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The evolution of handedness in humans and great apes: a review and current issues

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Summary - *Population-level right-handedness is a defining characteristic of humans. Despite extensive research, we still do not know the conditions or timing of its emergence in human evolution. We present a review of research into the origins of handedness, based on fossil and archaeological data for hand preference and great ape hand-use. The data show that skeletal asymmetries in arm and hand bones supporting a right-sided dominance were present at least in the genus Homo, although data are more robust for Neanderthals. The evidence from tool-use, production, and cave art confirms that right-hand preference was established in Neanderthals and was maintained until the present. The great apes can provide real-life models for testing the conditions that facilitate or enhance hand preference at both the individual and group levels. The database on great ape hand-use indicates that they do exhibit hand preferences, especially in complex tasks. However, their preferences vary between tasks, and while group-level biases have occasionally been reported, no human-like handedness bias has been found. We discuss the methodological problems encountered in these approaches. Shared problems include a lack of agreed terminology both within and between disciplines, small sample sizes, interpretation biases and a failure to replicate experiments. In general, there is a paucity of fossil material, with poor preservation hampering traditional metric methods. The archaeological data are often founded on unreliable methods. The primate database is plagued by the use of measures that could be inappropriate for revealing hand preference, and by methodological inconsistencies between studies. We emphasise the need to standardise the methods to allow between studies and species comparisons. We propose that when referring to 'handedness' it is more appropriate to use the terms 'hand preference' and 'hand use' , to avoid confusion with each discipline's own definition of handedness.*

Keywords - *Hominins*, *Asymmetry, Laterality, Hand preference, Great Apes.*

Introduction

The region of the hand has long been of interest to researchers in the field of palaeoanthropology, and the evolution of this key area of the hominin postcranial skeleton has received extensive treatment in the literature (Susman & Creel, 1979; Tuttle, 1981; Marzke & Shackley, 1986; Lewis, 1989; Susman, 1994, 1998; Niewoehner *et al.*, 1997, 2003; Marzke, 1997; Marzke & Marzke, 2000; Churchill, 2001; Niewoehner, 2001; Alba *et al.*, 2003; Tocheri, 2007). The reason for the continued fascination in the evolution of the hand is, in part, because of its distinctive modern morphology compared to non-human primates and the unique nature of its functional capabilities. Research in this field has been led by the desire to understand functional aspects of the upper limb and the relationship between anatomy and tool-making and using. Less attention has been paid to asymmetry between the upper limbs and what this implies about handedness and hand preference in the genus *Homo*.

Interest in hominin handedness has arisen from the observation that across modern human groups, there is a strong preference for using the right hand (Hécaen & de Ajuriaguerra, 1964; McManus, 1991). On average, 90% of individuals prefer to use the right hand for complex tasks (Annett, 1985; Fagard, 2004; Raymond & Pontier, 2004). This population-level right-handedness appears to remain relatively constant around the 90% mark, although there is some variation in the proportion of left-handers between groups ranging from 0 to 27 % (Coren & Porac, 1977; Marchant *et al.*, 1995; Marchant & McGrew, 1998; Fagard, 2004; Faurie, 2004; Faurie & Raymond, 2004; Raymond & Pontier, 2004). The fact that human-like handedness does not appear to be present in our closest primate relatives, the other great apes (McGrew & Marchant, 1997a), raises interesting questions about how, when and where this trait arose in hominins.

Laterality in hand-use may also be important for understanding the evolution of language capabilities within the human genus. A neuroanatomical link within the primary motor cortex of the brain for the control of the hands and the vocal apparatus has led some researchers (e.g. Corballis, 2003) to propose a co-evolutionary link between two uniquely human traits – complex language production and comprehension, and population-level hand preference. Although attempts have been made to identify the presence of spoken language in hominins (Arensburg *et al.*, 1990; Martínez *et al.*, 2004; Krause *et al.,* 2007; Martínez *et al.*, 2008), the general dearth of evidence, both skeletal and lithic, makes fossil indicators of handedness a potentially interesting avenue for assessing language capabilities within the human genus.

Handedness in the archaeological record

The study of the evolution of handedness must necessarily start with the archaeological evidence. While necessary, it is also problematic, as archaeological evidence of handedness can be hard to identify. Fossil remains of the hands are often isolated and fragmentary, making the related pairs of bones necessary to safely identify hand preference in an individual difficult to find. The difficulty of identifying handedness at the individual level soon becomes an impossibility when attempting to identify hand preference at the group or population-level, due to the paucity of available skeletal material. Researchers have therefore also investigated more imaginative methods of assessing the existence of handedness in hominins, such as lithic manufacture and rock art. The processes of manufacturing stone tools and creating art is of course inextricably linked to the anatomy and function of the hands and by studying these processes we can gain more of an insight into the use of the hands at the level of the individual as well as the group. This section will outline the key fossil evidence for the presence of hand preference in the hominin skeletal record. The other lines of evidence, both cranial (i.e. from dental modification) and non-skeletal will also be discussed.

Fossil evidence for hominin hand preference

Plio-Pleistocene fossils

Prior to the emergence of the human genus, there is a sizeable corpus of hand bones representing Miocene ape species such as *Proconsul* (e.g. Beard *et al.*, 1993; Begun *et al.*, 1994) and *Oreopithecus* (e.g. Susman, 1985, 2004; Moyà-Solà *et al.*, 1999, 2005). By the time we reach the emergence of the first possible tool-making in the African Plio-Pleistocene, the skeletal evidence for handedness is much sparser. The functional anatomy of the *Australopithecus* hand has been studied in detail (e.g. Bush *et al.*, 1982; Alba *et al.*, 2003; Ricklan, 1987; Stern & Susman, 1983; Susman, 1994, 1998; Marzke, 1997), but upper limb asymmetry and handedness in this genus has seldom been addressed. The largest collection of hand bones from this period comes from Hadar in Ethiopia and has been assigned to *Australopithecus afarensis* (Bush *et al.*, 1982). This collection consists of 5 carpals, 18 metacarpals (whole and fragmentary) and 28 phalanges, but as the sample comprises at least 5 individuals (2 of which are juvenile) and the bones were not found in anatomical association, no assessment of asymmetry was undertaken. Alba *et al.* (2003) reanalysed the Hadar material and compiled a composite *A. afarensis* hand from the material, believing the bones likely to have come from a single individual. As this hand is comprised of left and right bones, it is not possible to make an assessment of asymmetry. It is, however, possible to see that reconstructions of this nature have the potential to allow future asymmetry calculations to be attempted, if allowances were made for measurement error. In terms of the rest of the upper limb, the AL288-1 *A. afarensis* skeleton ("Lucy") retains fragmentary humeri and ulnae (Senut, 1981), although the asymmetry in these bones has not been studied to date.

More recently, an important discovery offers renewed potential for understanding the evolution of the hominin hand. The remarkably intact Stw 573 *Australopithecus* (potentially *A. africanus*) skeleton found at Sterkfontein, and dating to around 3.3 million years, appears to have a complete left arm and hand (Clarke, 1999). While this specimen is still being painstakingly extracted from the breccia of the Sterkfontein caves it is not possible to gather information about the metric properties of the upper limb bones so far exposed, but Clarke believes that a complete right upper limb will also be found. If this turns out to be the case then the Stw 573 skeleton will provide an unparalleled opportunity not only to study the *Australopithecus* arm as a complete functional unit, but also to allow comparisons of upper limb bilateral asymmetry for the first time in hominin evolution. An important step in understanding the evolution of hand preference in hominins will come from identifying the move from a more primate-like mixed pattern of upper limb asymmetry to the more human-like pattern of strong right-side dominance. It is hoped that analysis of the Stw 573 arm(s) will shed light on this question, if only for one individual.

The first tool-makers

With the emergence of the human genus and the first identifiable manufactured stone tools, there is a noticeable lack of postcranial material associated with these first tool-makers (e.g. Haeusler & McHenry, 2007). Fortunately however, the discovery of the OH 7 (*Homo habilis*) fossils in 1960 (Leakey *et al.*, 1964) provided the first instance of a set of hominin hand bones found in the same context as early Oldowan stone tools. Such was the importance of the association between the hand bones and the tools that the name given to this newly identified species, *H. habilis*, reflected how the role of stone tool-use was perceived as integral to the evolution of the hominin lineage. Napier (1962) reported the presence of hand bones from a juvenile and an adult from Bed I at Olduvai Gorge as being part of this new species of *Homo*. Although it was not possible to make attributions of hand preference to such a small sample, Napier highlighted the very modern morphology of the bones, suggesting that a modern pattern of hand-use would also have been likely in the new *H. habilis* species.

