderthals, 25 Neanderthals are right handed, two are left handed, and one (La Chapelle 1) shows incongruent asymmetries (Uomini, in press).

Looking to older species, very few studies of skeletal asymmetry have been possible for non-*Homo sapiens* fossil hominins (Cashmore et al., 2008). The most ancient postcranial asymmetry consists of a single instance, the right-sided shoulder and arm bias seen in the Nariokotome Boy (KNM-WT 15000, *Homo ergaster*), dated to about 1.6 Ma (Walker and Leakey, 1993). In addition, brain asymmetries revealed by endocasts suggest that *Australopithecus* and early *Homo*, including the Nariokotome Boy, had the modern pattern (reviewed in Cashmore et al., 2008).

#### Earliest evidence of population handedness

If the Toth method could be validated, the Koobi Fora data would represent the oldest evidence for handedness in a population (East African candidate species are *Australopithecus* [*H.*] *habilis*, *Homo ergaster*, and *Paranthropus boisei*). The next oldest evidence for a population bias is the use-wear on the Kariandusi artefacts, which likely pertain to *Homo erectus*. A rightward bias could be inferred for *Homo heidelbergensis* based on the dental striations and twisted bifaces, if these methodologies were validated. The flake data from La Cotte and fossil asymmetries show that right handedness also occurred at the species level in *Homo neanderthalensis*.

#### Comparing apes

In an ideal comparative perspective, the archaeological handedness data available for hominins would be directly compared to excavated material culture from extinct members of the extant great apes *Pan*, *Gorilla*, and *Pongo*. However, archaeological investigations of chimpanzee sites (Mercader et al., 2002; McGrew et al., 2006; Haslam et al., 2009) are just beginning, and there are virtually no post cranial pongid fossils that would be diagnostic for laterality. The most useful category of evidence pertaining to human origins is therefore found in a subset of laterality data from living non human apes. These can be found by observing wild apes doing tasks that are ecologically valid (McGrew and Marchant, 1997a).

The evidence from non human apes and other primates suggests that individuals often have task-specific hand preferences (Marchant and McGrew, 1996; Fletcher, 2006). In particular, observing chimpanzees across multiple spontaneous hand actions shows that individuals appear to be ambidextrous (they use both hands with equal preference) for most tasks and ambilateral (task-specialised [i.e., use the right hand for certain tasks and the left hand for other tasks]) for a few tasks (McGrew and Marchant, 1992, 2001; Fletcher and Weghorst, 2005). Some studies even fail to find any significant hand preference at the individual level across tasks (e.g., Mosquera et al., 2007).

On the population level, it appears that each separate population of non human primate has its own distinct profile of laterality biases, particularly when considering single tasks. For instance, there are claims of group level right hand biases in the chimpanzees at Yerkes Regional Primate Research Center, USA and in the Olive baboons at Rousset Primatology Center, France

(Meguerditchian and Vauclair, 2006). Populations with a predominance of left handed individuals are found among males of the M-group of wild chimpanzees at Mahale, Tanzania (this group's females are right handed; Corp and Byrne, 2004) and captive orangutans in Atlanta, USA (Hopkins et al., 2003). Although Lonsdorf and Hopkins (2005) report a group left hand bias in termite fishing by wild chimpanzees of the Kasekala community at Gombe, Tanzania, this result relies on the use of one-tailed statistical tests on each individual's Handedness Index, rather than the more appropriate two-tailed non parametric tests (Siegel and Castellan, 1988; Byrne and Byrne, 1991: 541). According to the binomial test, a population of twelve left handers and four right-handers is not a statistically significant departure from random (two-tailed  $p = 0.07$ ). Indeed, when Lonsdorf and Hopkins (2005: 12636) applied their analysis method to previously published data from other authors who had reported no population bias for termite fishing and ant fishing (two different actions), they found no significant differences between these and their own study. Similarly, in a recent meta-analysis, Papademetriou et al. (2005) report that the only statistically significant population level biases found in 118 publications since 1987 suggest a left hand preference for reaching in lemurs, rhesus monkeys, and Japanese macaques, and a right reaching preference in tamarins.

