‘Humans, tools and handedness’

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Chapter 15

Humans, Tools and Handedness

James Steele & Natalie Uomini

Precision tool use typically involves preferential use of a dominant hand in humans and some other animal species, and in humans the right hand tends to be the preferred hand. We outline conventional criteria for recognizing handedness in living subjects, and summarize some recent genetic models of the stability of human handedness as a polymorphism. We then summarize skeletal and (in greater detail) material-culture evidence for hand preference in the fossil and archaeological records. Such observations suggest that right handedness has been predominant even in early species of our own genus, although the fossil sample is exceedingly small.

The roles of the hands in tool-using tasks

Skilled tool manipulation usually falls into the category of asymmetric or differentiated bimanual activities (Guiard 1987, 487). With remarkable consistency, individuals divide the work between their two hands in a predictable and regular fashion. More specifically, one hand tends to be preferred as the one that executes an action on the object, while the other hand stabilizes the object. Most remarkably, in about eight or nine out of ten individuals it is the right hand that is selected to play the leading role (making it the dominant hand). This role typically involves finer movements, in terms of both spatial and temporal resolution (Guiard 1987, 497). The pattern is exemplified by stone knapping, where the dominant hand wields a hammerstone to strike a core that is supported by the non-dominant hand.

This pattern of population-level hand preference seems to distinguish us from other living primates, among whose populations and species it is hard to discern any such bias. Because our own right-handed bias seems to be related, via the linking mechanism of cerebral dominance, to another unique human feature (language processing: e.g. Hécaen & de Ajuriaguerra 1964; Bradshaw & Rogers 1993), an enormous volume of research has been dedicated to its understanding. In this chapter we shall introduce some aspects of the research literature in psychology and behaviour genetics, to provide context for our own archaeological interests. We shall then discuss some skeletal and material-cultural markers of hand preference that may enable us to track the evolution of human handedness empirically.

Measurement of handedness

Handedness is measured in a variety of ways, which are either preference based or performance based (McManus 1996). Skill and preference tend to be highly correlated, although there are exceptions. Skill is usually measured by comparing the two hands in rapid aimed movement tasks such as the Annett pegboard task (Annett 1970), which measures how fast each hand can move ten pegs in a board from one row of holes to another. Handedness is assessed by calculating the relative speed advantage of the more skilled hand, and is therefore treated as a continuous variable. Preference is usually measured by questionnaires which ask about the preferred hand for each of a series of tasks, and in which the respondent indicates the strength of the preference on an ordinal scale (e.g. Always Right, Usually Right, Either, Usually Left, Always Left). Responses are usually summed into a Laterality Index by allocating values (e.g. +2, +1, 0, –1, –2) to each position on such a scale. In younger children and non-human primates, for whom a questionnaire is inappropriate, preference may instead be directly observed in a series of simple tasks.

Both measures give comparable results when used to determine broad patterns of left- and right-hand use at the population level. The preference measure has been more widely used, perhaps because it is simpler to administer. Inevitably some questionnaire items are subject to culturally-learned biases, a factor that obviously complicates interpretation of the most simple preference measure used in literate societies (the writing hand). However, there is some well-designed research using both skill and preference measures, which indicates that questionnaire responses can be analyzed and a factor identified relating to precise motor control which is impervious to cultural influences (Connolly & Bishop 1992).

One group of researchers has attempted to collect data in an ethological manner, resembling the way handedness data is collected for non-human primates such as chimpanzees. They found that human manual preference in non-tool-using tasks is less right biased than implied by the questionnaire measures (which are heavily biased towards object manipulation tasks). Marchant *et al.* (1995) tabulated hand use observed in ethnographic videos from groups of three traditional cultures (G/wi, Yanomamo, and Himba) using the kind of task classification that would be used in an ecologically-valid primate study. Examples of behavioural categories of limb movements included reaching for objects, scratching oneself, eating, and using tools. Their results evidenced a barely-discernible right hand preference for all tasks at the population level, although a stronger right-hand bias was found for tool use only (particularly where it involved a precision grip, which agrees with Guiard 1987).

Asymmetries in hand skill and movement control

In explaining the functional neurology of human handedness, most researchers take the right-hander as their prototype. Hand skill is often measured by aimed movement tasks (such as the Annett pegboard task, described above), and right-handedness is generally explained by reference to a left hemisphere advantage for fine temporal resolution of sensory input and motor output (Carson 1993). An advantage for the dominant hand is usually seen not in simple ballistic movements, but in movements of greater difficulty (in the Fitts' Law sense, Fitts 1954; also in terms of finer spatial and temporal resolution, Guiard 1987). Flowers (1975) hypothesized that in movements of greater difficulty as measured using Fitts' Index, and which imply a 'corrective mode of control', the dominant hand would have an advantage because of an underlying advantage in the rate of information transmission. Carson (1993, 481) discusses two explanations for this advantage. One is the 'feedback processing' model, which proposes that the left hemisphere is more efficient in error correction using sensory feedback. The other is the 'output variability' model, which proposes that the left hemisphere permits more precise control of net forces and force durations. There is still considerable uncertainty regarding which of these models is more valid.

There is also considerable debate regarding the level of organization at which neurophysiological asymmetry is found. A voluntary bimanual movement can be analyzed in terms of three levels of organization (Peters 1995, 201). These are Level 1 (the level at which the goal is formulated), Level 2 (the level at which 'the precisely timed commands for the initiation and termination of the movement trajectories of the two hands are issued': Peters 1995, 202), and Level 3 (the level 'which governs the final outflow of control for the particular hand that allows the hand to perform the movement as required': Peters 1995, 203). Peters (1995) favours an asymmetry in attentional processes which influences hand skill at Level 1, while Sainburg (2002) suggests that the causal agent is an asymmetry in the control of limb segment inertial dynamics which occurs downstream from the trajectory planning level. It is beyond the scope of this chapter to do more than note these debates, and point out their relevance to understanding the kinds of skilled movement control involved in the knapping gesture (e.g. Roux *et al.* 1995; Roux 2000).

Explanations of the prevalence of left- and right-handedness

The observation that other living primates do not show as strong a right-handed bias as humans at the population level (MacNeilage *et al*. 1987; Marchant & McGrew 1991; Sugiyama *et al.* 1993) has led some evolutionary psychologists to conjecture that the initial ratio of right and left-handedness was 50:50 in early hominins. If this is correct, then the present ratio of about 90:10 in humans can only have arisen subsequently through natural selection. This implies that right-handed individuals had a reproductive advantage, namely that the genes associated with right-hand dominance were positively selected for and were able to spread via Mendelian inheritance through our species. From this argument it also follows that some explanation must be given for the persistence of a small proportion of left-handers, despite this selection towards right-handedness.

There are several competing explanations for the present-day incidence of right- and left-handedness, and three of these will be detailed below. Some postulate that human right-handedness is the norm, and that left-handedness is pathological; however, there is little empirical support for such an extreme position. Others have proposed that while there are disadvantages to left-handedness, compensating advantages may accrue which are frequency-dependent. Most commonly, however, the argument is made that handedness is under partial genetic control with significant environmental modification during development. In such models, it is argued that the advantage lies with those who are moderately right-handed, but that the interaction of genetic and environmental influences produces greater phenotypic variation, ranging from left-handedness to extreme right-handedness. All such explanations have to address the empirical findings of an apparently stable underlying prevalence of about 10–15 per cent left-handedness, and of a male excess (about five males are left-handed for every four females: McManus 1996).

The most famous of the explanations which propose that left-handedness is pathological is the Geschwind-Behan-Galaburda hypothesis (Geschwind & Behan 1982; 1984; Geschwind & Galaburda 1985a,b). This proposes that individuals, by default, develop to be right-handed unless there is some testosterone-induced developmental delay in the growth of the fetal left hemisphere, causing not just left-handedness but also atypical language lateralization (and other less intuitive disorders, such as a high rate of autoimmune disease). This hypothesis has been exhaustively examined in clinical studies, and the verdict must now be that it is not supported (e.g. Bryden *et al.* 1994). Other explanations exist which relate left-handedness to developmental neurological disorders, particularly in the context of fetal growth retardation and of premature birth (Bakan 1971; Bakan *et al.*1973; Satz 1972). While such trauma, however, may account for a small fraction of left-handers whose preference is genuinely secondary to fetal brain insult, it does not seem to explain left-handedness in more than about one in twenty cases (Bishop 1984).

A second class of explanation interprets the persistence of left-handedness in low frequencies as due to some cognitive or other advantage, which counteracts any developmental disadvantages. This only works if the frequency of left-handedness stays below some critical level. The evidence for an association between developmental delay and elevated frequencies of non-right-handedness is quite strong, with some studies indicating greater risk for short stature, reduced body mass, and delayed onset of puberty (e.g. Coren & Halpern 1991; Mulligan *et al*. 2001; but see also Eaton *et al*. 1996). Claims for some specific competitive advantage associated with left-handedness are based on apparently elevated frequencies of left-handedness in certain activities and professions (Peterson & Lansky 1977; but see Wood & Aggleton 1991; Mebert & Michel 1980; Gotestam 1990). More recently, an argument for a frequency-dependent advantage for left-handed fighting has been proposed, based on observed elevated incidences of left-handedness in interactive and combat sports (Raymond *et al.* 1996). In particular, because left-handers are in the minority, they are more successful when they fight against right-handers. Such proposals entail specific predictions about the interaction between culturally-variable selection coefficients for left-handedness, and the distribution of variance in reproductive success: higher fitness would be expected for left-handers who live in very violent societies. However, detailed genetic models to support such proposals have not yet been articulated, and until they have been, we should be wary of confusing correlation with causal explanation.