In contrast to the fragmentary nature of most early *Homo* remains, the relatively complete skeleton of the KNM-WT 15000 *Homo ergaster* specimen (also known as the Nariokotome Boy) provides a rare opportunity to assess upper limb bilateral asymmetry and thus make inferences about hand preference in this species. KNM-WT 15000 is a juvenile skeleton (the exact age at death has been debated but is likely to have been between 10 and 15 years [Smith, 1993]), but the state of preservation is such that asymmetry could be assessed in a number of bones (Walker & Leakey, 1993). Damage to the left scapula and the absence of a left humerus make asymmetry estimations impossible for these bones. The preservation of the clavicles is much better however, and a virtually complete pair exists. While there is very little difference in the lengths of the bones (right = 130.5mm, left = 130.4mm), there is a noticeable difference in the groove that houses the deltoid attachment (right = 22.0mm x 3.8mm, left = 17.0mm x 3.0mm). This has led Walker & Leakey (1993) to conclude that the Nariokotome Boy may have been right-handed. There are also faint markers which indicate the presence of attachments for the *pectoralis major* and *subclavius* muscles, and the costoclavicular ligament, but these appear to be more developed on the left than the right.

Apart from the missing (unfused) epiphyses, both ulnae of KNM-WT 15000 are also complete (Walker & Leakey, 1993). A bilateral difference exists in the lengths of the preserved bones. The right ulna (260.3mm) is longer than the left ulna (257.2mm), although the missing epiphyses must also be taken into consideration. Unfortunately, few hand bones have been recovered for the Nariokotome Boy, but Walker & Leakey (*ibid.*) have identified what they believe to be first metacarpals, once again missing the unfused epiphyses. The left shaft is longer than the right shaft in this instance (right = 34.7mm, left = 35.2mm), but the authors raise the possibility that these bones may belong to another, potentially unknown mammal species which may have also lived in the area. Therefore, these measurements need to be treated with caution.

Despite the small number of comparable measurements available, the trend for the Nariokotome Boy is for the right upper limb to be bigger than the left upper limb and, for the clavicles at least, for muscle development to be greater on the right side. Taken together this suggests that this skeleton exhibited a general right arm preference. The juvenile status of this specimen must of course be taken into consideration when drawing conclusions about its asymmetry, but this example shows that assessments of upper limb bilateral asymmetry are possible in fragmentary fossil hominin remains.

Out of Africa

The movement of early *Homo* out of Africa is documented at the fossil-rich site of Dmanisi, Georgia (Gabunia & Vekua, 1995). While the main focus of investigation has surrounded the cranial and mandibular material from the 1.77 million year old site (e.g. Gabunia & Vekua, 1995; Gabunia *et al.*, 2000; Vekua *et al.*, 2002; Lordkipanidze *et al.*, 2005, 2006; Rightmire *et al.*, 2006), postcranial material has also been recovered (Lordkipanidze *et al.*, 2007). While there are few hand bones represented in the postcranial material from Dmanisi, there are a pair of adult clavicles (missing the sternal and acromial ends) and a pair of subadult humeri (not complete). The clavicles are 137.3mm (left) and 135.6mm (right) long. The humeri have anterioposterior midshaft diameters of 17.1mm (left) and 16.8mm (right) and mediolateral midshaft diameters of 14.3mm (left) and 14.7 (right). While these values must be treated with caution due to the incomplete state of the clavicles and the subadult status of the humeri, it can be seen that this is little left/right difference between bones, and no clear pattern of side dominance in the metric properties is present.

The Sierra de Atapuerca in Spain has produced an extensive collective of hominin fossils from the Early and Middle Pleistocene of Europe (e.g. Arsuaga *et al.*, 1990; Carbonell *et al.*, 1995; Bérmudez de Castro *et al.*, 1997; Arsuaga *et al.*, 1999). The Lower Pleistocene site of Gran Dolina has produced fossils attributed to *Homo antecessor*, believed by some to be the last common ancestor of *Homo neanderthalensis* and *Homo sapiens* (e.g. Bérmudez de Castro *et al.*, 1997). Carretero *et al.* (1999) report on the upper limb material from Gran Dolina (TD6), where two adults and two subadults appear to be represented. Although several clavicular and radial fragments are present, there are no paired bones available for measurements of asymmetry. A total of 12 hand bones (2 carpals, one second metacarpal, a metacarpal distal epiphysis, four proximal and four intermediate phalanges) were also found in the Gran Dolina cave (Lorenzo *et al.*, 1999), again representing adults and subadults. However, once again it is not possible to take asymmetry measurements because there are no matched pairs of bones.

The Middle Pleistocene site of Sima de los Huesos at Atapuerca has produced large amounts of postcranial material belonging to *Homo heidelbergensis* (Carretero *et al.*, 1997), particularly clavicles, scapulae and humeri. While there are numerous left and right measurements available for each of these bones, individual pairs have not been identified, making comparisons of asymmetry unwise at this stage.

Neanderthals

With the appearance of *Homo neanderthalensis* in the fossil record, we start to find larger amounts of preserved upper limb material, making estimations of bilateral asymmetry more straightforward. The general trend in Neanderthal data is for a right-side dominance (see Steele, 2000; Steele & Uomini, 2005). For example, the Le Régourdou Neanderthal shows a right-side dominance in diaphyseal diameter in the clavicle and humerus, plus medio-lateral diaphysis diameter for the ulna and radius.There is also a right-side dominance for radial neck diameter, proximal clavicular curvature, radial interosseus crest development, and ulnar radial facet height (Vandermeersch & Trinkaus, 1995).

Trinkaus *et al.* (1994) quantified the asymmetries in the paired humeri of eight Neanderthal individuals: La Chapelle 1, La Ferrassie 1, Neandertal 1, La Quina 5, Spy 2, Shanidar 1, Tabun 1, and Kebara 2 using humeral length, distal articular breadth, cortical and medullary areas (at 35% and 50% of the length from the distal end of the humerus). Trinkaus and colleagues found a right-side dominance for all individuals except Shanidar 1, although this specimen has a pathological right arm and associated disuse atrophy on the left arm. The arms of Neandertal 1 also show pathologies, in the form of left-arm lesions which may have partly contributed to the strong rightward asymmetry in this pair of humeri. A possible left-arm trauma can be attributed to a third fossil, La Quina 5, despite the absence of visible lesions. The remaining five individuals are considered as having nonpathological asymmetries, indicating they were subjected throughout their lifetimes to differential loading patterns which favoured the right arm (Trinkaus *et al.*, 1994).

Indirect support for these findings comes from Niewoehner *et al.* (2003). Their work has found that a modern pattern of arm preference was present in the human genus prior to the appearance of *Homo sapiens*. Despite some anatomical differences in the carpometacarpal articulations, no differences were found that would have prevented Neanderthals from exercising a range of movement comparable to that of anatomically-modern humans. In fact, Niewoehner and colleagues suggest that Neanderthals would have likely exhibited more mobility at the trapezium-metacarpal joint of the thumb than is found in modern humans. With no reason to assume functional discrepancies between Upper Palaeolithic hominins, it can therefore be presumed that a similar pattern of upper limb dominance would also exist in Neanderthals as in anatomically modern humans.

More recent finds such as the *Homo floresiensis* specimens from the island of Flores, Indonesia (Brown *et al.*, 2004; Morwood *et al.*, 2005) provide new opportunities to study the evolution of hand-use and preference in this unique species. Research already undertaken by Larson *et al.* (2007) on the *H. floresiensis* shoulder and upper arm and Tocheri *et al.*(2007) on the wrist bones have found this hominin to have an unusual and distinctly primitive upper arm morphology, posing interesting questions about its tool-making capabilities. To date, only a few hand bones have been found belonging to this species (Morwood *et al.*, 2005), comprising 3 carpal bones, 1 unspecified metacarpal, and 5 phalanges, making the identification of asymmetry impossible at this stage. It can be hoped, however, that with further excavations on Flores, a larger sample will eventually be available for study.