Still other populations exist that lack any group level hand preferences (i.e., with even distributions of right- and left-handers within the population), such as the chimpanzees at the Mona Foundation Sanctuary, Girona, Spain (Mosquera et al., 2007); the lowland gorillas from Zoo Atlanta and Lincoln Park Zoo Chicago, USA (Hopkins et al., 2003); the wild gorillas at Karisoke, Rwanda (Byrne and Byrne, 1991); the chimpanzees in Barcelona, Madrid, Valencia, and Reus Zoos, Spain (Colell et al., 1995); and Chester Zoo, UK (Fletcher and Weghorst, 2005); or the bonobos at Twycross Zoo, UK; Wilhelma Zoo, Germany; and Apenheul, Holland (Chapelain and Hogervorst, 2009). For wild subjects, we can list the chimpanzees at Kasekala, Gombe, Tanzania (Marchant and McGrew, 1996; McGrew et al., 1999); chimpanzees at Bossou, Republic of Guinea (Sugiyama et al., 1993); mountain gorillas at Karisoke, Rwanda (Byrne and Byrne, 1991); and vervets in the Palmiet Valley, South Africa (Harrison and Byrne, 2000).

Thus, each primate population has a laterality pattern that must be assessed in its own context. Populations can be right handed, left handed, evenly divided between right- and left-handed, or comprised of ambidextrous individuals. In the meta review of Hopkins (2006: their Table 3), the number of right handed apes is smaller than the number of left handed and ambidextrous subjects. The existence of great ape populations with either a left hand bias or no bias indicates that we cannot generalise evidence of a given right handed population to the other members of the same species. These findings reinforce the uniqueness of the human pattern in that *Homo sapiens* show right handedness in many unrelated populations separated widely in space and time, and furthermore that no *Homo sapiens* population is left handed or ambidextrous.

Of particular interest are tasks that elicit the strongest laterality, as they may provide useful insight into the conditions that led to the emergence of handedness in hominins. If the differences between strongly and weakly lateralised tasks are related to task features, these could lead to predictions that are testable on the archaeological material. The tasks that elicit the most consistent lateralisation have been described by primatologists as relating to manual skill, tool use, bimanual complementarity, or sequence length. For example, Harrison and Byrne (2000) found individual vervet monkeys were more strongly lateralised for the tasks they considered more skilled (termite feeding and detaching skin from fruit) than for eating leaf shoots and sugarcane. Trouillard and Blois-Heulin (2005) show in De Brazza's monkeys that strength of

laterality increases with task complexity, using five experimental devices. Chapelain et al. (2006) found increased individual lateralisation in Campbell's monkeys for more complex experimental food reaching tasks.

For the great apes this strength effect is the same: hand preferences for termite fishing, a highly dexterous task, are very stable in chimpanzees, meaning that nearly all individuals have a consistent hand preference (Nishida and Hiraiwa, 1982). Boesch (1991) reports stable individual hand-use patterns for the most difficult or "complex" tasks of nut cracking and wedge dipping at Tai, whereas the same chimpanzees were ambidextrous for reaching and grooming. Sugiyama et al. (1993) and Biro et al. (2003) also found consistent individual hand preferences in wild chimpanzees at Bossou for nut cracking with stones, but not for picking or carrying food. Chimpanzees show exclusive or significant right- or left-hand preference for smashing *Strychnos* fruits on anvils (McGrew et al., 1999) and for bimanual processing of *Saba* fruit and lemons (Corp and Byrne, 2004), while gorillas show stable hand use patterns and a nonsignificant trend towards population right handedness for the finest manipulations in processing three of four edible plants (Byrne and Byrne, 1991; Byrne et al., 2001a, b). Orangutans are individually handed for feeding (Rogers and Kaplan, 1996; Peters and Rogers, 2008), as are bonobos (Harrison and Nystrom, 2008; Chapelain and Hogervorst, 2009). In contrast, simple tasks such as tripod reaching do not tend to elicit individual hand preference (Cashmore et al., 2008). Some of these findings may be explained by the higher level of skill required for tasks involving tool use (O'Malley and McGrew, 2006), but strong hand preference is also found in tasks that do not involve direct tool manipulation. Therefore tools may represent only one part of the skill element.