The third class of explanatory models invokes the genetic theory of a balanced polymorphism with heterozygote advantage. The single-locus theories for laterality propose that there is a gene, made up of two alleles (either one can be recessive or dominant), for left-hemisphere cerebral dominance, which causes strong right-handedness as well as language lateralization. Annett (1985; 2002) calls this the Right Shift allele (R+), and the alternative is simply an inactive allele (R–, which we will refer to here as 0). Since each person inherits one allele from each parent, there are three possible genetic combinations (genotypes): 2 R alleles (homozygous), 2 0 alleles (homozygous), or 1 R allele and one 0 allele (heterozygous). In the absence of the R gene, individuals may develop right- or left-hemisphere dominance with equal likelihood as a result of chance environmental factors during development (Annett 1985; 2002; McManus 1985; cf. Laland *et al.* 1995). The reason why we do not all have this gene is because there is an advantage for being heterozygous (R0) at this single locus. It is better to have one allele causing the 'right shift', and another allele which gives no such bias, because their interaction will tend to produce the optimal outcome — moderate left-hemisphere dominance, and thus, moderate right-handedness. Some individuals (00 homozygotes) will have a complete absence of the right-shift gene (which, cultural biases excepted, will tend to produce left-handedness in about half of the cases), and other individuals (RR homozygotes) will have a double dose of the right-shift gene (which will bias towards extreme right-handedness).

The idea of a heterozygote advantage is not new, the classic example being the malaria hypothesis for sickle-cell anaemia (Haldane 1948, cited in Durham 1991, 123). Among the populations of tropical West Africa there are three classes of haemoglobin genotypes: AA, AS, and SS. The A allele is the normal condition for haemoglobin. The recessive S allele is a mutation of the haemoglobin molecule which causes sickle-cell anaemia, but also confers resistance to malaria. People with the AA genotype have a normal (severe) reaction to malaria; people with the SS genotype have severe sickle-cell anaemia; but people with the AS genotype only show very weak sickle-cell symptoms and very low rates of malarial infection and mortality. The advantage of the AS genotype lies in the combination of normal and sickling haemoglobin. AS haemoglobin, only when infected with malaria, begins a sickling process which leads to the death of the malarial parasites. Normal AA haemoglobin does not have this capability, whereas the anti-malarial ability of SS haemoglobin is overshadowed by the high mortality caused by sickle-cell disease (Durham 1991, 106 ff. & 481).

These latter genetic models do quite well in accounting for the patterns we observe for heritability of handedness, and for the patterns observed in twinning. To date, however, the evidence for a quantifiable heterozygote advantage associated with moderate right-handedness has been equivocal. Several attempts to identify this advantage have investigated its possible behavioural origin (i.e. a cognitive advantage: Annett & Manning 1989; a link to schizophrenia: Crow *et al.* 1998; but see Nettle 2003), although there have been few if any studies of the measurable direct effects on reproductive fitness. Recent work by Yeo & Gangestad (1993; Yeo *et al.* 1993) does advance this field somewhat, although still not measuring direct fitness consequences of heterozygosity at the cerebral dominance locus. They have found that compared with moderately right-handed individuals, both left-handers and extreme right-handers have higher incidences of the minor physical anomalies that are associated with developmental instability (which is, in turn, associated with generalized homozygosity).

Skeletal correlates of handedness

To summarize our discussion so far, it seems that there is an advantage for the dominant hand in tool use that relates to an underlying efficiency in information-transfer rate in the contralateral cerebral hemisphere. This advantage is seen in the greater skill of the dominant hand when executing voluntary movement tasks with high levels of difficulty in the Fitts's Law sense, or tasks with very fine spatial and temporal resolution in the Guiard sense, and in which a corrective mode of control is indicated. It seems likely that the neurological basis of this asymmetry in skill is only weakly genetically determined, with considerable scope for environmental influence during development. Individuals vary both in their hand preference and in the degree to which one hand is more skilled than the other.

The evolutionary origins of the most commonly observed pattern, namely a left-hemisphere specialization for the executive role and consequent right-handedness, are of course matters of intense scientific interest and debate. It is beyond the scope of this paper to review such debates further, since that would require us to digress into the evolutionary anatomy of language. In this section, therefore, we shall summarize some forms of skeletal evidence enabling us to track the evolution of handedness in tool use as seen in the fossil record (see also Steele 2000, from which this three-page summary is abstracted).

Many studies in recent years have demonstrated the range of adaptive responses of the skeleton to patterns of mechanical loading *in vivo* (e.g. Carter 1987) These responses can include increases in bone strength due to increased bone density and/or cross-sectional area, increases in mechanical efficiency by shape change, and resistance to avulsion by increasing the surface area of the sites of attachment of muscles and ligaments on a bone's surface. Evidence suggests that in any particular case, the effect of muscle strength and mechanical loading on bone-mineral formation is localised to the specific site of muscle–bone interaction. Because a consistent hand preference leads to lateral asymmetry in the mechanical loading experienced by the two hands, arms and shoulders during life, we can diagnose the handedness of a deceased individual by studying right–left differences in the lifetime skeletal response to loading strains.

In humans, supporting evidence is found from a number of studies that have quantified skill and strength differences between the dominant and the non-dominant hand and arm. It is plausible that some skill differences are developmentally canalized, but that skill and strength differences are subsequently amplified by habitual patterns of use. Annett has found that in the pegboard task, the dominant hand is capable of performing with an average speed advantage over the other hand of 4.2 per cent in females and 3.4 per cent in males (Annett 1998). Other similar tasks produce larger skill asymmetries between the two hands (10–12 per cent: Tapley & Bryden 1985). It has also repeatedly been observed that in right-handed adults of both sexes, normal grip strength in the dominant hand tends to be about 10 per cent greater than the grip strength of the non-dominant hand (Thorngren & Werner 1979; Petersen *et al.* 1989; Crosby *et al.* 1994; Chau *et al.* 1998). A similar pattern of relative pinch strength between the dominant and non-dominant hand has also been reported (with the dominant hand about 10 per cent stronger than the non-dominant hand: Brorson *et al.* 1989; Bimson *et al.* 1997; Chau *et al.* 1998). Further contrasts relating to hand preference have been described for wrist extension, with the dominant side having on average about 10 per cent greater wrist extension strength (Richards *et al.* 1993). Perplexingly, however, left-handed subjects are equally likely to have a stronger grip in either hand (Crosby *et al.* 1994; Petersen *et al.* 1989); perhaps this reflects the need for left-handers to adapt their hand-use pattern to the constraints of a right-handed world. An effect of work pattern has been reported (Josty *et al.* 1997): heavy manual workers have the strongest grip and the least strength difference between the two hands, while office workers have the weakest grip and the greatest strength difference between the two hands. Light manual workers were found to be intermediate between these two groups.

The bones of the hand, arm and shoulder girdle

A repeated clinical observation is that the bones of the right hand tend to be larger than those of the left hand, as does the volume of the hand itself (Purves *et al.* 1994). This is seen in radiographs (McLeod & Coupland 1992), although in the earliest studies of side differences in the second metacarpals by Garn *et al.* (1976) and by Plato *et al.* (1980) no correlation was found with handedness (as measured either by hand preference or by grip strength). A correlation of relative hand size with handedness has been reported for right-handers, although not for left-handers (Purves *et al.* 1994). Most recently, Roy *et al.* (1994) have reported finding bilateral asymmetry of bone area in the second metacarpal correlated with hand dominance, in which handedness was assessed by the subject's own personal impressions of which handedness group they belonged to.

In right-handed adolescents and adults, muscle mass tends to be greater in the arm on the dominant side (Chhibber & Singh 1972; Schell *et al.* 1985; Neumann 1992; Taaffe *et al.* 1994). It is also well established that the right humerus and radius tend to be slightly longer and heavier than their left counterparts (Latimer & Lowrance 1965; Ruff & Jones 1981). There have been a number of recent radiographic studies of professional racquet sports players and other athletes, who may begin their training early in childhood, and whose dominant arms tend to experience unusually large mechanical loads during the playing years (Buskirk *et al.* 1956; Jones *et al.* 1977; Haapasalo *et al.* 1994; Tsuji *et al.* 1995; Kannus *et al.* 1996). These studies have concentrated on differences between the long bones of the two forelimbs in bone-mineral content, bone mineral density and cross-sectional cortical area. They repeatedly observe greater bone-mineral density and content in the long bones (humerus, radius, ulna) on the dominant side (a pattern also found, but less markedly, in normal control samples). Such modern radiographic studies converge on the finding that activity stresses produce adaptive responses in the bones of the dominant forelimb, effects that ought to be discernible as measurable asymmetries in paired skeletal elements in individuals from archaeological populations.

Asymmetrical loading patterns are also found in people without intensive sports training. Ingelmark, in an early and pioneering radiographic study (1946), found that greater forelimb length (as measured by the sum of the lengths of the humerus and radius) was correlated with the side of the preferred hand in children. In this study he classified as left-handers all children who reported the use of their left hands in at least two of seven everyday tasks. Consistent with modern behavioural data on handedness, females are also more likely than males to have longer long bones in the right forelimb. Two recent studies of tennis players and normal controls go some way to replicating, among adults, Ingelmark's finding (Krahl *et al.* 1994; Haapasalo *et al.* 1996).

Reichel *et al.* (1990), in a radiographic study of normal adults, also found a correlation between handedness and the side of greater bone-mineral density and bone width in the radius in its midshaft and distal segments. The ulna appears to be the bone with least bilateral asymmetry of the three long bones in the arm. In professional racquet sports players, the effect of prolonged unilateral loading on increase in bone-mineral content and bone mineral density in these bones is slightest at sites in the ulnar shaft and the distal ulna (Haapasalo *et al.* 1994; Kannus *et al.* 1996). Presumably this reflects its lesser role in distributing mechanical load in racquet sports. Kennedy (1983), however, has observed preferential development of the ulnar supinator crest in the right arms of males in some archaeological populations of modern humans, apparently reflecting the stresses involved in overarm throwing (as, for example, of a hunting spear).

