

Bilateral Asymmetry of the Humerus
Throughout Growth and Development

By

Amanda C. Blackburn

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Department of Anthropology
University of Manitoba
Winnipeg

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Abstract

This project investigates the development of asymmetry throughout growth by using bilateral asymmetry of the humerus as a proxy for handedness. A large skeletal sample of non-adults combined with a smaller sample of adults, primarily from British archaeological sites, was examined in order to detect when handedness appears in the human skeleton. Traditional measurements were combined with 3D data in order to provide a comprehensive picture of bilateral asymmetry. Results of this work indicate a striking trend from left to right-handedness during growth and development, with infants and toddlers exhibiting left-sided asymmetry and older children and adolescents demonstrating right-sidedness. Interestingly, this trend is consistent with what has been observed behaviourally in children, suggesting that biomechanical forces strongly influence bilateral asymmetry in the upper limb bones. In addition to examining handedness throughout growth, this research also explores bilateral asymmetry more generally as it is impossible to fully understand handedness without observing how asymmetry varies according to different factors. Although this work supports the hypothesis that all human populations are right-handed, there are subtle differences between groups. Results indicate that British populations became more asymmetrical over time, with this becoming most pronounced during the Industrial Revolution. Differences in degree of asymmetry between males and females was also noted, suggesting differences in activity between the two groups, as well as supporting the notion that the male and female skeleton differ in how they respond to biomechanical forces. Overall, this work provides a comprehensive analysis and discussion of how handedness presents in the human skeleton.

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Chapter 1 - Introduction

There are only a few traits that can be considered uniquely human, and among them is our seemingly inexplicable preference for right-handedness. It is well established that the majority of humans are right-handed, meaning they use their right hand for most unimanual tasks. Overall, approximately 90% of individuals exhibit right-handedness while left-handedness accounts for the remaining 10% of the population (Annett, 1985; Calvin, 1983; McManus, 2002). Although this proportion may fluctuate somewhat among populations, in general, right-handers far outnumber left-handers (Bryden et al., 1993; Faurie et al. 2005; Marchant & McGrew, 1998). However, the process through which handedness develops in children remains somewhat unclear, with many children exhibiting a preference for the left hand early in life (Corballis, 1983). Even less clear, is how hand preference is reflected in the bones of non-adult individuals. The purpose of this work is to investigate morphological variation of the humerus in past human populations for evidence of the development of hand preference in childhood.

In order to investigate the emergence of handedness in children, this project will use shape and size of the upper arm bones as a proxy for hand preference. The basis for this investigation lies in the knowledge that bone is a highly malleable tissue that responds to mechanical forces throughout life (Frost, 2003; Ruff et al., 2006; Wolff, 1892). As such, the skeleton can alter its mass, density, and shape in response to physical activity. These changes are adaptive, helping the bone maintain integrity and decrease the likelihood of fracture. As humans exhibit the tendency to use one arm more than the other, behavioural laterality will be reflected in directional asymmetry of upper limb bones (Blackburn & Knüsel, 2006; Lazenby, 2002).

Although this asymmetry is well-documented in adult skeletons, it is unclear whether bones of the upper limb display asymmetry early in development or if this only becomes apparent later in life. Subsequently, this raises uncertainty about whether biomechanical or genetic factors are primarily responsible for asymmetry. Through the investigation of upper limb asymmetry, this study will help determine whether handedness is a trait present at birth or one developed throughout life. If analysis of morphology reveals that a right-sided asymmetry is present in the majority of infants and young children, this study will support the hypothesis that genetic factors play a strong role in determining upper limb asymmetry. Alternatively, if a trend toward right-sided dominance does not become evident until later in development, this will suggest that biomechanical forces are necessary to make handedness observable in skeletal remains.

The majority of skeletal populations used in this study are British in origin, ranging from the 1st century B.C. to the 19th century A.D., although most are medieval. Many of these individuals would have lived in rural agricultural settings and, therefore, would have engaged in a wide variety of activities associated with this lifestyle. However, over such a large span of time, tasks were bound to change or be modified, particularly following the Industrial Revolution. Bilateral asymmetry can also be used to compare individuals from different sites and time periods in order to elucidate any variations according to these factors. This study also includes a small Sadlermiut sample from Native Point, Nunavut. The Sadlermiut are an extinct Inuit population who remain somewhat mysterious. Little is known of the Sadlermiut as ethnographic accounts are scarce, but evidence suggests this group had a strong emphasis on marine resources and were excellent whalers. Therefore, the differences in activity patterns between the

Sadlermiut and British populations should be acute and potentially observable on the skeleton.