Dental indicators of hand preference

Analysis of the postcranial skeleton is not the only way of determining asymmetries, and handedness in hominins has also been inferred in other, perhaps less obvious, ways. Bermúdez de Castro *et al.* (1988), for example, have identified striations made by tools on incisors and canines attributed to Middle Pleistocene hominins. From striations on the buccal surface of 19 teeth found at the Atapuerca site of Sima de los Huesos, Bermúdez de Castro *et al.* (*ibid*) inferred that these hominins were predominantly right-handed, as the location and orientation of the striations suggested that material of some nature was being held between the teeth and cut or scraped with the right hand. This assertion was further supported by experimental replication of this activity which identified the same striation patterns as found on the Sima de los Huesos teeth. A further study by Fox & Frayer (1997) looking at the teeth of Neanderthal individuals from Krapina found a similar right-handed pattern of non-dietary striations in six out of seven of the individuals who showed a side preference (and 90% of all documented cases they reviewed). As a control sample, the authors note striations of a similar morphology to those found in the Neanderthal teeth in a sample of bear teeth also analysed from Krapina. They conclude that there is no particular pattern of side dominance in the bear teeth sample, supporting the assumption that the hominin teeth striations are non-dietary in origin.

In contrast, Bax & Ungar (1999) urge caution when interpreting patterns of tooth striations. Their study compared striations on the teeth of 66 individuals from modern populations where subsistence strategy was known and found no relationship between striation orientation and handedness (although it should be noted that the authors assumed a right-hand dominance for the individuals represented in the study). The lack of a significant relationship was also evidenced for the modern populations where tools were known to be scraped along the incisors. The results lead Bax & Ungar (*ibid*) to question the link between hand-use and tooth striations unless the hominins studied were using their teeth in different ways to modern humans as represented in their study.

Neuroanatomical evidence for hand preference

Fossilised cranial material also provides an opportunity to make assessments of hand preference in hominins, albeit in a more indirect method than either the postcranial or dental material. From preserved cranial vaults it is possible to make endocasts, which take an impression of the inner surface of the cranium and can potentially provide information on the size, structure and organisation of the cortical surface of the hominin brain. Perhaps the main focus of the study of hominin endocasts is to ascertain the language capabilities of these individuals; however, it is also possible to use this information to make tentative assessments of their hand preference. This is based on the assumption that handedness and language arise from a single brain mechanism related to brain asymmetry (Crow, 1998).

Holloway & De La Coste-Lareymondie (1982) assessed petalial asymmetry in 41 partial and complete endocasts of australopithecines and members of the *Homo* genus for which data were available. Petalias are defined as the "greater protrusion of one cerebral hemisphere relative to the other as expressed at the frontal and occipital poles of the brain" (Phillips & Sherwood, 2007: 2398). In *Homo sapiens*, the predominant pattern is for a left hemisphere occipital protrusion and a right hemisphere frontal protrusion. What Holloway & De La Coste-Lareymondie found is that, when compared to asymmetry in modern *Homo sapiens*, australopithecines and early *Homo* did not show any significant differences in their patterns of left-occipital and right-frontal petalias, while significant differences did exist when *Australopithecus* and *Homo* specimens were compared with great ape endocasts. Falk (1983) compared the partial frontal lobe endocasts of two early hominins (1.75 - 2mya) from Koobi Fora, KNM-ER 1470 (*H. rudolfensis*) and KNM-ER 1805 (probable *H. habilis*) and concluded that, while KNM-ER 1805 showed an ape-like pattern of frontal lobe fissure morphology, the left frontal lobe endocast of KNM-ER 1470 had a human-like morphology of the analogous Broca's region. While the taxonomic assignment of these crania is problematic, these findings suggest that there was likely to have been some change in brain organisation (and therefore potentially in lateralisation also) around the time of the emergence of the genus *Homo*.

Several endocasts have been made for both Asian and African *H. erectus* specimens. Holloway (1980) analysed endocasts for five *H. erectus* specimens from Solo, Indonesia (Ngandong) and found that four out of five endocasts exhibited the left-occipital, right-frontal petalia pattern common to modern humans. While it was not possible to gain any information about the sulcal morphology of the Solo specimens, Holloway noted that the left lobes were 'pronounced' in the region of the Broca's area in all of the endocasts. Together, these findings led Holloway to propose that right-handedness was present in these individuals. For the African *H. erectus* KNM-WT 15000 (the 'Nariokotome Boy'), Begun & Walker (1993) also identified a human-like petalia asymmetry, although the occipital lobes were approaching symmetry.

What has emerged from the study of hominin brain endocasts is that a human-like pattern of petalia asymmetry was established in early *Homo* and is likely to have been present in *Australopithecus* also. In addition, there is evidence of expansion of the Broca's region (or its homologue) in early members of the human genus. However, caution should be exercised when interpreting the results of such analyses. As Falk (1986) points out, data gained from endocasts, while useful, must be regarded as superficial. From a methodological stance, Watkins *et al.* (2001) note that petalias may result from displacement of the hemispheres, rather than a difference in the amount of brain tissue. The deformation present in some endocasts should therefore be taken into consideration when interpreting petalia data. With regards to the functional significance of petalias, Amunts *et al.* (1996) highlight how little is known about the relationship between brain morphology and neurological function. Chance and colleagues (Chance *et al.*, 2005; Chance & Crow, 2007) have suggested that petalia asymmetry is not related to lateralisation of language. Through their work on the brains of individuals with schizophrenia, Chance *et al.* (2005) found that the brains of individuals with schizophrenia did not differ significantly in their petalia asymmetry from the brains of individuals without schizophrenia. They did however find significant differences between these groups in terms of hemisphere volumes. Therefore, caution needs to be exercised when relying on the evidence from hominin brain asymmetry to make assessments of hominin hand preference. While it may be possible to draw firmer conclusions regarding language capabilities from this data, conclusions regarding hand preference should be considered tentative at best.

Problems with assessing fossil evidence

There are clear problems with attempting to identify handedness in hominin skeletal material. The most obvious of these is the paucity of fossil material available for study. Handedness has most traditionally been assessed from the bones of the arm (due to the more common occurrence of these larger elements in the fossil record), with hand bones very rarely being represented. As was illustrated above, many species of hominin are represented by very few and fragmentary hand bone remains, and for some species (e.g. *Homo rudolfensis*), there appears to be no hand bones at all (or indeed upper limb bones in general). During excavation, if it cannot be determined that all bones come from the individual being studied, then of course this will affect the asymmetry that can be determined from the individual.

When suitable material is available for study, the lack of paired bones makes an assessment of individual asymmetry challenging at best. For the hand bones in particular, ordering and siding of bones can also be an issue. Unless damaged, the metacarpals are easily identifiable, but for the phalanges this can be much more difficult and is often not attempted in studies. This has led to finger asymmetry being poorly understood, both in extinct and extant populations.

The methods by which asymmetry is assessed can also be an issue in this research. Traditionally, asymmetry has been determined through analysis of metric properties of the bone such as length, diameter and circumference. Problems arise using this methodology when the bone is fragmentary, damaged or altered during fossilisation. The complete size of fragmentary bones can be estimated, and this adjustment must always be taken into account when drawing conclusions regarding asymmetry. Analysis of muscle attachment site development can also be used to determine asymmetry. When paired attachment sites differ in the nature and degree of their development, then it can be assumed that the more strongly developed of the two will be on the arm that was most commonly stressed. Of course, a pair of muscle attachments sites is required to make this kind of comparison. Information about sex and age of the individual is also required, as it has been shown that muscle attachment morphology is affected by these variables (e.g. Robb, 1998; Wilczak, 1998).

One final problem is that, for the reasons outlined in this section, very little research into the hominin arm and hand is directly concerned with hand preference and asymmetry. The majority of research is focused on the tool-making and using capabilities of the hominin upper limb. But as outlined in the introduction, understanding the development and expression of asymmetry in *Homo* will allow a fuller understanding of the evolution of our genus. The information needed to make asymmetry assessments can be found in the published literature and further attempts must now be made to use it to its full potential.