Effects of activity on the bones of the shoulder girdle (scapula, clavicle) have been less frequently studied than they have on the long bones of the forelimb, but all these bones often show clear asymmetries related to handedness. It is usual to find a greater range of motion in the gleno-humeral joint (where the humerus articulates with the shoulder blade) on the side of the preferred hand (Bonci *et al.* 1986). In the clavicles, the right bone tends to be both shorter and more robust than the left. Mays *et al.* (1999), in a study of the clavicles from the predominantly mediaeval population of Wharram Percy, have found this same pattern and have also found a tendency for the areas of attachment of the costoclavicular ligament (the site of a feature known as the rhomboid fossa) and of the trapezoid ligament to be more developed on the right side. These authors support the hypothesis that loading of the dominant limb exerts greater axially compressive forces on the ipsilateral clavicle, leading both to shape changes (greater robusticity) and to greater development of the attachment sites of those ligaments which stabilize the clavicle within the shoulder girdle during axial compression.

These post-cranial skeletal markers of asymmetrical development in the shoulder, arm and hand appear to provide us with a very extensive tool kit for diagnosing handedness in past populations. However, a number of other processes may affect the development of asymmetry in paired skeletal elements in the forelimb and shoulder girdle, and these should also be taken into account in any such analysis (cf. Steele 2000, 213–14). These other processes include both fluctuating asymmetry, and directional asymmetries favouring growth in one member of a pair of bones when these are due to innate developmental biases and not to mechanical loading history. Pathological development of elements of one side of the body is a third potentially complicating variable.

Skeletal markers of handedness in human evolution and prehistory

If our inferences about the relationship between handedness, tool use and the adaptation of bone to loading are correct, then we would expect asymmetrical skeletal development to occur only in primate species which are extremely tool-dependent (i.e. humans, and their tool-dependent hominin ancestors). Schultz (1937) recorded asymmetries of the lengths of arm bones (humerus and radius) in a large sample of ape skeletons (including 130 gorillas, 82 chimpanzees, 8 orangutans, and 21 gibbons). In marked contrast with the 722 human skeletons in his sample, he found no tendency for the right arm to be dominant in apes as assessed by this measure. He also found that the mean degree of asymmetry (unsigned) in apes was about half that found in the arm bones of humans. These findings concur with the observation, mentioned above, that apes do not exhibit either the population-level right-handedness seen in humans, or the degree of loading of the individually-dominant side which is seen in the human bones.

If we examine skeletons of relatively recent populations from the historical period, the patterns suggest that frequencies of right- and left-handedness have been relatively stable across the centuries. Steele & Mays's (1995) study of asymmetry in the summed lengths of the humerus and radius in the medieval Wharram Percy cemetery population found a pattern in adults very similar to that reported by Annett for the distribution of manual performance asymmetries in the modern British population, with 81 per cent showing the right-handed pattern, 3 per cent showing no significant asymmetry, and 16 per cent showing the left-handed pattern.

These frequencies of arm-length asymmetry were almost identical to those recorded by Schultz (1937) in anatomy collections in the US, where the percentages of instances falling into each of the same categories were 80:4:16 in a pooled sample of 232 Americans of European ancestry. Schultz (1937) recorded data on long-bone length asymmetries for the humerus, radius, and for both combined, partitioned by sex and also by population (his sample also included 233 Americans of African origin, 122 Alaskan Eskimo-Inuit, 118 North American Indians, and smaller samples of Chinese and of Aboriginal Australians). The overall incidence for the whole pooled sample is 79 per cent longer right arms, 3 per cent equal to measurement precision, and 18 per cent longer left arms. For all the populations for which sex information was tabulated, the females were always less likely to have longer left arms and more likely to have longer right arms (which is consistent with sexual dimorphism in the incidences of right- and left-hand preference: cf. Seddon & McManus 1991).

Moving back slightly further in time, we can also analyze skeletal samples from earlier populations of modern humans (*Homo sapiens sapiens*). Thould & Thould (1983) examined 416 adult skeletons from Romano-British Poundbury, and found that the arm bones were longer on the right side in 210 individuals and on the left in 65 (the rest were not measurably asymmetrical). A study of asymmetries in the radii in a sample of 27 individuals from three Neolithic farming sites in the Middle Elbe-Saale region, Germany, found a right-dominant pattern in 70 per cent of individuals, with 15 per cent left-handed and 15 per cent 'ambidextrous' (Reichel *et al.* 1990). However, the discriminant function used to predict handedness in this study is likely to have somewhat inflated the estimated frequencies of non-right handedness. In foraging peoples of early Holocene (Mesolithic) northern Europe, most individuals studied had longer right forelimbs, a pattern seen slightly more strongly in females (Constandse-Westermann & Newell 1989). 24 adult males had longer right arms (summed lengths of the humerus and radius), and 9 had longer left arms. For the females, the ratio was 19 with longer right arms to 5 with longer left arms.

Moving significantly further back into evolutionary time, fossil hominin remains can also be analyzed. There is only a very small number of individuals of extinct species whose skeletons are preserved in sufficient completeness to enable left–right comparisons of paired upper-limb elements. This limited evidence suggests, however, that predominant right-handedness extends back in time to at least the early members of our own genus *Homo*, around 1.6 million years ago (mya). The skeleton of the Turkana boy from Nariokotome, WT-15000 (early African *Homo erectus*, also called *Homo ergaster*), has greater development of the clavicular area of attachment of the right deltoid muscle and greater length of the right ulna, consistent with right-handedness (Walker & Leakey 1993). Asymmetry in the shafts of the humerus consistent with right-arm dominance is also prevalent in Neanderthal skeletons: of six skeletons in which the relevant measurements could be taken bilaterally, all were more robust in the right arm (Trinkaus *et al.* 1994). The Neanderthal individual buried at Le Régourdou, dated to between 75 kya and 60 kya, also shows several markers for right-handedness, such as a thicker and more curved right clavicle, ulna, radius, and humerus (Vandermeersch & Trinkaus 1995).

Material cultural markers of handedness

The skeletal evidence is very sparse for Pleistocene and earlier hominins. Technology provides another, more abundant data source. Archaeological evidence from tools and other artefacts can also be used to infer the evolution of human handedness, and is summarized first by method of estimating handedness (subjective fit in the hand; tool production including multiple flake analyses and knapping gestures; lateralized retouch; asymmetrical tool use and use-wear; teeth marks; and art including representations of tool use, engravings, cave paintings, and hand prints), and then within each method, by time period (from earliest to most recent evidence) and by material (stone, bone, wood, antler, bronze, etc.).

Subjective and early assessments

A number of early archaeologists involved in excavations have observed that certain tools fit better in the right or left hand. Nowadays archaeologists refrain from making such comments because they are seen as unscientific, but in the last century they were acceptable. For example, Gabriel de Mortillet (1890) claimed that there were more left-handers in prehistoric times, based on Neolithic double-edged scrapers from France and Switzerland. Strangely, he had previously (1883) argued for the opposite, finding that most 'hand-stones' of 'very early tribes' found in the Somme gravels were made for right-hand use (cited in Brinton 1896). Other right-hand supporting declarations were also made by Black *et al.* (1933), by Evans (1897) about handles and hafts for bronze sickles and swords in Swiss lake dwellings and English barrows (see also Wilson 1891, 138), and by Sarasin *et al.* (cited in Spenneman 1985 and Posnansky 1959).

Such subjective observations were based on an intuitive supposition of how to hold the tool, because the grips, purposes, and manners of tool use were not known. Nonetheless, it is interesting that separate researchers have made similar judgements of material from vastly distant sites both in time and space. These early assertions are therefore worth including in this review and may be worth revisiting in the future, especially now that the methods of gripping and using tools are becoming better-known. Semenov's (1964) volume is a good example of the level of detail that can be obtained in a study of use-wear in order to specify the precise kinds of hand configuration that were used to grip tools during their use. Also, recent papers by Takeoka, Phillipson, and Posnansky, which will be discussed below, do take grip position into account.

Another early argument was proposed by Dart (1949), although his ideas are now considered fanciful. He hypothesized that baboons from Sterkfontein had been hunted by tool-wielding hominins, as the crania seemed to show signs of crushing from hand-held bone weapons. These patterns, Dart suggested, indicated predominant right-handedness because a right-hander holding a tool will tend to strike the front left (if from a face-on attack), or rear right (if from a stealthy rear attack), parts of the victim's skull. Although Dart's hypothesis was developed with the scientific reasoning of his time, our current knowledge of taphonomy, as well as continuing excavations at Sterkfontein, has enabled criticisms of Dart's ideas. For example, Brain (1981, 263–4; 1994) describes the types of taphonomic processes involving carnivore gnawing and roof collapses that can produce the damage patterns observed by Dart.

Tool production

Two studies have analyzed large assemblages of flakes to find proportions of right and left flakes; they are those of Bradley & Sampson (1986), and Toth (1985). In addition, four studies look at scatters from single knapping events. Fischer (1990), Högberg (1999), Newcomer & Sieveking (1980), and Wenban-Smith (1997) present data from experiments and archaeological sites showing that the knapper's handedness produces a distinct scatter pattern on the ground. The knapping gesture also imposes constraints on accuracy and, therefore, on the homogeneity of flake-surface attributes. Three studies have used arguments from the knapping gesture to indicate asymmetrical features on tools and flakes (Rugg & Mullane (2001), Takeoka (1991), and White (1998)). Finally, we include an anecdotal report of a left-handed knapper who was buried with his core and hammerstone in hand.