Overall, this work represents a comprehensive examination of how bilateral asymmetry of the humerus, and by proxy handedness, develops throughout growth. Results will contribute to our understanding of what forces are primarily responsible for bilateral asymmetry and whether this trait is subject to strong genetic control (Lovejoy et al., 2003). This study will also be able to demonstrate if there are any variations between populations based on differences in activity patterns throughout time, or geographic region. As such, the cumulative knowledge gained from these analyses will allow for a more complete picture, not only of how handedness presents throughout growth, but what implications this has for lifestyle and the types of activities being performed by individuals in the past.

Chapter 2 - Literature Review

The exact nature of handedness, including our universal preference for the right hand, the persistence of left-handedness, and the evolutionary mechanisms that have led to the presence of this trait in humans are questions that have long perplexed researchers. The extreme propensity for right-handedness exhibited by *Homo sapiens* as compared to other animals, including non-human primates, suggests this trait may be unique to the human species. Through the examination of modern non-human primate populations and archaeological evidence, particularly skeletal asymmetry, it may be possible to infer both how and when handedness appeared in human evolutionary history. Working on the basis that handedness has deep evolutionary roots, it then becomes possible to investigate how this trait appears in individuals, specifically how it develops throughout growth.

Historical and Archaeological Evidence of Handedness

The universality of human right-handedness is supported not only by observation of modern populations, but through examination of the historical and archaeological record as well. Faurie and colleagues (2005) used old films and photographs taken from anthropological investigations of traditional societies in order to investigate hand preference in these groups. The researchers discovered that in all cases, right-handedness was observed in between 75% and 97% of individuals. A more highly influential study, however, was conducted by Coren and Porac (1977). As it is clearly not possible to directly observe handedness in past populations and written references to lateral preference are rare, Coren and Porac (1977) deduced that artwork should reflect the distribution of handedness witnessed by the artist. Therefore, works of art can be

considered representative of handedness patterns in the culture that produced them. The study focussed on 1200 pieces of art depicting uni-manual weapon or tool use, and spanned a time period of approximately 5000 years (3000 B.C. to A.D. 1950). Results were consistent with those from modern populations in that the majority of individuals were depicted as right-handed. Furthermore, the proportion of left- to right-handers was similar to modern populations, with right-handed tool or weapon use observed in 93% of instances. Although this study provides valuable evidence indicating that for at least the past 5000 years humans have been right-handed, it should be noted that the proportion of left- and right-handers observed may not necessarily reflect true numbers of these individuals. For example, a right-handed artist may be more inclined to depict subjects as right-handed also. Also, left-handedness has often been stigmatized and, therefore, may not have been fully represented by art in some cultures (Brackenridge, 1981; Coren, 1993). Nevertheless, both Coren and Porac's (1977) work and the study by Faurie and colleagues (2005) provide strong evidence that right-handedness is not merely a characteristic of modern Westernized populations.

Archaeological evidence has been used to support the hypothesis that species-level right-handedness was present even earlier in the human past than demonstrated by the above-mentioned studies. In a review of prehistoric cave art Uhrbrock (1973) found that there is a predominance of left handprints depicted. Presumably, these were produced by blowing coloured powder through a hollow bone. In this technique, one hand would be used to hold the bone implement while the other would necessarily become the subject of the handprint. Uhrbrock (1973) reasoned that, as the dominant hand would have held the hollow bone, the predominance of left handprints indicates that most artists were

right-handed. However, this conclusion rests on the premise that the depicted hand belongs to the artist, which is unknown. These cave drawings date to the Upper Pleistocene, between 10,000 and 40,000 years ago. Bradshaw and Nettleton (1983) also examined human and animal depictions from the same period. These researchers found that most subjects of cave art faced left, a tendency that is mimicked by modern right-handed artists. Therefore, Bradshaw and Nettleton (1983) suggest that this trend is evidence for right-handedness toward the end of the Upper Pleistocene.