Summary of fossil data

Although severely hampered by the paucity of suitable paired remains, there is potential for studying the development of asymmetric hand-use over the course of hominin evolution. With the current available material, a right-side dominance in metric and muscle properties has been shown for the Neanderthals. Earlier in the course of hominin evolution, the evidence for hand preference is much less clear, although it can be tentatively concluded from the evidence that a right-side dominance was present in *Homo* prior to the emergence of the Neanderthals. When this move towards a right-hand preference would have occurred is unclear based on the skeletal evidence alone. It is possible that the archaeological evidence or the great ape evidence may be able to shed more light on this issue and determined in more detail whether modern human-like hand preference was emerging prior to the appearance of *Homo*, or whether it was the development of stone tool-making and using behaviours that drove a move towards population-level right-handedness.

The skeletal record does have more to offer, however. The discovery of the Stw 573 *Australopithecus* skeleton (Clarke, 1999) will eventually provide the opportunity to study what will hopefully be a complete set of upper limb bones, from what is a crucial period of hominin evolution. The existing upper limb material may also be able to tell us more about upper limb asymmetry. Until now, the main focus of research into the upper limb has been to understand the functional evolution of the hand and arm. While paired bones that can be confidently said to originate from the same individual are extremely rare, careful comparisons between bones controlling for body mass, age and sex may allow more general asymmetry analyses to take place, thus increasing our understanding of this uniquely modern human trait.

Archaeological evidence for hominin hand preference

The emergence of stone tool manufacture

Toth (1985) is perhaps the most commonly cited study that attempts to identify handedness in the lithic record. In his study, Toth uses the orientation of cortex on flakes detached from a core as an indicator of the hand preference of the knapper. This is based on the assumption that a right-handed knapper will rotate a core clockwise (anti-clockwise for a left-handed knapper) and this will be reflected in the position of the cortex left on detached flakes. This, of course, will only work for those flakes taken from the outer surface of the core. Toth's experimental findings were interpreted as supporting the presence of preferential right-handed knapping at the Lower Pleistocene site of Koobi Fora, Kenya (1.9 – 1.4 ma) and the Middle Pleistocene site of Ambrona, Spain (0.4 – 0.3 ma).

Although widely cited, Toth's methodology has attracted criticism. Analysing the flakes produced by a group of modern-day knappers, Pobiner (1999) found that handedness as indicated by flakes did not necessarily correspond with the handedness reported by the knapper. When flakes from multiple knapping sessions were compared, it was found that handedness (as identified from the flakes) changed from session to session for some knappers. Two of the knappers produced equal amounts of right- and left-handed flakes, and one of the right-handed knappers only produced left-handed flakes in certain sessions. In addition, this method does not take account of the fact that many tools are not made using the core rotation technique identified by Toth. Bifacial flaking, for example, is ignored (John McNabb, pers. comm.). Even when focussing replication experiments only on single-platform core production, the clockwise knapping direction is not maintained (Patterson and Sollberger, 1986; Uomini, 2005; *contra* Ludwig and Harris, 1994). The nature of these results, as well as their inconsistency, suggests that examining the orientation of cortex on flakes is unlikely to be a reliable method of assessing handedness in the lithic record.

In response to some of the problems found in Toth (1985), Rugg & Mullane (2001) outlined a methodology that uses the degree of skew in the cone of percussion of knapped flakes to identify the handedness of the knapper. The use of direct percussion to remove flakes for a stone core leaves identifiable traces on the core and the detached flake. The cone of percussion is, as the name suggests, a cone-shaped feature from which ripples extend, originating at the point at which the core was struck. The hypothesis was tested that hand preference would influence the direction from which the core was struck and therefore it would be possible to identify the hand preference of the individual knapping from the angle of the cone of percussion. Rugg & Mullane (2001) found that 75% of their sample could be accurately sided by this method when the hand preference of the knapper was known. Although the sample size (N = 75) was small, this methodology has potential to add to the techniques available for the analysis of hand preference in stone tool manufacture.

Homo heidelbergensis to early Neanderthals

According to experiments by White (1998), the knapping method for making twisted ovate bifaces can reveal hand preference. This is related to the flaking order that reveals which hand held the handaxe (see Uomini [2008] for a detailed discussion) (see Fig. 1). A right-handed knapper produces the Z-twist that is characteristic of most archaeological twisted bifaces, found in Britain from 362 kya to 334 kya (Evans, 1897; White, 1998), in France from 478 kya to 242 kya, and at Melka Kunture in Ethiopia around 800 kya (Galloti & Piperno, 2003). However, all the possible production methods for twisted ovates are not yet established (Saurel, 1990; Winton, 2004). Therefore, alternatives remain to be confirmed through detailed technological analyses of lithic assemblages.

The use of asymmetrical tool form to identify handedness in production has been continued by Cornford (1986), who found asymmetry in long sharpening flakes at the La Cotte de St Brelade site in Jersey, presumed to have been knapped by Neanderthals. The method of producing these sharpening flakes led Cornford to suggest that asymmetry in the position of the bulbar surfaces could be used to ascertain the hand preference of the knapper. The right-side bias in the position of bulbar surface facet on the flakes in this sample suggested that between 71% and 84% of the flakes were made by right-handed people.

Homo sapiens

The Palaeolithic tools studied by Semenov (1964) were examined for their use-wear traces. These consist of asymmetrical evidence from use. Semenov's reconstructions of how these tools (bone retouchers, stone scrapers) were held and used led to the conclusion that most of the tools were used by right-handed people (Uomini, 2008). Further use-wear traces indicating a right-hand preference were found on Mesolithic and Neolithic drilling tools (Cahen *et al.*, 1979; Cahen & Keeley, 1980; Spenneman, 1984) and on one Lower Palaeolithic handaxe (Keeley (1977).

A consistent pattern was also found in an assemblage of French Mesolithic engraved pebbles based on S.E.M. (Scanning Electron Microscopy) analyses of the direction and angle of movement of the engraving tool (D'Errico, 1988, 1992). All 27 pebbles were engraved with the right hand. The bimanual holding configuration corresponds to the preferred modern-day pattern for spontaneous engraving, in which the pebble is held in the left hand and the engraving is done with the right hand (Uomini, 2006a).

Taken together, the results of these studies support the dominance of the right hand in tool manufacture as far back as early Oldowan tools. These studies also provide a number of interesting avenues for further research regarding identifying handedness (and therefore laterality) in the lithic record.

Parietal art

The archaeological record provides an additional way of assessing hand preference in Upper Palaeolithic populations, through the analysis of cave and rock art. The oldest rock art identified so far has been found in western Europe, dating back some 30,000 years or more (Valladas *et al.*, 2001). Hand images have been dated (using uncalibrated carbon-dating) at two sites in southern France, at Cosquer Cave and Gargas Cave, to between 24 and 27 kya (Clottes, 1998). At Gargas, a bone chip embedded in a hand stencil was dated, and at Cosquer, charcoal from the stencils themselves was analysed.

Representations of the hand are one of the most enduring and numerous of all forms in prehistoric rock art, thus providing a large body of evidence from which to assess hand preference in past populations. In rock art, hand preference can be tentatively ascertained through assessment of one of the most prevalent forms of prehistoric art – hand prints or hand stencils. Hand prints are created by covering the palmar surface of the hand with a paint substance and creating a 'positive' print of the hand on a surface. Hand stencils are created by placing the hand upon a surface and then applying pigment (either by blowing paint through a tube, spitting or using a brush) around the hand to create a 'negative' print of the hand (Fig. 2). Hand prints can therefore be considered to represent an impression of the dominant hand, whereas the hand stencils are likely to represent an impression of the non-dominant hand, if we assume that the 'artist' needed his or her dominant hand to assist with the painting process. However, it has been suggested (Pager *et al.*, 1991) that 'positive' hand prints can feasibly be made by both the dominant or non-dominant

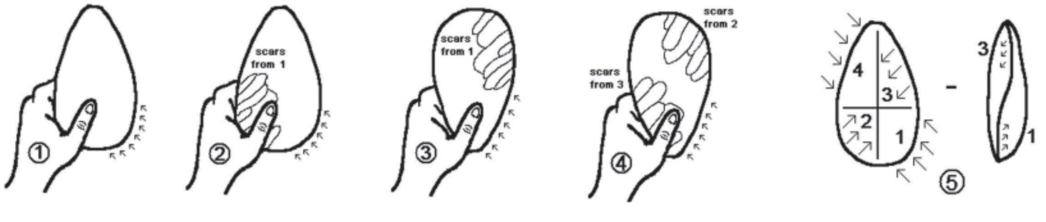

Fig. 1 - Diagram of right-handed knapping sequence for twisted ovates proposed by White (1998), reducing one "quarter" of each face of the piece at a time: 1. base of first face; 2. base of second face; 3. tip of second face; 4. base of first face; 5. the finished handaxe with Z-twist. Drawn by N. Uomini.

hand, whereas the 'negative' stencils are likely to have been made with the non-dominant hand, thus leading Pager *et al.* (*ibid*) to propose that hand prints are not a reliable indictor of handedness.