However, in the human sciences as among primatologists, there is no agreement as to what constitutes skilled or complex tasks (Sambrook and Whiten, 1997; Olausson, 2003; Trouillard and Blois-Heulin, 2005). Some relate manipulative skill to motor precision (Fagot and Vaclair, 1991; McGrew et al., 1999; Harrison and Byrne, 2000). Complementary hand role differentiation may also add complexity (Beck and Barton, 1972; Rogers and Kaplan, 1996; Harrison and Byrne, 2000). Novelty has also been discussed (Young et al., 1983; Fagot and Vaclair, 1991; Chapelain et al., 2006). Others relate complexity to the number of combined elements or multiple movements (MacNeilage et al., 1987; Steenhuis and Bryden, 1989; Boesch, 1991; Matsuzawa, 1991, 1996; Harrison and Byrne, 2000; Hayashi and Matsuzawa, 2003; Rugg, 2004, 2007; Hayashi, 2007b).

These definitions are compatible with the two levels of skill as defined in prehistoric activities: the execution of elementary gestures through physical motor know-how and the realisation of the chaîne opératoire, or sequence, through operative ideational know-how (Roux, 1990; Karlin and Julien, 1994; Roux et al., 1995; Steele, 1999; Apel, 2001). In cognitive psychology terms these operate on two levels, motor and conceptual, that relate to procedural and declarative knowledge (Pelegriin, 1991, 2005). The motor level (Byrne and Russon's [1998] action level) requires physical motor know-how to execute the elementary gestures; these involve implicit learning and they are responsible for precision and accuracy (i.e., ballistic movement or with visual feedback; temporal and spatial error tolerance of the movement), as well as bimanual action (i.e., yoked/identical; independent parallel; complementary). The conceptual level (Byrne and Russon's [1998] program level) requires operative ideational knowledge to implement the series of actions in the chaîne opératoire. This can involve both implicit and explicit memory, unlike the motor level. The conceptual level controls object combinations and their relationships (Matsuzawa, 1991, 1996), numbers, and orders of multiple movements (sequence length; serial or hierarchical order). Novelty would also work on this level.

This two-level scheme is useful for a comparative approach because it provides a common framework for understanding the influence of task complexity or skill on the lateralised hand preferences of human and non human apes alike. Tool involvement, of course, is inherent in all archaeological data. What the primate data provide, in complement, is information on complex manual behaviours not related to tool use. Gorilla plant food processing involves long sequences, but if such acts were at the root of human handedness, we would never find them in the archaeological record.

In summary, overall task complexity can be influenced by increased precision and accuracy requirements in the elementary gestures, longer sequences of actions, complementary hand role differentiation, and greater numbers of elements to be combined. The greater lateralisation seen in tool use can be explained by the inherent complexity in using a tool because it implies bimanual cooperation, combining elements, and additional action sequences (i.e., in selecting and/or manufacturing the tool before use [cf. Haidle, 2009]). As the literature suggests, the effect of complexity on lateralisation strength appears to hold for the great apes, as well as some monkeys (Trouillard and Blois-Heulin, 2005). However, the disparity in research methods prevents direct comparison of results between humans and our nearest evolutionary cousins.

#### *Towards a comparative ethology*

The robust findings from chimpanzees and other non-human apes that manual preference becomes more stable with increasing complexity and tool use, lead to the question of how to compare these data to the results from humans. In contrast to observational data from wild apes, the experimental data that are often cited as evidence for a uniquely human pattern of hand use usually derive from laboratory tests or questionnaires (e.g., Oldfield, 1971; Bryden, 1977). Despite the fact that some apes can communicate with humans using sign languages or lexigrams, to our knowledge nobody has tried to administer such a questionnaire to one of these apes. Regarding hand performance, the human experimental tests tend to be restricted to artificial contraptions in laboratories, often requiring serial repetitions of hand movements (e.g., Bryden and Roy, 2005). The ecological validity of such performance trials is questionable (Marchant et al., 1995). Furthermore, a comparative palaeoanthropological-primatological approach would benefit from testing evolutionarily meaningful tasks (McGrew and Marchant, 1997a). Performance need not be measured experimentally, since it can be determined through natural outcomes of spontaneous tasks; for example, chimpanzees are more efficient for termite fishing (i.e., obtain more termites per tool withdrawal) when they commit to an exclusive hand (McGrew and Marchant, 1999).

One possible way to bridge the disciplines with comparative research on laterality is by using the same methods to study all species. Therefore, direct comparison with the non human great ape data will require observation in naturalistic settings (McGrew and Marchant, 1996). Rather than testing wild apes in laboratories, we can "put humans in the wild," for example by using the ethological approach pioneered by Marchant et al. (1995).