It has been proposed that stone tools can be used to determine the hand preference of the tool maker (Toth, 1985). During the manufacturing process, if a striking platform is oriented upwards with the exterior surface facing the maker then a right-handed blow with a hammerstone will produce flakes with cortex only on the right side (Pobiner, 1999). In this manner, examination of patterns of cortex on flakes can reveal the handedness of the tool maker. Based on this method Toth (1985) suggested that right-handedness could be detected as far back as the Lower Pleistocene, 1.4 – 1.9 million years ago. Several researchers, however, have noted that there are many problems associated with this method (Davidson & Noble, 1996; Patterson & Sollberger, 1986). For example, Pobiner (1999) has noted several assumptions intrinsic to this technique, including the requirement that all flintknappers must rotate a core clockwise. Additionally, raw material and individual flintknapping skill can affect cortex patterns (Pobiner, 1999). In an experiment conducted by Patterson and Sollberger (1986) it was demonstrated that there is no consistent correlation between a tool maker's hand preference and the type of flake produced. Based on these conclusions, stone tool

evidence must be viewed cautiously as its ability to accurately reflect handedness remains questionable.

Postcranial Evidence of Handedness

As handedness is a highly elusive trait in the archaeological record, skeletal remains of the upper limbs offer the most direct evidence of hand preference in past populations. Behaviourally, hand preference can be detected by various means, including what hand is dominant in fine motor tasks, such as writing, and also which hand is used for coarse strength tasks like using a hammer (Auerbach & Ruff, 2006; Blackburn & Knüsel, 2006; Harris, 2000), with the evaluating criteria often having the potential to affect reported proportions of left and right-handers. This results from a tendency for many individuals to exhibit some degree of ambidexterity. As such, it is best to view handedness as a continuum, with only some people being very strongly left or right-handedness, and most individuals falling somewhere in the middle (McGrew & Marchant, 1996). In general, however, an individual's handedness can be considered the hand that is used in performing the majority of tasks.

In order to understand how skeletal evidence can provide information about what is primarily a behavioural trait it is first necessary to understand the manner in which bone adapts to activity. Essentially, bone is a dynamic, malleable tissue that responds to mechanical forces throughout an individual's lifetime (Knüsel, 2000a; Lazenby, 2002). The skeleton is particularly responsive to unusual, short-term loads to which it will respond by altering its mass and density. These changes are adaptive, helping the bone maintain its integrity. As humans exhibit the tendency to use one arm more than the other,

this behavioural laterality should be reflected in directional asymmetry of size, shape, and pattern of remodelling in the skeleton. However, it is necessary to demonstrate this trend in living individuals of known handedness before applying it to past populations.

An examination of biomechanical theories, and how bone models and remodels can provide a basis upon which to interpret morphological aspects of the humerus. Wolff's law is commonly cited in bioarchaeological and palaeoanthropological studies as a means of explaining that bone adapts to its mechanical environment and, consequently, morphological differences can be used to examine past activity and mechanical strains (Ruff et al., 2006). However, it is interesting to note that Wolff (1892) actually intended to develop mathematical rules which could be used to explain trabecular orientation in long bones. Although that aspect of his work has not stood the test of time, the more general concept that emphasizes the importance of mechanical loading on skeletal form is still predominantly accepted among bioarchaeologists and palaeoanthropologists (Ruff et al., 2006).

Frost (1987; 1996; 2003) built on Wolff's law by proposing a mathematical theory for bone biology known as the "mechanostat". This model is based on the idea that the skeletal system evolved primarily for mechanical needs. Frost (1987; 1996; 2003) hypothesizes that there is a mechanical feedback system that controls bone mass, so that whenever the skeleton is challenged by a non-mechanical signal, its response is channelled through a mechanosensory system and any changes are designed to preserve optimum mechanical function. The skeletal system has a series of minimum effective strains which serve as set-points. If bone is in disuse and strain falls below the minimum value (set-point), it will undergo high turnover bone loss, whereas strains above the set-

points will stimulate new bone growth. Frost (1987) also proposes that hormones and biochemical agents can artificially change set-points so that the minimum effective strain is altered. Although the essence of the mechanostat theory has some validity, its predictions do not appear to conform well to experimental observations (Turner, 1999). Ruff and colleagues (2006) point out that feedback models do tend to have issues in effectively dealing with the complexity of the skeletal system. For example, the amount of strain needed to elicit an osseous response is not the same throughout the entire skeleton but varies by location. Nevertheless, complexity in a model does not necessarily make the approach invalid (Ruff et al., 2006)