From the collections of hand prints/stencils where it has been possible to assign the hand used to make the image, it would appear that the overwhelming majority suggests a right hand dominance. The reported frequencies hand stencils and prints in Europe, Australia, the Americas, and Borneo show statistically significant departures from 50% ($p< 0.01$) in all cases (detailed in Steele and Uomini, 2005). The universality of these proportions is consistent with a right-handed pattern. In experimental cave painting, right-handers prefer to make stencils by pressing their left hand against the wall (C. Gilabert, pers. comm.), especially when spraying pigment through a tube held in the right hand (Faurie & Raymond, 2004). The left-hand stencil preference may reflect a postural bias to standing on the left leg (Auerbach & Ruff, 2006), or it may be constrained by a preference to hold the pigment container, torch, or blowing tube in the right hand. Conversely, the right-hand print preference may be related to a more direct link with the hand used to paint cave art when the pigment is applied with fingers, which would indicate a right-hand dominance for drawing in the Upper Palaeolithic. Together, this research supports the establishment of a strong right hand preference for most activities before the appearance of Upper Palaeolithic rock art in Europe.

It may also be possible to assess hand preference from the orientation of animals in paintings. Pager *et al.* (1991) found that, in a study of a hundred school children, all the left-handed children drew animals that faced to the right, whereas all the right-handed children studied drew their animals facing to the left. This trend was also found by Perelló (1970) and Alter (1989). This suggests an interesting alternative avenue of investigation. On the basis of these results, Willcox (1959) found that between 50.6% and 62.3% of the European and African rock studied showed animals facing to the right, i.e. consistent with being drawn by a left-handed person. Such a high percentage of apparently left-handed individuals, when compared to other lines of evidence, suggests that, unless there is a unique activity represented by the paintings, the orientation of animals in rock paintings may not be the most reliable method for assessing handedness in these populations. Further research is needed in living humans to ascertain whether handedness does in fact influence drawing orientation and what possible role language may play in the representation of these images.

Fig. 2 - Hand stencils from Gua Masri, Kalimantan, Borneo. Photo by L.-H. Fage.

Problems with assessing archaeological evidence

The prehistoric evidence for hand preference is fraught with similar problems as the fossil material. While stone tools have somewhat better preservation than bones, their indirect link to hand-use makes them ambiguous. Although material culture data abound throughout prehistory, very few have been studied for lateralised traces. The lithic material that has been studied for hand preference is often based on methods that have been subsequently shown to be unreliable (e.g. the Toth study), or on methods that remain to be validated with large-scale controlled experiments (e.g. the cone of percussion method, twisted ovate production, handprints and hand stencil making, drawing animal figures). Furthermore, some of the older handedness data (Semenov's scrapers, drilling tools) could benefit from being revisited with modern techniques and tools.

It is difficult to identify individual signatures in tool manufacture and use. Well-preserved traces of individuals are rare (Gamble & Porr, 2005), and these often do not yield any hand preference data. Nonetheless, the La Cotte scrapers and the Mesolithic engraved pebbles illustrate how an experimentally-validated, large-scale study can yield rich information about the hand preferences of people at a specific site. These are isolated points in time but they give important windows into contemporaneous groups. The archaeological data for hand preference exist, but they have not yet been interrogated for their full information potential.

Hand preference in great apes

As our closest living relatives, the great apes provide an interesting model for the evolution of human handedness. If precursors of human handedness were present in a common ancestor of humans and apes, the laterality of great apes would help us to understand the evolution of human handedness. In addition to their phylogenetic proximity, the great apes also display some particularly interesting characteristics. Their hands are similar to those of humans in terms of morphology and manipulative skills (Byrne *et al.*, 2001). They can manufacture and use tools (Goodall, 1964). They can use bipedal locomotion (Videan & McGrew, 2002). They exhibit some abilities for language (e.g. bonobos, Savage-Rumbaugh *et al.*, 1986). All of these features have been proposed as mechanisms fostering the evolution of hemispheric specialisation. Hand preference has been extensively studied in non-human primates, but the results have often been contradictory and inconsistent. Therefore, despite a substantial database, this topic remains highly controversial (Warren, 1980; Palmer, 2002; Papademetriou *et al.*, 2005). We present here four of the main hypotheses regarding hand preference, and the associated predictions for hand-use in non-human primates. We review the relevant data in great apes, and discuss how these relate to the hypotheses presented.

The *'postural origins theory'* of MacNeilage *et al.* (1987) proposes that laterality arose from an adaptation to unimanual predation in primitive primates. In 1987, MacNeilage *et al.* examined the available data in non-human primates. They reported that left-hand preferences were found for reaching, while right-hand preferences were found for manipulation, among other things. They suggested that "primate handedness patterns evolved with structural and functional adaptations to feeding, that they are precursors to aspects of human left- and right-hemisphere specialisation patterns, and that they evolved in the following order" (MacNeilage *et al.,* 1987: 247). First, the left hand would have been specialised for visually guided reaches, the right hand being specialised for postural support (MacNeilage, 1993). This pattern would have evolved in arboreal prosimians. Later, as primates became more terrestrial, and with the development of the opposable thumb, the right hand would have become specialised for manipulation and bimanual coordination. According to this hypothesis, left hand preferences should be found for reaching (particularly in low primates species), and right hand preferences should be found for manipulation in higher primates.

The *'bipedalism theory'* suggests that the appearance of handedness in humans was related to the emergence of bipedalism. Bipedalism could have directly led to brain lateralisation and handedness. The shift from a quadrupedal posture to a less stable bipedal posture (less postural support, higher centre of gravity) would have made the problem of balance control more complex, which would have required an increase in cerebral skills. Lateralisation would have been selected as a solution to improve brain abilities, for maintaining balance in a bipedal posture (Sanford *et al.*, 1984; Falk, 1987; Westergaard *et al.*, 1998).

According to this theory, when in a bipedal posture, non-human primates should exhibit hand preferences more similar to those of humans. The bipedal posture should enhance the use of the right hand and reveal human-like group-level right bias in primates. Alternatively, bipedalism could have indirectly influenced the emergence of brain lateralisation and handedness by releasing the hands from the duties of postural support, making them available for some other activities that have been proposed to be related to the emergence of handedness (e.g. gestural communication, tool-use) (Bradshaw, 1991).

The *'tool-use theory'* proposes that handedness evolved as an adaptation to bimanual coordination for tool manufacture and use (Kimura, 1979; Frost, 1980; Provins, 1997). A related theory proposes that brain lateralisation would be linked to throwing (Calvin, 1983). The cognitive requirements of tool-use and throwing are high, and may have created selective pressures for the emergence of brain lateralisation and handedness. From this hypothesis, non-human primates are expected to exhibit strong and right-biased preferences for tool-use and/or throwing.

The *'task complexity theory'* was formulated by Fagot & Vauclair (1991). Based on consistent evidence from primate hand-use data, it predicts that strong individual preferences and group-level biases for hand-use should be more likely to appear in complex tasks. Task complexity can be related to different factors such as novelty, precision of the action, accuracy of the action, number of stages necessary to solve the task, number of elements to be combined, the need to use both hands (in similar or complementary roles), sequences of actions, subordinate hand used for postural support, and complex balance control (Uomini, 2006b). According to this theory, more complex tasks should elicit stronger laterality in non-human primates.