Tool production: multiple-flake analysis

An influential study by Toth (1985) proposed that right-handedness can be seen in the archaeological record by reconstructing the preferential direction of core rotation during initial flaking. The direction of rotation of the core was inferred from the presence of cortex (the outer surface of a flint nodule) on the right or left side of the dorsal surface of a flake. He studied flakes from Koobi Fora (Kenya) from a number of sites dated to between 1.9 and 1.4 mya, predominantly of the Oldowan industry, but included one Early Acheulean site (dated to between 1.4 mya and 700 kya). It is important to note that Toth's method only applies to a specific reduction strategy, namely the use of single-platform cores. This involves removing all the flakes from the same platform, in sequence. On a round cobble, this reduces the number of possible flaking locations to two: in front of the previous removal, or behind it. Toth's own replications of Karari scrapers produced 56 per cent right-biased flakes, caused by rotating the core clockwise in the left hand. He argues that this decision is dictated by 'the musculo-skeletal structure of the left hand and arm, in which the superior power of the supinators and flexors produce a preferential rotation in this direction for a stronger and more controlled turning motion (O. Lovejoy pers. comm.)' (Toth 1985, 611). The finding of 57 per cent right-oriented flakes at six Koobi Fora sites suggested that the Koobi Fora knappers, hominins from 1.6 mya, were at least as right-handed as Toth. He also studied Acheulean flakes from Ambrona (Spain), dated to 400–300 kya, and found 31 left-oriented for 48 right-oriented flakes, a R:L ratio of 61%:39%.

In a study of Acheulean handaxes from Caddington, UK (dated to 115–130 kya), Bradley & Sampson (1986) replicated biface and Levallois reduction sequences by a right-handed knapper. They classified the flakes with respect to cortex retention as well as the presence and location of relict margins. A tentative analytical method was created which yielded a handedness index of 62 per cent R for the experimental collection, and 54 per cent R for the archaeological sample. The authors interpret these results as a weaker bias towards right-handedness in Caddington compared to the experimental knapping.

Bradley & Sampson's classification according to relict margin location means that reduction sequences are taken into account, a notion which also appears in Toth's argument although it is open to criticism. This has to do with extending the Toth method to other archaeological collections. In fact, for most types of knapping, the order of flake detachment is mostly contingent on the shape of the core or flint nodule (Patterson & Sollberger 1986; Pobiner 1999). The fact that the Karari cores were flaked from a single platform certainly allowed good serial flaking. This was demonstrated by Ludwig & Harris (1994), who confirmed that right-handers rotated the core clockwise and left-handers counterclockwise when making Karari scrapers. Therefore we must be cautious when applying Toth's method to industries whose reduction strategies were not restricted to serial flaking. With other kinds of flake production, the figures seem to approach 50:50 as the sample sizes increase (Noble & Davidson (1996), 170; Pobiner 1999; Uomini 2001).

Tool production: knapping scatters

Although there are very few high-resolution sites with *in situ* knapping scatters (e.g. Högberg 1999), they are valuable because they can reveal handedness. It has been shown experimentally that a knapper sitting on a seat produces a central concentration of debris which is skewed to the side of the knapping hand. For example, Fischer (1990) describes a series of conjoined artefacts found in place at the Trollesgave site, Denmark, near a large stone. The site is dated to 9100 BC and the artefacts are referred to the Bromme technocomplex. Fischer, a right-hander, experimentally replicated the Trollesgave blades while sitting on a similar stone seat, in the event producing a scatter which was most dense in front of his feet, fading out to the sides, and right-oriented. The archaeological scatter was also orientated to the right, located similarly in front of the stone. When sitting directly on the ground, with one leg folded and one leg straight out, a clear triangular scatter appears. Newcomer & Sieveking (1980) replicated 16 Neolithic axe roughouts at the site of Grime's Graves, UK. The left-hander, Newcomer, sitting on the ground with his right knee bent and left leg out, produced a right-skewed scatter ending abruptly where the legs were. It must be noted that there is another action which can produce a concentrated scatter: the use of a piece of hide or cloth for leg and crotch protection. The pieces which fall on the material collect into a distinct heap when they are dumped onto the ground, for example when emptying the debris or when the person stands up. It is important to note that the dumped heap looks identical whether the knapping is done sitting on the ground, on a seat, or squatting (Newcomer & Sieveking 1980). Specifically,

> the manner in which the roughout was held during flaking did not seem to have much effect on the size and shape of flake scatters. When the [sheepskin] thigh pad is used, it catches the flakes as they are struck and the flakes then tend to drop in a circular heap below. Without the pad, which is difficult to use when standing or seated on the floor, the flakes are either caught in the fingers and then dropped, or allowed to shoot off freely; in either case the roughly circular shape of the scatter is recognisable. (Newcomer & Sieveking 1980, 350)

Similarly, Wenban-Smith (1997), a right-hander, sat on the ground with the left leg folded and right leg out (the inverse of Newcomer) and produced a left-skewed scatter bounded by the legs.

Tool production: knapping gesture

With respect to knapping gestures, Takeoka (1991) defines two kinds of movement which affect the position of the flake blank (or core), and thus the angle at which it receives the hammerstone blows. One is wrist abduction/adduction, the other is forearm pronation/supination. When knapping, the axis of wrist movement (if the palm is placed flat on a table, this would be a side-to-side motion of the hand) affects the direction of fracture force propagation within the core; this is the effect that the cone of percussion method exploits, although they argue for an entirely hammerstone-based cause (Rugg & Mullane 2001). Forearm rotation affects the working angle (angle between the platform and hammerstone trajectory); a more pronated wrist results in an obtuse angle (because the platform is tilted towards the body) while a more supinated wrist results in an acute angle (platform tilted away from the body). A third factor, wrist flexion/extension, affects the horizontal position of the striking platform, bringing it closer to the knapper's eyes (Takeoka 1991, 503–5).

Rugg & Mullane hypothesize that:

> the angle at which the cone of percussion occurs relative to the striking platform is usually around 90 degrees, but can vary ... Because the human arm has pivot points at the shoulder, elbow and wrist, it is plausible that some blows would lead to cones of percussion that were angled to the right or left relative to the striking platform. (Rugg & Mullane 2001, 252)

Because the Hertzian cone indicates directionality, its skew should reflect the exact trajectory of the hammerstone. Rugg & Mullane experimentally validated their recognition criteria, with four left-handed knappers and four right-handers: in a blind test they were able to assign 75 per cent of those flakes that had a clear cone of percussion to the correct handedness.

The fact that right-handers produced right-skewed cones and left-handers produced left-skewed ones indicates that the tendency to skew the blow comes from either slight, unintended supination of wrist or unintended flexion at the elbow of the knapping arm. The basic knapping gesture, as described above, consists of partially pronating the wrist and simultaneously adducting the forearm, so any deviation to orient the blow towards one's body is caused by extra supination and/or flexion. These biomechanical suggestions depend on the bimanual configuration used in knapping, which is discussed below.

For simplifying purposes, we will say that knapping can be done with five general hand positions, or configurations. The first four involve holding the core against one leg and are grouped as two different techniques: Flake Support and Free Fall. We suggest these names to reflect the immediate intention for the resulting flakes. Newcomer & Sieveking (1980) refer to 'Free Fall' vs 'Deliberate placing in a heap', to distinguish ways of treating blades as they come off the core. Generally, Flake Support is used when the flake itself is the intended product, meaning the knapper wants to prevent it from falling to the ground where it might break; the core is pressed against the thigh so that the resulting flake will lie sandwiched between the core and leg. In Flake Support, the core is held either against the outer surface of the ipsilateral (same side as core hand) thigh, or the inner surface of the contralateral thigh. Conversely, Free Fall tends to be used when the flakes are waste products; in this case, the core is pressed against the leg so that the flake comes off the 'free' side of the core and falls to the ground. In Free Fall, the core is held either against the inner side of the ipsilateral thigh (flaking between the legs), or the outer side of the contralateral thigh (flaking on the outside of the body, where the knapping arm has lots of space to move).

However, these suggestions are by no means strict rules, as the shape of the flake is dictated by the way the hammer's energy is transferred. Specifically, in Flake Support, the hammer arm's trajectory is stopped by the leg, causing the energy to flow into the leg; this tends to produce curved thinning flakes. In Free Fall, the hammer arm can follow through its trajectory, resulting in the energy going through the core, producing flat thinning flakes (B. Bradley pers. comm.).

An important factor affecting knapping configuration is the technique, defined by the type of hammer (F. Sternke pers. comm.). A soft hammer (i.e. antler) requires much greater velocity, meaning one tends to knap with Free Fall so as not to smash one's leg. Hard hammers (i.e. most stones) can be wielded with less speed, so it is possible to use Flake Support. Also, when thinning a handaxe, the core is normally held in the hand or with Flake Support. This gives more control of core spatial configuration, and prevents end shock (an unpredictable accident causing the handaxe to snap in two).

Additionally, one can entirely support the core in one hand (Newcomer & Sieveking call this Freehand: 1980, 349). For large or heavy objects the forearm can be supported in turn by the ipsilateral thigh (this configuration is observed in knappers from Papua New Guinea: see Stout 2002). For small objects or when finer control is needed, the core is held in the unsupported hand, such as in the thinning stage of handaxe production.

In addition to the five mentioned above, other configurations do exist, such as holding the core between the two legs (as in indirect percussion for blade production), or holding the core against an object (anvil, tree stump, ground, etc.). It is also important to note that some methods (core-reduction strategies) make use of more than one knapping configuration. For example, making blades by direct percussion first requires making a crest, which 'is done on the outside of the thigh' (Newcomer & Sieveking 1980, 350), and second, platform preparation followed by blade removals, both 'done between the legs' (Newcomer & Sieveking 1980). In his blade experiments, Newcomer produced two distinct scatters separated by his leg, containing two different types of debitage, reflecting the use of these two configurations.