Importantly, the findings from the ethological study of Marchant et al. (1995) suggest that the pattern of population level lateralisation in humans may be similar to that of non human apes as reviewed above with respect to the complexity hypothesis. In at least three traditional cultures, lateralisation at the group level is stronger for tool using tasks. Observational data were collected from ethnographic video footage of the daily lives of people in three traditional cultures: the G/wi Bushmen from the Central Kalahari in Botswana, the Himba from northern Namibia, and the Yanomamö

from the Orinoco forest in southern Venezuela. This study revealed that hand actions not related to tool use (such as waving at insects or poking) produced ambidexterity in individuals and a random distribution of laterality in the population. Strong right hand preference was found individually and in each group for using tools, particularly those requiring a precision grip. This effect is consistent with the complexity hypothesis and highlights the need for further ethological research.

### The pilot study

In order to obtain ethological data for humans on a task that would be directly comparable to chimpanzee data, a pilot study was conducted at Land of Legends Lejre, Denmark in July 2006, following Marchant et al.'s (1995) approach. The spontaneous hand use patterns of children and adults doing archaeologically valid activities were recorded (preliminary results in Uomini, 2006b). A naturalistic experimental setup, using provisioning but not manipulation, was created where participants could be observed in spontaneous manual behaviour. This followed the method introduced by Sakura and Matsuzawa (1991) and applied by Inoue-Nakamura and Matsuzawa (1997) and Hayashi et al. (2005) to study the acquisition of nut cracking in chimpanzees. Objects were made available in an area of heavy visitor traffic and presented as "prehistoric games" for visitors to try.

The games (tasks) included nut cracking and flint puzzles. The nut cracking station consisted of three stone anvils, 21 hammerstones, and hazelnuts and walnuts. Nut cracking is attested from pitted anvils dating from the Oldowan onward (Joulian, 1996; Goren-Inbar et al., 2002; de Beaune, 2004) and is also customary in West African chimpanzee communities (Whiten et al., 1999). The abstract flint refitting puzzles were made of four flint nodules that had been flaked into pieces, the number of pieces to be refitted ranging from four to nine. In order to discreetly note their writing hand, the experimenter asked visitors to sign their name and age in a notebook.

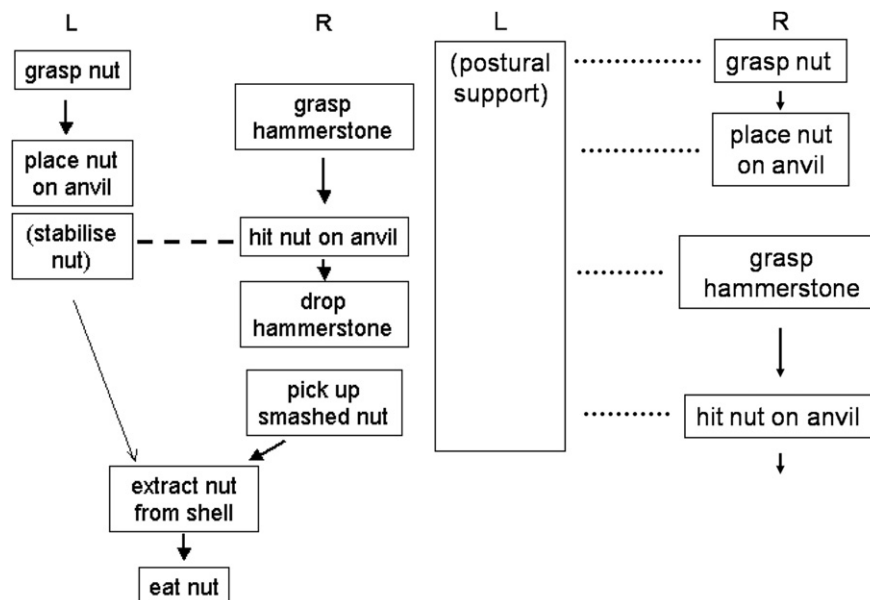
Video recordings of the spontaneous gesture sequences of visitors doing these activities were analysed in detail according to bouts of actions (McGrew and Marchant, 1997a). Sequences of action units

(Inoue-Nakamura and Matsuzawa, 1997; Hayashi et al., 2005; Hayashi, 2007a, b) were extracted from the analysis; examples are shown in the flow diagrams (Figs. 1a, b and 2) following the format of Byrne and Byrne (1991). In Figures 1 and 2, dashed lines show simultaneous complementary collaboration where the hands focus on one goal but do different actions; dotted lines show simultaneous but independent actions of the hands where each hand achieves a separate goal; straight arrows show continuity of objects; and curved arrows show potential recursiveness in the sequences.