We now investigate whether the available data on great ape hand preferences could favour any of the proposed hypotheses. All the studies discussed below involved captive apes, except when they are specified as wild or rehabilitated.

Tripedal reaching

For reaching for items on the ground from a tripedal posture, great apes have been found to be weakly lateralised. Few individuals displayed preferences, with many individuals exhibiting no preference; and no group-level bias has been found (*chimpanzees* - Finch, 1941; Marchant & Steklis, 1986; Hopkins, 1993; Colell *et al.*, 1995a; Hopkins & Pearson, 2000; *bonobos* - Hopkins *et al.*, 1993a; De Vleeschouwer *et al.*, 1995; Hopkins & DeWaal, 1995; *gorillas* - Fagot & Vauclair, 1988; Olson *et al.*, 1990; *orang-utans* - Heestand, 1986; Olson *et al.*, 1990; Hopkins, 1993).

Bipedal reaching

Studies have compared reaching from a tripedal posture with reaching from an experimentally induced bipedal posture (food placed at height). These are reviewed by Westergaard *et al.* (1998). The great apes showed enhanced right hand use to reach from a bipedal posture compared to a tripedal posture (*chimpanzees* - Hopkins, 1993; *bonobos* - Hopkins *et al.*, 1993a, but the reverse was found by De Vleeschouwer *et al.*, 1995; *gorillas and orang-utans* - Olson *et al.*, 1990). Group-level right biases have been found in chimpanzees (Hopkins, 1993) and gorillas (Olson *et al.*, 1990) for bipedal reaching.

Feeding

For the hand that brings food to the mouth, individual preferences have been reported (*wild chimpanzees* - Marchant & McGrew, 1996; *bonobos* - Hopkins *et al.*, 1993a; Shafer, 1997; Harrison & Nystrom, 2008; *wild gorillas* - Parnell, 2001; *orang-utans* - Rogers & Kaplan, 1996 [rehabilitated subjects]; O'Malley & McGrew, 2006). For bimanual feeding, when one hand takes food to the mouth while the other hand holds another food item, a group-level right bias has been reported in captive chimpanzees (Hopkins, 1994), and a right side trend has been found in bonobos (Hopkins *et al.*, 1993a; Hopkins & DeWaal, 1995). A few individual preferences have been found in wild orang-utans (Peters & Rogers, 2008).

Manipulation

In bimanual manipulative tasks, the two hands are engaged in a collaborative action. The hands have different but complementary roles: one hand manipulates the item while the other hand holds the item (Guiard, 1987; Corp & Byrne, 2004). This can occur in food processing and in object manipulation. Wild chimpanzees have been shown to be strongly lateralised for the bimanual processing of *Saba* fruits and lemons (Byrne & Corp, 2003; Corp & Byrne 2004). They had strong preferences, often with the exclusive use of one hand, and almost all of the individuals were lateralised. No group-level bias appeared (Byrne & Corp, 2003; Corp & Byrne 2004). Wild gorillas showed a strong laterality for the bimanual sequential manipulation of plants with defenses (Byrne & Byrne, 1991). The majority of the individuals were lateralised, and the preferences were often exclusive. For one category of plants, there was a group-level trend for using the right hand for fine manipulation while the left hand held the item (Byrne & Byrne, 1991). Rehabilitated orang-utans have also shown some strong individual preferences for holding and manipulating food (Rogers & Kaplan, 1996).

For manipulating an object (e.g. ball, tube) held by the other hand, the great apes have shown strong preferences, with most individuals being lateralised. Preferences appeared at the individual-level in gorillas (Hopkins *et al.*, 2003) and bonobos (Chapelain & Hogervorst, 2008). A group-level left bias has been reported in orang-utans (Hopkins *et al.*, 2003) and a group-level right bias in chimpanzees, which has been replicated in several studies (e.g. Hopkins, 1995) ('tube task', reviewed in Hopkins & Cantalupo, 2005). For tasks requiring to open a box or slide a panel, most individuals appeared to be lateralised, with no reports of group-level bias (*chimpanzees* - Colell *et al.*, 1995b; *bonobos* - Shafer, 1997; *gorillas* - Fagot & Vauclair, 1988; Olson *et al.*, 1990; *orang-utans* - Olson *et al.*, 1990).

Throwing

There is very little data on laterality in throwing. Chimpanzees have been found to exhibit strong hand preferences for throwing (Hopkins *et al.*, 1993b; Colell *et al.*, 1995a), and a group-level right-side trend and bias have been reported (Hopkins *et al.*, 1993b; Hopkins *et al.*, 2005a) (but see Marchant, 1983). A behaviour related to throwing is the pounding of *Strychnos* fruits onto an 'anvil'. Wild chimpanzees showed very strong individual hand preferences for this ballistic movement (McGrew *et al.*, 1999).

Tool-use

The majority of studies on tool-use have focused on chimpanzees. These studies are reviewed in McGrew & Marchant (1997b) and Marchant & McGrew (2007). They reported a strong laterality for tool-use (Marchant *et al.*, 1999, but with the exception of Marchant & McGrew, 2007). Wild chimpanzees have been found to exhibit strong individual preferences for the use of a probe to extract termites from their nests (termite fishing) (Nishida & Hiraiwa, 1982; McGrew & Marchant, 1992; Marchant & McGrew, 1996; McGrew & Marchant, 1999; Lonsdorf & Hopkins, 2005), to use a 'sponge' to drink water from tree holes

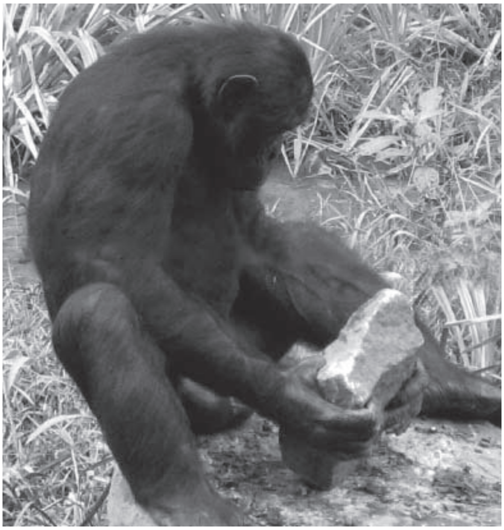

Fig. 3 - A bonobo (*Pan paniscus*) cracking nuts. Lola Ya Bonobo Sanctuary, D.R. Congo. Photo by A. Chapelain

(wadge dipping) (Boesch, 1991), and to use stones to crack open nuts (nut cracking) (Fig. 3) (Boesch, 1991; Sugiyama *et al.*, 1993; Matsuzawa *et al.*, 2001). At the population-level, the majority of individuals were lateralised for tool-use. Individuals were found to have extremely strong preferences, with almost exclusive use of one hand (McGrew & Marchant, 1997b). No group-level bias has been found for tool-use (McGrew & Marchant, 1996). One study reported a group-level left trend for termite fishing (Lonsdorf & Hopkins, 2005). In orang-utans, individuals have shown hand preferences for making, modifying and using tools, with tool-use evoking the strongest laterality relative to the other tasks (O'Malley & McGrew, 2006). For bonobos, data indicate individual preferences for tool-use (Chapelain, unpublished data; Harrison & Nystrom, 2008).

Gestures

Laterality has also been found in gestural communication, both spontaneous and induced (Hopkins *et al.*, 2005b). Chimpanzees showed a group-level right preference for begging for food from the experimenter (Hopkins & Leavens, 1998; Hopkins & Wesley, 2002; Hopkins *et al.*, 2005b). For clapping the hands together to attract the attention of humans, chimpanzees showed strong, quasi-exclusive, individual preferences, and almost all individuals were lateralised (Fletcher, 2006). In bonobos, a weak laterality has been reported for various spontaneous gestures (intraspecific and interspecific), with most individuals being ambipreferent (Hopkins *et al.*, 1993a; Hopkins & DeWaal, 1995; Shafer, 1997; Harrison & Nystrom, 2008), but strong individual preferences have also been found for spontaneous and induced gestures (Chapelain *et al.*, unpublished data).