The manner of holding the core can also interact with the reduction strategy, indicating handedness. White (1998) identified four possible bimanual configurations for manufacturing twisted ovates. These bifaces exist in British sites dated to from late OIS-11 to early OIS-10 in significant proportions (20–46 per cent) at sites like Bowman's Lodge, Wansunt Pit, and Swanscombe (all three in Kent), Elveden and Foxhall Road (Suffolk), Allington Hill (Cambridgeshire), and Hitchin Lake Beds (Hertfordshire), and in France dated from OIS-12/11 to possibly OIS-8. Twisted ovates are made with a particular method, usually at the finishing stage: first, one quarter of the edge is flaked unifacially. Then the handaxe is inverted through the long axis and one quarter of the opposite face is flaked. These two sets of unifacial removals, on opposing faces, are now joined at one tip of the handaxe. Next, the piece is rotated (clockwise or counterclockwise) 180 degrees and one more quarter flaked unifacially. Finally, the piece is inverted through the long axis again and the opposite quarter is flaked, bringing the last two sets of removals to join at the other end of the handaxe. The result is a handaxe with an edge alternating four times between the two faces. This makes the profile look 'twisted' in the same way, no matter how you hold it.

For all four edges that are knapped unifacially, it is the handaxe which is rotated so that the hammer hand always knaps in the same 'active zone' of the core hand (White 1998, 99). The interpretation of handedness comes from the fact that nearly all twisted ovates have a Z-shaped profile rather than an S shape. This means that there are two possibilities for the active zone: either the area near the wrist for a right-hander, or the area near the fingers for a left-hander. (A right-hander using the fingers area, as well as a left-hander using the wrist area, would produce an S twist.) The use of the fingers area can only be justified if the prehistoric knappers were mostly left-handed, and so this possibility can be excluded, leaving only the right-handed option as an explanation of the Z-shaped profiles.

Finally, a remarkable burial was found at Hazelton North, Cotswolds, UK, dated to 5500 BP (Saville 2003). This tomb contained a male, 30–45 years old, with a flint core beneath his right elbow, and a hammerstone at the place of his left hand. The core and hammer were most likely placed into the burial after his death; they were either placed faithfully, meaning he was a left-handed knapper, or he was right-handed and they were placed incorrectly, meaning his buriers disregarded the hand he used when knapping.

Lateralized retouch

Five authors (Cornford 1986; Phillipson 2000; Semenov 1964; Blankholm 1990; Brinton 1896) describe evidence of handedness from asymmetrically-retouched tools. This asymmetry can be due to lateralized use, making it necessary to retouch the more worn side of the tool, or simply from constraints in knapping when holding the piece. Cornford (1986) describes flakes resulting from a *coup de tranchet*. The site of La Cotte de St Brelade, France has a long stratigraphy spanning the last two interglacials (from 240 kya to 122 kya). The tools were resharpened with a tranchet blow to freshen one edge of one face of the tip. These sharpening flakes were removed by right-handers in proportions ranging from 77 per cent to 91 per cent, from oldest to youngest layers of the site. Further evidence comes from the use of bone retouchers (Semenov 1964, 163). The artefacts come from Middle Palaeolithic (Kiik-Koba and Teshik-Tash) to Upper Palaeolithic (Kostenki 1) sites in Russia, dated to 37–34 kya. Semenov indicates dents on the convex side of bone retouchers which met at an angle of 75–85 degrees to the long axis, suggesting they were used by right-handers. Blankholm (1990) also found lateralized retouch on microlithic armatures of the Maglemosian industry (9.5–8 kyr BP) in southern Scandinavia. These lanceolates and triangles were mostly retouched on the left side, in proportions from 50 per cent to 100 per cent, and this was not due to any functional constraints. Phillipson (2000 and pers. comm.) notes a site containing chert scrapers at Aksum, Ethiopia, dated to the fifth to sixth centuries AD, which are asymmetrical in shape. They consistently have one spurred corner, usually on the left, and which Phillipson attributes to habitual use in the right hand. An early study of North American Indian tools by Brinton (1896) measured three asymmetrical criteria: offset point asymmetry, side of lateral retouch, and blade 'twisting'. He found about two-thirds more right-handed features than left-handed ones in undated blades of chert and jasper (Ohio), chert, quartz, and jasper (Wisconsin), and argillite, jasper, quartz, and black chert (New Jersey).

Use and use-wear

Two authors examined the traces left on stone tools by use, specifically scrapers and flakes (Frame 1986; Semenov 1964). Three authors include specific constraints about grips in their analysis (Takeoka 1991; Phillipson 1997; Posnansky 1959). Two authors and colleagues studied use-wear from a rotating motion (Keeley 1977; Cahen *et al.* 1979; Cahen & Keeley 1980; Spenneman 1987). Roosevelt (1974) describes asymmetrical wear on wooden spoons. Gerharz & Spenneman (1985), along with Wilson (1885; 1886; 1891), report evidence of use-wear and use patterns from bronze sickles. Three authors point to the necessity of hiring left-handed miners in Roman times.

The La Cotte artefacts were examined for microscopic use-wear traces to determine handedness by another technique. Frame (1986, in the Cornford volume) inspected the striation orientation and bands of polish from working wood, hide, or other materials on long sharpening flakes. Of 18 right-asymmetrical sharpening flakes, 4 had oblique rightward marks, 1 left, and the remainder either perpendicular, parallel, or multidirectional. Of 4 left-asymmetrical flakes, 2 had traces of moving leftward, 1 perpendicular, and 1 multidirectional. Frame proposed that these marks, in relation to the working edge indicating the direction of tool use, showed they were preferentially used by right-handers.

Semenov (1964, 87f.), in his volume on use-wear, described the mechanism for asymmetrical scraper wear. The scrapers were used on hide, without handles, simply held in the hand. Because the tool is held 'with its axis at an angle of 75–80 degrees to the skin surface', by implication, there is a constraint on simultaneous abduction of the upper arm and pronation of the wrist/forearm (in orienting the tool-using hand perpendicular to the surface being worked). This implies that force is more efficiently exerted when the arm is less abducted and the forearm less pronated. Semenov counted that about 80 per cent of end-scrapers are worn on the right side. His data include Russian (Kostenki 1, Timonovka, Mezin, Suponevo, Sakajia) as well as other Upper Palaeolithic sites. Takeoka (1991) further argued from scraper usage, with the assumption that the scraper was pulled towards one's body, the ventral surface at the front. In this motion, the thumb is pressed against the ventral surface, fingers supporting the dorsal surface. Takeoka argued that the working edges of the scrapers are mostly located on the side of the flake that will put the proximal (thickest) end of the flake inside the cupped palm, rather than the fingers, and therefore were made for right-handers. Phillipson (1997) confirmed this effect. She scrutinized 54 handaxes and cleavers recovered by an LSB Leakey excavation in 1931 in Kenya. Their stratigraphy is dated to about 1 mya. Starting from the premise that the trailing face, not the leading face, of a used edge, would show greater signs of use, Phillipson reconstructed possible grip types for each piece. Of 54 tools, 6 (11 per cent) could be assigned to probable left-hand use, 45 to the right hand, and 3 were indeterminate. Constraints of use involve the efficient exertion of force and resistance of finger and hand muscles:

> rotation of the wrist without shifting fingers permits the concave edge to be used as a pull scraper. (Phillipson 1997, 180)

Some implements had more than one working edge, and so by implication were held in several different ways:

> These positions would have allowed for a number of types of force to be exerted in several directions with the tool, depending upon exactly how the hand was placed. A line of force from the working edge through the central mass of the tool to the base of the palm of the hand, for example, permits steady pressure to be applied while the fingers are partially freed to rotate the tool in subtle scooping, twisting or scraping motions. A grasp in which the handaxe is compressed between the tips of the fingers and the palm of the hand is needed to prevent loss of control when it is used for heavy cutting or sawing in a direction parallel to the utilized edge. The shock of chopping or digging motions is best absorbed by the front of the palm of the hand or the base of the fingers, although a posture with the fingers well spread and the force falling somewhat further forward is also effective. (Phillipson 1997, 174)

Furthermore, an asymmetrical weight distribution on the tool can facilitate use:

> a hand-hold was provided by a retained area of the original cortex or a flake striking platform on an otherwise bifacially worked specimen. In most instances this more rounded area was associated

> with an asymmetric bulge on one or both faces of the handaxe which fit comfortably into the concavity of the user's grasp and greatly facilitated the controlled manipulation of the tool. (Phillipson 1997, 174)

This latter statement, like the next one below, is an example of how to reconcile the nineteenth-century subjective observations mentioned above with the rigorous scientific approach preferred today. A similar observation on the use-constraining effects of asymmetrical weight distribution in the artefact was made by Posnansky (1959), in studying a collection of Early to Middle Acheulean handaxes from the Trent Valley (UK) and 118 handaxes from the Furze Platt site (UK). He states:

> it is found that the displacement of the weight away from the cutting edge, which a non-central median ridge implies, increases the efficiency for cutting. (Posnansky 1959, 42)

Like Phillipson, Posnansky tested the handaxes for ease of use in either hand, assuming a cutting function. Specifically, 'the most efficient method of cutting is one in which the butt of the tool is held in the palm of the hand with the fingers splayed around the blunter of the two edges and the flat face of the tool faces the inner cut face' (Posnansky 1959, 43). Of 40 complete tools in the Turton collection, 35 per cent were found to better accommodate the right hand, 12.5 per cent the left hand, and 52.5 per cent either hand. Two independent observers found similar proportions: they assigned the following respective proportions to the same handaxes 37.5 per cent-15 per cent-47.5 per cent and 22.5 per cent-10 per cent-67.5 per cent.