In total, 238 visitors spontaneously manipulated at least one of the "games." The mean age of the 128 visitors who signed their age was ten (range 3 to 49, s.d. 7.5). Statistical analyses were conducted for the subset of 48 participants who did at least six bouts of nut-cracking or puzzle manipulation. Among the 14 visitors who did six or more bouts of the nut cracking task, 12 showed an exclusive or significant ( $p \leq 0.01$ ) preference for one hand configuration (holding the hammer in the right hand). This corresponds to a Level 4 bias according to the model of McGrew and Marchant (1997b), where most of the population is significantly biased to the right side. Writing hand was congruent with the nut hammer hand in all cases ( $n = 12$ ). In contrast, the flint puzzle showed the least stable lateralisation, with most subjects showing ambidexterity (34 of 38). The four participants who did six or more bouts of both nut-cracking and the puzzle, showed congruent hand preference between the two tasks in all cases. However, the puzzle task remained at Level 1 of McGrew and Marchant's (1997b) model, with the majority of individuals using either hand equally frequently.

### Discussion

As reviewed above, the most robust evidence for population level handedness in prehistory begins with the Neanderthals, although data from East African sites as early as 1 Ma indicate right handedness was also the norm. As in the living human hand preference surveys, there are no reports of predominant left handedness in any prehistoric data sets. These findings contrast sharply with the situation in non human primates, especially great apes, in which we find large geographical variation in hand preference profiles. There are



**Fig. 1.** (a) Typical sequence for nut cracking, showing distinct hand roles. (b) Example sequence for nut cracking showing entirely unimanual nut cracking with left hand engaged in postural support.

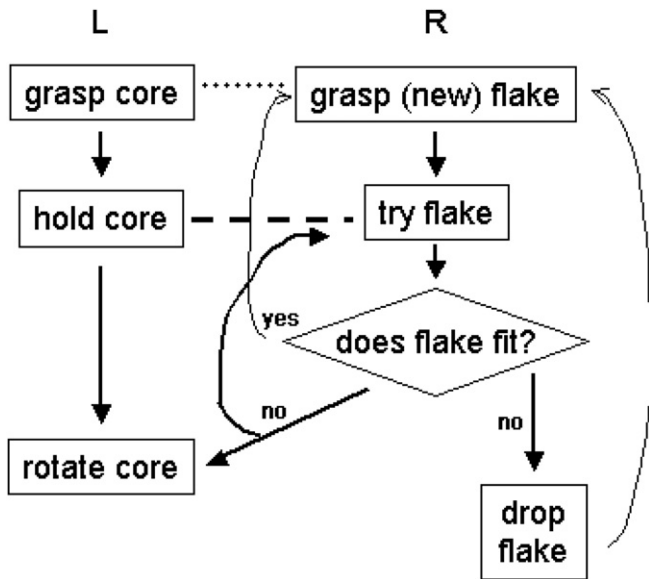


Fig. 2. Typical sequence for flint puzzle, showing distinct hand roles and recursive programs.

populations of right handed apes, as well as populations of left-handed apes and monkeys and populations with equal numbers of right handers and left handers. Populations of ambidextrous non-human primates also exist. Therefore, in terms of species level patterns, humans show a unique directional bias to the right side.

Comparing individual level biases suggests that hand preferences in humans and other apes are similarly influenced by the effects of task complexity on lateralisation strength, that is, the degree of consistency within an individual. A direct comparison with chimpanzees can be made with the nut cracking data. The human ethological study presented here showed a group bias towards holding the hammerstone in the right hand (12 right-handed and two ambidextrous), which is greater than any of the figures found for chimpanzees who crack nuts in the wild (Boesch, 1991; Sugiyama et al., 1993; Biro et al., 2003).

The Danish children at Lejre revealed a case of de lateralisation that may also be related to this effect. The puzzle task elicited more ambidextrous responses than expected. Any of the proposed “complexity” factors may account for this. For instance, the puzzle requires shorter action sequences than nut cracking. Nut cracking requires the five basic actions of grasp nut, place nut on anvil, grasp hammer, hit nut, and eat nut (Inoue-Nakamura and Matsuzawa, 1997); whereas the puzzle only requires two or three (grasp flake, grasp core [optional], fit flake to core). The nut cracking task also requires more motor precision than the puzzle due to the aimed ballistic movement involved.