Other behaviours

Individual preferences have been found in self-directed behaviours (e.g. *in bonobos* - Hopkins *et al.*, 1993a; Hopkins & DeWaal, 1995; Shafer, 1997; *in wild and captive chimpanzees* - Boesch, 1991; Marchant & McGrew, 1996; Fletcher & Weghorst, 2005; Mosquera *et al.* 2007). Group-level preferences have been reported for cradling, for which great apes could exhibit a left side bias (see Damerose & Vauclair, 2002 and Hopkins, 2004 for a review and discussion). Individual preferences have been found for carrying in chimpanzees (Marchant, 1983; Fletcher & Weghorst, 2005) and a group level left bias has been found in bonobos (combined data from Hopkins et al., 1993a and Hopkins & DeWaal, 1995).

In summary, these studies have shown that great apes exhibit degrees of hand preferences. Manual laterality has been found to be weak for simple tasks such as tripedal reaching, but strong for complex tasks that require developed cognitive skills. For bimanual coordinated actions and for tool-use, individual preferences were very strong and the majority of the individuals were lateralised. At the group-level, biases have been found only for certain behaviours (e.g. bimanual feeding, bimanual 'tube task', bipedal reaching, gesturing) and they never reached a human-like handedness bias.

With regards to the four hypotheses, these data bring further clues to the discussion of handedness origins and expression, but the current database does not allow us to draw any final conclusions.

Regarding the *'postural origins theory'* (MacNeilage *et al.*, 1987), there may be some support for a group-level right bias for manipulation (e.g. the trend in gorillas for food processing [Byrne & Byrne, 1991] and the tube task in chimpanzees [Hopkins & Cantalupo, 2005]), but there are many negative findings (e.g. bimanual coordination and object manipulation), and this theory is generally refuted by the data (McGrew & Marchant, 1997a; Papademetriou *et al.*, 2005).

Consistent with the *'bipedalism theory'*, an induced bipedal posture enhanced the use of the right hand, and some group-level right biases have been reported in chimpanzees and gorillas for bipedal reaching (Olson *et al.*, 1990; Hopkins, 1993. However, further controlled studies would be necessary to disentangle the factors involved, as high laterality may be related to the complexity of the task rather than bipedal posture *per se*.

For tool-use, the majority of individuals were lateralised and with very strong individual preferences, which would support the tool-use hypothesis. This strong laterality could be related to the specific cognitive requirements of tool-use (McGrew *et al.*, 1999; Harrison & Byrne, 2000), or to the cognitive skills related to complex manipulations (Steenhuis & Bryden, 1989; Boesch, 1991; Byrne & Byrne, 1991; Matsuzawa, 1991, 1996; McGrew & Marchant, 1992, 1997a, 1997b; Marchant & McGrew, 1996; Harrison & Byrne, 2000; Byrne *et al.,* 2001; Hayashi & Matsuzawa, 2003; O'Malley & McGrew, 2006; Hayashi, 2007), and/or coordination with the object (same temporal and spatial coordination skills as bimanual actions) (Fagot & Vauclair 1991; Rogers & Kaplan, 1996; Harrison & Byrne 2000; Corp & Byrne 2004). There was a case of weak laterality for tool-use, but this was for an arboreal tool-use where the postural requirements may discourage lateralised behaviours (Marchant & McGrew, 2007). No group-level right bias has been found for tool-use, which fails to support the prediction of the *'tool-use theory'* (Kimura, 1979; Frost, 1980; Provins, 1997). The 'throwing theory'(Calvin, 1983)may be supported by Hopkins *et al.* (2005a), who reported strong preferences and a group-level right bias for throwing in chimpanzees.

The theory of *task complexity* (Fagot & Vauclair 1991) is strongly supported by the data. Manual laterality appeared to be weak for simple tasks such as tripedal reaching, and strong for complex tasks that require high cognitive skills like bimanual coordinated manipulations. In complex tasks, the apes have shown strong hand preference, and these tasks have elicited group-level trends or biases in some cases.

Problems with assessing hand preference in non-human primates

Several important methodological issues emerge from the literature review, and these are discussed in the following sections.

Task specificity

Since the earliest studies on non-human primates (e.g. Kounin, 1938), researchers have shown that hand preference depends on the task that is used to assess laterality (Warren, 1980; Fagot & Vauclair, 1991; McGrew & Marchant, 1997a; Papademetriou *et al.*, 2005). This has been consistently reported and is generally accepted: the strength and direction of preference vary according to the task (Sanford *et al.*, 1984; Heestand, 1986; Fragaszy & Mitchell, 1990; Byrne & Byrne, 1991; Hook-Costigan & Rogers, 1995; Anderson *et al.*, 1996; Marchant & McGrew, 1996; Ward & Cantalupo, 1997; Spinozzi & Truppa, 1999; Teichroeb, 1999; Harrison & Byrne, 2000; Chapelain *et al.*, 2006). This raises important issues because the results thus depend on the task that is used to assess the preferences. It is therefore essential to standardise the methods between studies to allow comparisons of the data between studies and species. Disappointingly, there is no consensus between studies regarding their measures. Thus, when considering the available database, it is difficult to get an understandable overview of laterality in non-human primates and to draw any general conclusion.

Task complexity / inappropriate measures

Regarding task specificity, studies have consistently shown that strong preferences and group-level biases would be more likely to appear for complex tasks (as seen above). For humans and non-human primates, the more complex the task is, the stronger the hand preferences are (*for humans* - Annett, 1972; Healey *et al.,* 1986; Bishop, 1989; Steenhuis & Bryden, 1989; McManus & Bryden, 1992; Marchant *et al.*, 1995; Fagard & Corroyer, 2003; Fagard, 2004; Faurie, 2004; Leconte & Fagard, 2006; *for non-human primates* -Warren, 1980; Fagot & Vauclair, 1988; Fragaszy & Mitchell, 1990; Byrne & Byrne, 1991; Colell *et al.*, 1995a; Anderson *et al.*, 1996; Spinozzi *et al.*, 1998; Phillips & Sherwood, 2005; Trouillard & Blois-Heulin, 2005). Complex tasks would then be the most appropriate measures for revealing hand preferences. When considering the methods used to measure hand preferences in apes, Marchant & McGrew (1991) concluded, "the typical task for assessing laterality of function [is] one-handed, non-sequential and gross in movement" (p. 423). Simple tasks tend to be the rule in laterality research. Therefore, the negative results observed could be related to the simplicity of the task rather than reflecting an absence of lateralisation in non-human primates (Byrne & Byrne, 1991; Hopkins, 2006). For future research, there is evidence that an appropriate measure for revealing laterality would be a very complex task, like those involving a precise sequential bimanual manipulation on one object, with a different role for each hand (manipulate vs hold item) (Byrne & Byrne, 1991; Rogers & Kaplan, 1996; Byrne *et al.*, 2001; Uomini, 2006a).

Sample size

One of the main issues with studies of non-human primates is the small size of the samples considered (Marchant & McGrew, 1991; Hopkins *et al.*, 1993a; Hopkins, 2006). This raises important problems in terms of generalisation of the results and weak statistical power of the analyses (McGrew & Marchant, 1997a). Due to the limited availability of primate subjects, most studies have tested very small samples. In their meta-analysis of studies on apes, Marchant & McGrew (1991) reported that, "the paucity of subjects in the typical study of laterality is indicated by the fact that in 78 reports that specify numbers, only 26% had more than 10 or more subjects" (p. 429). In a more recent review, Hopkins (2006) reported that "nearly all individual studies of handedness fail to obtain adequate sample sizes to have a reasonable amount of statistical power"(p. 548). According to Hopkins (2006), a minimum of 59 subjects would be required to detect a group-level bias of the type present in non-human primates (around 65%). Only five of the ape studies reviewed by Hopkins (2006) had sample sizes greater than 59 individuals of the same species. It is therefore possible that the absence of group-level bias, which is the most common result reported, might be related to a small sample size issue. However, an extreme human-like bias would likely appear even with small samples.