Keeley (1977) describes a biface from Clacton (200 kya) with microscopic use-wear showing it was used with a vertical rotating motion, such as boring holes, in a clockwise direction. Keeley's argument implies that greater torque forces are exerted during wrist supination (clockwise for a right-hander) than pronation. Indeed, supination produces more torque than pronation (Sellers 2004), and this is the reasoning behind the design of screws: they must be screwed in clockwise, which exploits the stronger supinating torque of the right hand. The mode of prehension is not specified, but a tool being vertically rotated can be held either with the elbow up and palm facing outward (screwdriver grip), or with the elbow down and palm inward (stabbing grip). This presupposes that whatever the grip on the tool, people grind in a direction outward from the centre. In a screwdriver grip, the wrist must produce mainly supinating forces, while grinding with a stabbing grip, the wrist produces mainly extensor forces. Both of these could reflect a preference to supinating/extension rather than pronation/flexion (which would be the forces required if the grinding motion went inward). Cahen *et al.* (1979) confirm this constraint:

> Although a back-and-forth turning of the borer is efficient when the borer is hand-held, the outward turn of the wrist is more powerful. Experimental observations have shown that the return stroke in the weaker, inward direction is usually accompanied by a slackening of the vertical pressure. (Cahen *et al.* 1979, 668).

In other words, boring is usually done with a back-and-forth motion, but the outward stroke produces the bulk of the striations. In addition, microwear polish and edge damage indicate the principal direction of turning:

> Generally speaking, microwear polish forms on the aspect of edge ridges and projections facing toward the principal direction of turning, while utilization damage is created most heavily (sometimes only) on the aspect facing away. (Cahen *et al.* 1979, 681, in reply to objections from Newcomer and Odell).

Using the same analysis method, Cahen and colleagues (1979; Cahen & Keeley 1980) studied flint tools from Meer. This Belgian site was excavated in the 1960s and 70s, and is dated to 9 kyr BP. The lithic assemblage is characterized by Tjonger points, which are backed blades used in projectiles. They examined the use-wear on 31 tools which had been used for boring holes in, and engraving, bone and antler. These thick-bitted borers are called becs. The becs were grouped according to which flint block they could be refitted to; there were 6 refit groups in this sample. 21 becs had been used clockwise and 3 counterclockwise. These three becs were all knapped from the same block, suggesting they were made and used by a single person. The authors conclude that the main knapping scatter, called Concentration IV, was produced by at least two people, one of whom was left-handed (Cahen *et al.* 1979, 671).

Another study using the marks from rotating motions was made by Spenneman (1984a), who examined Swiss and German Neolithic bone, antler, and stone grinding tools. These tools display striations running from the top left to bottom right (for a right-hander) and top right to bottom left for a left-hander. The sites are all dated to between 4050 and 2900 BC, contain 19.4 per cent (of 31) left-handed tools at Burgerroth, Germany, 19.6 per cent (of 51) at Bodman, Germany and 6.3 per cent (of 597) at Twann, Switzerland.

Roosevelt (1974) examined a series of wooden and bone spoons and spatulas from northern Chile. They come from the Chiu Chiu site and are dated to AD 1000–1500. Roosevelt also created an experimental set of wooden spoons used, right-handedly, to stir and scoop food in a coarse ceramic bowl, and these showed lateral wear on the distal end. The archaeological spoons consisted of 76 determinable tools, of which 48 were right worn, 4 left worn, and 26 bilaterally worn. Because the archaeological and experimental spoons show identical wear patterns, their usage for mixing food as well as pigment and snuff was confirmed. Bone and wooden spatulas were also probably used with the concave part facing toward the user and the handle slightly angled (not vertical), as this is the most effective way to hold them (Roosevelt 1974, 102). This implies particular constraints on combinations of motor acts when performing a stirring or ladling motion.

Spenneman (1987, 22) offers some suggestions for identifying use-wear in adzes:

> In general, the movement of a hafted adze blade is not vertical but oblique in relation to the operator's body. This is due to the nature of the ball joint between the shoulder blade and the humerus. This angle is more oblique if the adze is held in one hand, than when held in both. In case of a right-handed individual, the movement runs from top left to bottom right (as viewed by the worker). … Due to this slightly oblique movement the edge of the stone adze does not hit the worked material in an optimal manner, one end of the edge making contact earlier than the other.

In application of these constraints, Gerharz & Spenneman (1985) describe two bronze farming tools from northern Ethiopia showing use by left-handers. The tools can be related typologically to industries around 1000 BC, although direct dating of the site disagrees. Several cast adzes from Yeha, a site contemporary with Haoulti, have asymmetrical use-wear. The upper face is more worn on the right corner, indicating it was used by a left-hander. Another adze from the same site shows right-handed use, as do two other adzes from other northern Ethiopian sites. Furthermore, one cast sickle from Haoulti, dated to between 300 BC and AD 100, is worn from intensive use. It was made for a left-hander because it has a strengthening rib running along the upper face, and the upper face was hafted on the left, meaning it was held in the left hand. The authors report finding, among 8000 bronze sickles, only four other left-handed sickles (two German ones, one Hungarian and one Romanian).

The use of left-handed workers has been documented in Roman times, in the context of mining. Röder (1957) describes the Roman mines for tuff (consolidated ash) in the Pellenz, Brohl Valley, Rheinland (Germany), in which there were usually 3 left-handers for 2 right-handers (3:2), or even 2:1.The workers used rods to dig out the walls of the mines, making vertical walls. The left walls were straightened by right-handers, and the right walls had to be straightened by left-handers (Bedon 1984, 158). In the Gallo-Roman mine at Saint-Boil (France, 1st century AD), the rectangular blocks had to be carved out by two miners working together, one of each handedness (Monthel 2002, 96). The biomechanical constraints of working close to a wall with a mining rod meant that the proportions of right and left handed miners had to be carefully selected; these should be visible in the written records that some miners kept of their workers (G. Monthel pers. comm.).

Cut marks on teeth

Three studies have studied the marks left on Neanderthals' anterior dentition by using stone tools to cut meat held between the teeth. This is ethnographically common (Semenov 1964, 104):

> Generally pastoral or hunting people (like the nomads of Mongolia, Tibet, Abysinnia and other countries) eat such meat with a knife in one hand. Meat is normally cut into strips, and baked or cured in this form. Then each person takes a piece and, holding one end in his teeth, cuts it free with a quick movement of the knife at his mouth, repeating the operation until the whole strip has been consumed. The cutting is done upwards from below. We have seen this done among Nenetz reindeer herdsmen in the Kanin peninsula in 1928.

The striations on Neanderthal and pre-Neanderthal hominins' teeth were examined by Bermúdez de Castro *et al*. (1988) and by Fox & Frayer (1997). In addition, the Boxgrove hominid has similar marks on its two teeth. If one dislikes the idea of using the teeth as tools (e.g. Bax & Ungar 1999, who explicitly reject a connection between handedness and striation orientation), there is also the interesting possibility that these marks were made by chipping flint with the teeth, an action which has been observed in Plains Indians (USA) and Australian Aborigines (Hester 1973).

Bermúdez de Castro *et al.* (1988) reported on striations found on the front teeth of *Homo heidelbergensis* individuals from the Sima de los Huesos site (Atapuerca, Spain) (19 teeth, comprising 4 individuals and 10 unassigned teeth), the La Quina 5 Neanderthal (2 teeth), one isolated tooth from Cova Negra, Hortus (several anterior teeth from 5 individuals), and include published data on Saint Brais (1 isolated tooth), Angles-sur-l'Anglin (1 isolated tooth), and the Shanidar 2 Neanderthal (2 teeth). Rough dates for these fossils are as follows: Atapuerca about 300 kya; La Quina 35–30 kya (a French cave with artefacts from a Mousterian area and an Aurignacian-Châtelperronian area); Cova Negra 120–35 kya (a Spanish cave with many stone tools, faunal, and Neanderthal remains); Hortus 60–55 kya (a French cave with many Neanderthal remains and stone tools); St Brais 50–40 kya (a Swiss cave); Angles-sur-l'Anglin 14–13 kya (a middle Magdalenian rock shelter with paintings); Shanidar 60 kya (a Neanderthal cave burial in Iraq).

For comparison, a prognathic mouth-guard with fake enamel Neanderthal teeth was worn by a right-hander. The experimental procedure involved holding a piece of meat between the front teeth and cutting off bite-sized pieces with flint flakes. The experimenter made striation patterns consistent with a right-handed downward motion from left to right (when viewed from the front), matching those on the fossil teeth. All of the fossil samples (except Angles, which has horizontal marks, and Hortus VIII) show striations pointing downward to the right. The teeth from Hortus VIII has inversely oriented striations, suggesting this individual was a left-hander.

The authors state that 'in the experimental study, the action that would produce striations as in scheme C [consistent with a right-handed operator cutting leftwards] was uncomfortable and felt less efficient' (p. 410). This implies that it would be equally uncomfortable and inefficient for a left-hander to cut rightwards, and therefore the observed rightward fossil striations preclude a left-handed product. The inefficiency of the right-handed leftward motion implies a constraint on simultaneous pronation at the wrist and extension of the forearm. A right-hander cutting from below (as described by Semenov) would produce pattern D on his/her teeth, consistent with a left-hander cutting leftward from above. But Bermúdez de Castro *et al.* (1988) did not observe pattern D in the fossils, suggesting the cutting was done downwards by right-handers. Furthermore, the authors identified partial Hertzian cones in the striations which indicate a downward cutting direction.

Fox & Frayer (1997) studied the teeth of Krapina Neanderthals, which also show striations consistent with cutting meat held between the teeth. Six of the thirteen individuals above age thirteen were found to display rightwards scratches, with one showing leftwards scratches. The remaining six individuals showed no predominant pattern (judged by the 50 per cent mark). Fox & Frayer also include published data from Kabwe and Tabun individuals, who also have right-handed striations. Further evidence comes from the two Boxgrove (400 kya) hominin teeth, which both came from the same mouth and were adjacent bottom front teeth, and show similar striations. They also indicate right-handed cutting with flint (Pitts & Roberts 1997, 265).

In total, these three studies reveal only 2 left-handed hominins for 19 right-handers. The number of individuals of unknown or indeterminate handedness is 7 in these studies, but we might assume that the proportion of right to left (10.5 per cent) is roughly similar in the indeterminate samples.