The ambidexterity shown by most of the experimental humans on the puzzle task is consistent with the little that is known about hand preferences for three-dimensional puzzle manipulation. As Marschik et al. (2007) found in a study of tower building with blocks, children did not show stable hand preferences until age 7. The puzzle may not have elicited distinct complementary hand roles because the supporting hand adopted a more active role than usual by frequently turning the core to meet the flake. Alternatively, postural constraints of the non active hand may have hindered laterality, as was found by Marchant and McGrew (2007) for arboreal ant fishing in chimpanzees. Furthermore, the puzzle did not reach the same level of hierarchical complexity as nut-cracking. This involves Level 2 tool use according to Matsuzawa’s (1996) grammatical framework, where the nut and anvil are subordinate

to the hammerstone. The flint puzzle was also probably more novel than nut cracking, since most visitors had never handled flint before, but several visitors reported familiarity with cracking nuts at home. Finally, the puzzle did not involve using a tool. In summary, the lack of lateralisation shown in the puzzle task may result from its lesser complexity and lack of tool involvement.

The results from the Marchant et al. (1995) human ethological study and the Lejre pilot study are compatible with a continuity framework. Specifically, we can conclude that the manipulative skills of human and non human apes are not qualitatively, but rather quantitatively, different. The findings that hand preference is strongest and most stable for “complex” actions in at least three members of the great ape clade (human, chimpanzee, gorilla) can be explained by the learning required to master complex tasks. Sugiyama et al. (1993) propose that the long-term learning required for bimanual nut cracking at Bossou encourages lateralisation. This is consistent with the positive correlation between learning time and skill acquisition for humans (Provins, 1997; Teixeira, 2006). As Teixeira and Okazaki (2007) suggest, hand preference may be modulated largely by experience once a basic role differentiation has been established. Namely, a feedback loop can reinforce the choice of the more experienced hand for new tasks, which in turn improves the performance of that hand. Therefore, the complementary hand role dichotomy of infants gains reinforcement with increasing task complexity as related to practice and learning in the child’s development.

Practicing increasingly complex actions may differentiate humans from other apes; Corballis (1998) proposed that most of the manipulations done by other animals are not complex enough to elicit hand preference. As the primate data show, the complex tool using skills of great apes may be related to their stronger laterality compared to other primates. In this perspective, tools are therefore an important piece of evidence for handedness evolution. If human handedness is related to an unusually high level of task complexity, then the archaeological evidence for hand use patterns is predicted to reveal a correlation with increasing tool complexity, and this could be tested in future research. The archaeological evidence for handedness shows that a right hand preference was already established in Neanderthals. The earliest stone knapping attests to the high technological proficiency of palaeohominins (Delagnes and Roche, 2005), suggesting that stone technology was not the first kind of material culture, and thus that complex manipulations on organic materials were customary in the Pliocene. The emergence of consistent handedness in a population may therefore have been related to the technology dense lifestyles of early hominins, which would have required stable hand preferences.

Furthermore, the acquisition of skills implicated in a technology rich society can be related to the uniquely human pattern of a population wide bias to one hand. Learners gain an advantage by using the same hand configurations as their peers for complex manual sequences, such as knot tying (Michel and Harkins, 1985). Whether this learning advantage would be sufficient to drive selection for a population wide bias to one side is unclear. This question may eventually be resolved by ongoing research into the genetic determinants of laterality, aided by genetic models of handedness (McManus, 1999; Annett, 2007). One way forward may be to investigate the genetic diversity of each species (Kaessmann et al., 1999) compared to the level of bias and heritability of hand preference.

In conclusion, primatological studies of laterality draw attention to the role of learning, tool use, and complexity in prehistory. Similarly, the archaeological data for handedness bring support to primatological findings and theories. New cross-disciplinary methodologies, such as the ethological approach of Marchant et al.

(1995) and the comparative neuroethology of Llorente (2007), the experimental ethology done in the pilot study, and the excavation of ancient chimpanzee technologies (Mercader et al., 2007; Haslam et al., 2009), must be encouraged. It is hoped that this paper has shown how palaeoanthropology and primatology can work together towards elucidating one of the most interesting topics in human origins, the evolution of species-level right-handedness.

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