Number of data points per subjects

The number of data points per subject has to be large enough to allow detection of the biases with statistical tests (McGrew & Marchant, 1997a). There is a controversy regarding the effect of sample size on laterality, and a debate regarding the most appropriate number of data points (Marchant & McGrew, 1991; McGrew & Marchant, 1997a). For instance, Palmer (2002) has shown an influence of the sample size, and argued that findings calculated on fewer than 25 data points would not be reliable. Other researchers stated that even 50 trials may be too few to reveal laterality (Marchant & McGrew, 1991). The number of data points is a trade-off between testing a great number of subjects and collecting a great number of data points per subject (Hopkins, 2006). This number varies considerably between studies, from 1 (e.g. Hopkins & Leavens, 1998) to 500 (e.g. Peters & Rogers, 2008) data points per subject. It is therefore possible that some studies yielded negative findings because the number of data points was inappropriate.

Data independency

To avoid sampling biases, it is important to ensure that the data points recorded are independent of each other (Byrne & Byrne, 1991; Marchant & McGrew, 1991; McGrew & Marchant, 1997a). This requirement is not always respected in research on laterality. Some researchers record every consecutive action in a behavioural sequence ('frequency'). But the use of one hand may influence the following use of this hand in the subsequent trials of the sequence, and data points would therefore not be independent. In such cases, the sample size would be inflated, and the findings could be biased toward false-positive effects (Byrne & Byrne, 1991; Lehman, 1993; Palmer, 2003). To avoid such effects and ensure data independency, it is advised to record only the first pattern of a sequence of identical actions ('bout'). Each sequence of identical actions is recorded as one bout. The different bouts are separated by an intervening event, 'when a different behavioral pattern performed by the same hand intervenes between two instances of the same pattern' (McGrew & Marchant, 1997a: 206). Thus two different bouts are recorded if separated by an action by which the subject could change its hand, e.g. after the individual has dropped the item.

Individual factors: sex, age, fluctuating asymmetry

It has been thought that only group-level laterality would stem from evolutionary processes, because individual-level laterality could be suspected to derive from individual factors (e.g. fluctuating asymmetry, sex, age) (Vauclair & Fagot, 1987). The effects of sex or age on laterality are unclear. Some studies found no effect of age or sex, while others reported an influence of sex or age on laterality (McGrew & Marchant, 1997a). These factors seem to be insufficient to explain the observed individual variability. However, it would be preferable to avoid including young individuals for which maturation may be incomplete (McGrew & Marchant, 1997a). Fluctuating asymmetry has been suggested to create behavioural asymmetries. It is unlikely, however, because physical developmental asymmetries have been shown to be unrelated to laterality in behaviour (Bisazza et al., 1997, 2002) and much weaker in degree (e.g. Sarringhaus *et al.*, 2005).

Settings: captive vs. wild

We study hand preference in non-human primates to investigate the evolution of human brain lateralisation, to understand when lateralisation would have appeared, and what could have been the selective factors for its emergence. The evolutionary and biological validity of studies on handedness in non-human primates would be challenged if laterality could only be found in captive settings. There are inconsistencies between data from wild and captive animals (see McGrew & Marchant, 1997a; McGrew & Marchant, 2001; Fletcher & Weghorst, 2005; Hopkins & Cantalupo, 2005; Marchant & McGrew, 2007 for discussions). Studies on wild animals generally reported weak laterality with most individuals being ambipreferent (Fletcher & Weghorst, 2005; Hopkins & Cantalupo, 2005). This pattern contrasts with the strong individual preferences and group-level biases that have sometimes been reported in captive animals (e.g. Fagot *et al.*, 1991; Hopkins, 1993). One could argue that this difference between captive and wild findings suggests that the laterality observed in animals might be an artefact of captive conditions. McGrew and Marchant (1997a, 2001) have proposed several factors related to captivity that could have an influence on laterality: disturbed sociality, contact with right-handed keepers, asymmetrical cages, stimuli availability, action repetition, unnatural and complex tasks, and so on. Some differences between the two datasets may be related to some methodological differences (Fletcher & Weghorst, 2005). The methods used in captive and wild studies differ; field studies focused mainly on daily spontaneous activities for which laterality is known to be weak (even in humans, Marchant *et al.*, 1995), while captive studies were mostly interested in experimental complex tasks that are more likely to reveal strong preferences (Rothe, 1973; Trouillard & Blois-Heulin, 2005; Chapelain *et al.*, 2006; Raymond, pers. comm.). Thus the weak laterality observed in wild animals might be related to the simple tasks considered. The strong laterality observed for complex actions in the wild supports this view.

Conclusions

What is known about the evolution of handedness?

The available evidence regarding the emergence and expression of hand preference (and later handedness) suggests that lateralisation may be a shared feature of great apes. Research has demonstrated that great apes exhibit hand preferences that can reach the exclusive use of one hand in complex tasks, and that can be present at the group-level in some cases. However, the strength and direction of laterality depends on the task, and group-level biases are infrequent and never reach the human-like handedness bias. Thus the pattern of laterality observed in apes can be seen to differ from the human pattern. As with brain endocasts, the difference between humans and apes may be one of degree: the brain asymmetry patterns and the hand preference patterns are present, but less prominent, in apes. These similar situations would support the idea of a relationship between hand preference and brain lateralisation.

Furthermore, these allow us to reconcile the two apparently conflicting positions about the origins of human brain lateralisation. A precursor of laterality may have existed in the common ancestor several million years ago (Hopkins, 2006), while at the same time the much stronger laterality seen in *H. sapiens* may be a derived trait specific to humans (Warren, 1980; Byrne & Byrne, 1991; McGrew & Marchant, 1997a; Fagard, 2004). In a continuity framework, this means that the modern state of extreme brain lateralisation and hand preference is likely to have evolved in the hominin lineage after the divergence from the last common ancestor. The fossil and archaeological data only tell us that this was established by the time of the first known hominin explorations out of Africa at 2 mya.

Methodologies

This review has highlighted several methodological problems that are common to all three fields of research, as well as discipline-specific problems. The fossil data available at present yield little information about group-level hand preference due to the general paucity of finds. Individual hand preference can only be ascertained when paired arm and hand bones are preserved. In contrast, stone tools are abundant, making a potential source of data for the group-level. However, the archaeology is less reliable for indicating hand preference in individuals. The living primate data could potentially address both levels of resolution. However, many studies have considered sample sizes that are too small, and are plagued by experimental biases or inappropriateness of the methods. All three disciplines suffer from disparities in methodology, which hinder comparisons and interpretation of their findings. Therefore we would like to underline the need for an increased communication within and between research areas.

What is the potential for future research?

The lack of agreed terminology is a potential hindering factor. Because it is difficult to identify ‘handedness’ in the modern human sense of population-level right hand preference from fossil data, the terms ‘hand preference’ and ‘hand-use’ are rather more appropriate when discussing past handedness. Regarding the available archaeological data, there is a real lack of centralised, standardised experimental reference bases to validate the hypotheses. As discussed above, many experiments have not been replicated and this would be an avenue to pursue.

Regarding research on laterality in non-human primates, the most important issue relates to methodological inconsistencies between studies. This absence of standardisation in the methods makes data comparisons and interpretation very difficult. Therefore, for future research, we would like to emphasize the need to standardise the methods between studies to allow comparisons between studies and species. It is also important to use tasks that are appropriate to reveal laterality, and to consider large samples. To understand the pattern and evolution of hand preference in non-human primates and humans, more data are needed, particularly on wild primates (Miller & Paciulli, 2002) since “the more natural the settings are (close to the environment of evolutionary adaptedness) the more valid the results are likely to be” (McGrew & Marchant, 1997a:210).

One can note that there is little cross-disciplinary interest between the different laterality research areas. For instance, studies on non-human primates often only cite human data very briefly (e.g. ‘there is a 90% right bias in humans’) in the introduction, and then go on to discuss non-human primate data without considering humans. To understand the evolution of laterality it will be necessary to consider studies on humans and non-human primates, as well as other vertebrates. Such a wider approach could shed important new light on the evolution of brain lateralisation. We therefore encourage cross-disciplinary collaborations for future research into this fascinating feature of human evolution.

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Info on the web

www.talkorigins.org

Information and debates relating to all aspects of hominin evolution

www.atapuerca.com

Up-to-date information regarding the ongoing excavations at Sierra de Atapuerca

www.bradshawfoundation.com/hands

Compilation of rock art images of hands

http://airto.bmap.ucla.edu/BMCweb/Consent/edinburgh.html

Reproduction of the Edinburgh Handedness Inventory, commonly used to assess hand preference in modern humans

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