Art

Upper Palaeolithic and later art is a further source of evidence for handedness. One suggestion is that the paintings and engravings are easier to read, and therefore were made, with a light source coming from above on the left side (Delluc & Delluc 1993, 44); meaning the artists held their torch in the left hand because they needed to use their right hand to draw and engrave. Other forms of evidence are images of people using their hands, engraved pebbles whose characteristic traces show the direction of engraving, the drawing of animal silhouettes, and the proportions of handprints and hand stencils made with the right and left hands.

Representations of lateralized tool use

Five studies have counted the number of depictions of right- and left-handed tool use in works of art. Uhrbrock (1973) made an extensive review of laterality depicted in paintings, sculptures, medallions, coins, and stamps. He reports higher proportions of left-facing profiles on US coins and medallions, but more right-facing profiles on European coins and medallions dating from 600 BC to AD 1964. Painted portraits are also slightly more likely to depict right-facing people. Depictions of tool use in sculptures, columns, and drawings from the Renaissance to modern times show right- and left-handedness, and representations of the Madonna holding her Child frequently show her holding him on her left side (Uhrbrock 1973). This might reflect either a conscious choice of the painter/sculptor, or the need for right-handed mothers to keep their dominant hand free. Another review was made by Coren & Porac (1977), who tabulated 1180 instances of unimanual tool and weapon use depicted in drawings, paintings, and sculptures from Europe, Asia, Africa, and America, spanning the time 15,000 BC to AD 1950. 92.6 per cent of these images portrayed right-hand use, remaining significantly consistent across geographical areas and time periods. Other such studies are described by Spenneman (1984a, 613); Dennis (1958) studied Egyptian paintings in tombs and found 7.5 per cent ($n = 120$) left-handed actions in the 2500 BC-dated sample, and 4.76 per cent ($n = 191$) left-handed depictions in the more recent sample. An assessment of hand use depictions was made by Spenneman (1984b), for a decorated Buddhist pyramid in Central Java which was constructed between the eight and tenth centuries AD. Spenneman studied 1504 scenes (none depicting the Buddha). These reliefs depict 14,892 people, 1085 of which are using their hands unimanually. Most (926 = 83.5 per cent) were simply holding an object, and only 153 (= 16.52 per cent) were performing a skilled action. The unskilled actions include leaning on a stick, holding a horse, a sword, a flower, axe, fan, umbrella, or reaching for something. The skilled actions include playing an instrument, manipulating food, riding an elephant, and using a weapon such as a sword, knife, bow and arrow, or spear. The right to left ratio for skilled actions was found to be 137:16 (89.5 per cent right-handed), while the ratio for unskilled actions was 578:348 (62.4 per cent right). Spenneman takes these figures to reflect reality, and rejects the possibility of artistic stylization, as the pyramid shows no signs of mirror-image symmetry or 'other kind of arts-connected constraint' (p. 165). It is possible, however, that such a constraint existed in the totem poles studied by Marrion & Rosenblood (1986). They examined 110 depictions of hand use in carved standing poles (nineteenth to twentieth century) used for houses and totems in the Kwakiutl Indian areas off the west coast of British Columbia. They found 20 per cent right-handedness, 24 per cent left-handedness, and 56 per cent simultaneous use of both hands.

Engravings

D'Errico (1992, 100, 99) reports on four possible ways of configuring the two hands and arms, derived from his experimental replications of engraved Azilian pebbles at Rochedane, le Mas d'Azil, and Pagès, France. The Azilian culture was Mesolithic, between 11 kya and 8 kya. D'Errico showed (1988) that the engravings were made working towards oneself, and therefore they tend to produce the frequently-observed pattern of right to left juxtaposition. Observing the clockwise direction of turning while working the pebbles, he notes that 'in all the engravings with two opposed series the surface was rotated 180 degrees between one series and the next' (1992, 100). This is a similar constraint to that mentioned by White (1998) for the working of twisted ovates. Studying the grooves with scanning electron microscopy, d'Errico (1988) showed that a right-hander engraving from left to right creates a groove which is compacted along the edge closest to the user. Drawing from top to bottom, the compact area runs along the left side (1988, 172–6). The incisions on the 27 Azilian pebbles are consistent with having been made from left to right by a right-hander.

Profile drawing

There have been many suggestions that, when drawing a person or animal in profile, a right-hander tends to draw the face to the left, and a left-hander facing right. Proponents of this hypothesis include Wilson (1885, 132; 1891, 33), Breuil (1952), Leroi-Gourhan (1965), Perelló (1970, 141), Alter (1989), and Willcox (1991, 146). One of the earliest mentions is from J.S. 1870 (cited in Uhrbrock 1973, 28), who wrote

> Most boys know that it is easier to draw a profile with the face looking toward the left hand; yet on looking over the hieroglyphs in the British Museum the faces will be generally found toward the right.

Alter (1989) made an experimental study of 231 subjects (19 L handers and 148 R) who were asked to quickly draw six shapes (bicycle, dog, bus, face profile, airplane, pitcher). The results showed consistent J-distributions in the location of the leading feature (i.e. the 'direction' of the drawing). Namely, the direction was strongly correlated with handedness, with most subjects consistently directional and a sharp drop-off to weaker and weaker consistency. Like Wilson, Perelló (1970) confirms this tendency to draw leading features on the side contralateral to the drawing hand:

> We have observed that when right-handed children draw man or animal faces, these faces always look left. On the contrary, left-handed children draw faces looking right. (Perello 1970, 141)

The only one so far to argue for more left-facing (and hence more right-handed artists), Wilson (1886, 17) refers to hieroglyphs at Palenque (Mexico, Mayan site), in which 'most' of the animals are depicted looking to the left.

On the opposite side, some argue that prehistoric painters were more left-handed than nowadays, or ambidextrous. This is the case of Perelló, Breuil, Leroi-Gourhan, and Willcox. Breuil (1952) reported finding 50.56 per cent right-oriented profiles in European cave art (n = 720) (cited in Willcox 1991). Similarly, Leroi-Gourhan (1965) reported 58.9 per cent right-oriented profiles in European cave art (cited in Willcox 1991). Perelló found, in the Spanish cave of Altamira, equal numbers of right- and left-facing bison (Perello 1970, 142). From these and other references (books on cave art, etc.) Perelló agrees with the high proportions of left-handers among prehistoric 'artists'. André Leroi-Gourhan (1965, cited in Willcox) found 58.9 per cent right-facing animals, as did Breuil (1952), who found 50.56 per cent right-facing profiles (Breuil (1952). From a survey of several site records, Willcox (1991) found figures ranging from 53 per cent to 64 per cent right-facing animals in South African, San, and nearby rock art. He speculates that the right hemisphere's superiority in face/pattern recognition, colour perception, and other visual abilities causes a higher proportion of left-handers to be artists, and agrees that the African data supports greater prehistoric left-handedness than in living San bushmen. Pales, cited in Delluc &

Delluc (1993, 44) also found more animals facing to the right, and concluded there must have been more left-handers in prehistory.

Handprints and hand stencils

A substantial body of literature has been published on counts of right and left handprints and stencils in caves. As these are frequent throughout the world, easy to count, and were directly created by the hands of actual prehistoric people, they contribute valuable data. There are three ways of making representations of hands in caves or rock shelters: 1) by dipping the hand in paint, or painting a motif onto the hand, then pressing the hand against the wall; 2) by putting the hand on the wall and spraying, or outlining, or dabbing paint around it; 3) by drawing a hand, either stylized or realistic-looking. The first method results in positive handprints, the second method produces negative hand stencils, and the third will not be considered here because it is disconnected from any real, actual human hand.

Handedness can be interpreted through these images if we make the basic assumption that the nondominant hand was preferentially placed on the wall, and that it was placed palm down. If the dominant hand was needed to hold the paint palette, the blowing tube, the candle or torch (since most cave paintings were made beyond the light of day), or anything else, then the nondominant hand would naturally have been the one selected to press against the wall. When using a blowing tube to spray pigment, the implied biomechanical constraint is that the dominant hand (the one with more precise control) will hold the tube, leaving the nondominant hand free to be painted on. Without a tube, one mixes pigment powder with water and/or saliva and sprays it directly from the mouth. It may be necessary to hold a container of pigment, for which the dominant hand might be used. Even without holding anything in the other hand, it appears more natural to press the nondominant hand against the wall (see below Gilabert pers. comm.; Faurie & Raymond 2004).

For positive prints, there is no question that the palm must have been down, since the skin on the back of the hand has its own distinctive pattern which is not that of a palm print. For negative images or stencils, in which we only see the outline of the hand, it is possible to distinguish between palm up and palm down by several methods: the clarity of the outline, the spreading angle between fingers, the presence of the forearm, and the position of the hands on the cave wall. Gradín (1994, 153) explains that a distinct contour can only be achieved with the palm down; the back of the hand cannot be applied with enough pressure on the wall to make a tight seal. In discussing the practice of making fingers look deliberately distorted (such as missing fingers), Walsh (1983, 4) indicates that some Australian Aborigines avoided the underspray problem ‘either by greasing the hand to make it fit close to the surface, or by placing the back of the hand against the rock and then holding the fingers down’. Barrière & Sueres (1993, 52) conducted experiments showing that a dorsal hand position, even with the fingers held down, produces this invasive pigment in between the fingers due to the lack of a tight seal, and furthermore that the hand cannot reach its maximum spread of fingers when it is dorsally placed. This is one way to rule out the possibility of faking missing fingers: the maximal spread between fingers cannot be faked if the fingers are bent. Kirchner (1959), from her own experiments, concluded it was possible to replicate, with clear outlines, the Gargas hands (with missing fingers) by bending the fingers.

In addition, the very position and angle of handprints can rule out the use of one hand. First, the height above ground (usually eye-level: Henneberg & Mathers 1994) constrains the angle at which the elbow can bend. Second, if part of the outline of the forearm is present, then it is clear which hand was used; but even without the forearm, some left hand stencils with a bent wrist coming from the left side (see for example the frieze of 21 aligned hands at Gua Ham, Borneo: Fage & Chazine 2001) can only have been made with the left hand palm down. This kind of wrist-bending can be seen in many photographs of hand stencils around the world, and seems to be a natural effect of trying to make a vertical hand stencil (because the distance required to blow pigment from one’s own mouth is around 40 cm (Barrière & Sueres 1993, 49) the elbow must bend outward from the body). Furthermore, it appears more natural for a right-hander to place the left hand against the wall. It has been observed by one right-handed painter with four years’ experience making hand stencils, that it feels more comfortable and natural to press the left hand against a wall (C. Gilabert pers. comm.). This is because the body must twist slightly to position the left hand on the wall while leaving the correct distance between mouth and wall. This seems to imply some sort of biomechanical preference on torso twisting.

Barrière & Sueres (1993, 50) give two examples from Gargas Cave (France, Gravettian era, 26–21 kya) that would have been impossible to make with the right palm up. One stencil is a hand placed horizontally with the wrist to the left, located 2 m above the ground in a narrow niche. In order for the right hand to be used palm up, the person would have had to hang upside-down while a second person sprayed the pigment, and yet the niche was only big enough for one person. The second example is a left hand with the arm extending to the elbow, oriented 45 degrees to the right, located beneath a sloping wall.

The techniques and methods for making negative and positive hand images have been extensively studied experimentally (e.g. Ringot 2002). The technique used 30,000 years ago can be determined by microscopic features of the pigment on the cave wall, such as degree of pigment invasion into the porous surface, the size of pigment particles, and their distribution (Clot *et al.* 1995). These authors identified three techniques used at Gargas, for different colours of pigment. For red and yellow, and black carbon-based pigment stencils, liquid paint was applied by spraying from the mouth. For black manganese stencils, the pigment was applied by dabbing with a brush or piece of fur (Clot *et al.* 1995, 231).

Paunero (1992, 53), in a study aiming to replicate the negative hands (or stencils) at Cañadón de Los Toldos, Patagonia, experimentally tested numerous variables in order to create the negative hand painting process which gives results 'most closely approximating the observed archaeological reality'. He tested the technique in which paint is directly sprayed from the mouth. The variables were: paint density, velocity of application, quantity of air, distance between the mouth and hand, temperature of the paint, basal area (area covered by sprayed paint), angle of dispersion (indicates the amplitude of spraying), angle of mouth position (measured from 0 degrees for the horizontal to the direction of spraying). He concluded that the Patagonian hand stencils at Cañadón de Los Toldos were made with mouth spraying.

The method of spraying with a tube was experimentally tested by Faurie & Raymond (2004). They tested 179 naive subjects for throwing hand, and instructed them to make a negative hand using a pen which sprays ink when blown into, mimicking the technique of prehistoric painting with a tube. Finally the subjects were asked which was their writing hand. Although most subjects held the tube in the same hand as the throwing and writing hand — making stencils of the opposite hand, as expected — a surprising number of right-handers made right-hand stencils (17 per cent). In contrast, only one left-hander made a left-hand stencil. These results suggest that the archaeological record should show more right-hand stencils than expected, if a certain proportion of right-handers are adding their right-hand outlines to the total of right hand outlines produced by left-handers. Furthermore, it can be deduced that the actual number of right stencils indicates the very maximum possible number of left-handed people, since some of the images could have been produced by right-handers. Thus the number of left-handers can be estimated from the number of right stencils, if 93 per cent of right stencils were made by left-handers. Conversely, nearly 100 per cent of left stencils can be attributed to right-handers. Compared with the summed data from Europe, Faurie & Raymond's proportions are almost identical to those of several European caves, suggesting that similar proportions of right- and left-handers existed in the last 10 kya. Aside from the assumption that painters only painted their own hands, Faurie & Raymond are also based on the supposition that negative hands were painted with a blowing tube. (Barrière & Sueres 1993, 50 describe a single painting event in Gargas, two adult hands framing a pair of child's hands, which implies they were painted hands-free, unless a third person held the tube. The evidence for spraying directly from the mouth suggests that the use of a tube must not be taken for granted).

Taking into account the assumptions that the preferred way of making hand images was palm-down placing of the nondominant hand, we can now turn to the archaeological data. The oldest cave paintings are currently in Chauvet Cave (France), and are dated to 32–30 kya (Valladas *et al.* 2001; Clottes n.d. website).

In the Cosquer cave (France, dated to 27–19 kya: Valladas *et al.* 2001), Clottes & Courtin (n.d. website) counted 54 negative hand stencils and one positive print. The proportion of left and right hands is unclear, but there is a panel with 8 left stencils sprayed in black.

Delluc & Delluc (1993, 34–5) review the literature from France and Spain, finding majorities of left hands everywhere: 17 caves with 319 hands yield 228 left hands for 52 right hands. In Kirchner's study (1959, 110) on hand representations in the Franco-Cantabrian area, combined with data from the rest of prehistoric Europe and ethnographic data from Australia and the Americas, she counted 304 left-hand stencils for 71 right, and 83 right-hand prints for 15 left-hand prints. This makes a total of 473 hands, consisting of 82 per cent right-handedness and 18 per cent left-handedness. Kühn (1955) had already counted 9 right- and 35 left-hand stencils at the site of El Castillo, in Spain.

In a study of several caves on the Nullarbor Plain, Australia, Lane & Richards (1966, 46) report that 'the majority' of stencils are left hands. The stencils are found in Murrawijinie Cave Numbers 1 and 3, Knowles Cave, and Abrakurrie Cave. The dates given for nearby Koonalda Cave are 13,700 and 18,200 ya.

Fage and colleagues (Fage & Chazine 2001; Fage *et al.* 2002) report on recent discoveries in Kalimantan, Borneo. There are 1500 hands in 26 caves, which have been dated to about 9900 ya (Plagnes *et al.* 2003). The sample taken from a calcite drapery covering a hand stencil at Gua Saleh was dated to 9870 ya, so the image must predate the drapery. Total hand stencil counts for one of the caves, Gua Tewet level 1, are 189. Of these, 114 are left hands, 50 right hands, and 25 indeterminate. This follows the general pattern of about two-thirds left hands to one-third right hands in all the Kalimantan caves (L.-H. Fage pers. comm.). The magnificent frieze at Gua Ham, for example, is made of 21 aligned hands, of which 20 are left and 1 right. The only exception is in one section of the 'Tree of Life' in Gua Tewet, consisting of 20 right and 2 left hands. The uniqueness of Borneo's hand images are the composition of interconnected 'trees' of hands, connected with lines, and decorated with symbols painted onto the palms.

Gradín (1994, 153) studied the Río Pinturas (Painted River) region of cave art in Central Patagonia. Hand stencils date to at least 9 kya and extend to 5300 ya. Two caves, Cueva de Las Manos and Cueva Grande of the Arroyo Feo, yielded counts of 329 left hands to 31 right ones, and 97 left hands for 2 right hands, respectively.

Greer & Greer (1999, 60) report on 708 rock-art sites in Montana, USA. These caves, bluff faces and rock shelters can be dated as beginning in the Middle Archaic period (3000 BC) and extending to AD 1400. The majority are positive prints (only 7 hand stencils exist). There are 429 identifiable prints with respect to laterality; 317 (74 per cent) are right hands and 112 (26 per cent) are left hands.

Gunn (1998) describes two rock-art complexes in the Levy Ranges, Australia, Kulpi Mara and Irtikiri. They have unique patterned handprints which were made by first painting patterns onto one hand, then pressing the painted hand onto the rock surface. In 7 sites there are 109 patterned handprints, 84 hand stencils, and 7 handprints. Reliable counts reveal 4:1 right to left prints, 1:4 right to left stencils, and generally more left- than right-patterned prints. Gunn proposes this latter fact reveals the tendency for right-handers to paint with the right hand onto the left. Suggested dates for these sites are fairly recent, i.e. within the last 2000 years, although one shelter was occupied in the last 30 kya.

Conclusions

We shall conclude by discussing the question that structured this symposium — namely, is knapping stone a uniquely hominin behaviour? It seems that humans routinely use a single 'preferred' hand to play the leading role in tool use, and that nearly nine times out of ten the choice is of the right hand. As we have mentioned, and as is discussed by other contributors to this volume, there is only weak and inconclusive evidence for a similar population-level bias towards the right hand in the tool-using behaviours of other living primates. This suggests that there may also be something unique about the organization of the neural substrate that controls these voluntary manual actions. If we analyze the skeletal and material cultural evidence for a population-level bias towards right-handedness, we see that the bias is consistently observed in the remains of anatomically modern human populations, and that there is a limited quantity of evidence which consistently indicates that such a bias also existed among the earlier members of our own genus. Whether this reflects selection for tool-making and tool-using capacities, or selection for some other adaptive capacity, is unfortunately beyond the scope of this paper.

Although the study of human handedness certainly opens an intriguing window onto the past, and onto the evolution of human tool making and tool use, there are other questions about hand skill which also need to be asked. It is logically quite possible that the evolution of handedness addresses only a part of the problem of the evolution of skill and complexity in the *chaîne opératoire*. If the evolution of a bias towards right-handedness preceded the evolution of a fully-modern capacity for complex serial order in planning and executing tool-making and tool-using actions, then we may be over-estimating the significance of handedness as an evolutionary marker of 'left hemisphere' executive functions of a fully human kind, including linguistic ability. An integrated assessment of both dimensions of the organization of skilled tool-using actions in the archaeological record is thus long overdue. For some handedness researchers this could amount to 'thinking the unthinkable'; but thinking the unthinkable is always a stimulating (if unsettling) exercise.

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