The inability for mathematical models to reliably predict bone modeling and remodelling forms one of Lovejoy and colleagues' (2003) primary arguments for the dismissal of mechanical strain hypotheses. While they do not deny that bone is susceptible to mechanical loading, Lovejoy et al (2003) suggest that too little is known about the mathematical laws governing skeletal modification to be useful. As an alternative, they propose that bone morphology and modification can be much better explained through genetic mechanisms, especially in light of technological developments in recent years. Pearson and Lieberman (2004) also acknowledge the potential that recent advances in genetics hold for our understanding of skeletal development. However, unlike Lovejoy and colleagues (2003) who strongly downplay the role of mechanical strain, Pearson and Lieberman (2004) suggest that it may indeed be possible to develop a greater understanding of bone structure and function (i.e. predicting activities based on skeletal form) although they question the usefulness of Wolff's law as an organizing principle due to its oversimplification of complex phenomena. Pearson and Lieberman

(2004) also point out the value of considering factors other than mechanical strain in triggering the resorption and deposition of bone. Of particular importance, is the difference observed in skeletal response to mechanical strain throughout the ageing process, with non-adults being more susceptible to activity-induced change than adults, probably as a result of cellular and hormonal mechanisms (Pearson and Lieberman, 2004).

Despite recent criticisms of Wolff's law, its basic underlying premise still maintains validity. As such, Ruff and colleagues (2006) propose that the general concept of bone functional adaptation replace Wolff's law in order to avoid issues with the more specific aspects of the law. Overall, functional adaptation essentially encompasses what the majority of researchers are referring to when Wolff's law is cited. However, as with other recent studies, Ruff and colleagues (2006 p.494) emphasize that "the function of the skeleton is not purely mechanical, and therefore its mass and morphology represent a compromise between different physiological demands, of which mechanical competence is only one." Furthermore, the perspective of Pearson and Lieberman (2004) dichotomizes genetic mechanisms and mechanical stimuli in the production of skeletal morphology. Such a polarizing viewpoint may be detrimental to interpretive frameworks, as both mechanical loading and genetic factors clearly influence the development of skeletal morphology (Ruff et al., 2006).

With regard to handedness and bilateral asymmetry, in general the dominant hand and arm are stronger and capable of performing more skillfully than their non-dominant counterparts (Steele, 2000). Among right-handed adults and adolescents, muscle mass is also greater in the dominant arm (Dorado et al., 2002; Schell et al., 1985; Taaffe et al., 1994). This pattern is less reliable in children, although some research suggests that the

dominant arm can be identified at a young age, even as early as in foetal development (Hepper et al., 1991; Pande & Singh, 1971). Clinical studies have also demonstrated that the dominant side tends to have a greater range of motion. For example, the humeral head tends to have a larger angle of retroversion on the dominant side, a feature that allows for an increased range of rotation (Kronberg et al., 1990). Schulter-Ellis (1980) discovered similar results when examining a sample of scapulae taken from individuals of known handedness. From this sample, it was determined that greater dorsal inclination of the glenoid fossa corresponds to handedness, although it is unclear whether this trait is established at birth or is increased by preferential limb use. In this study, Schulter-Ellis (1980) also examined several aspects of the humerus and radius and found that the greater total length of the long bones (humerus and radius combined) could be used as a predictor of hand preference. Additionally, the width between the epicondyles of the distal humerus was also greater on the dominant side. Work by Blackburn and Knüsel (2006) found a similar positive correlation between epicondylar breadth and hand preference in a living population. However, this trait appears to be complicated by individual activity patterns, such as the necessity of using the left-hand in certain tasks even though an individual may actually be right-handed. This subsequently affects the usefulness of size asymmetry as a handedness predictor and points to the need for taking several features into account when examining skeletonized individuals of unknown handedness. Although some morphological features may be affected by factors such as the performance of left-handed tasks, the majority of measurements should point towards true handedness.

Unusually high levels of activity can also create interesting patterns of asymmetry in the skeletal elements of the upper limb. Research involving professional tennis players has revealed that these individuals have some of the most exuberant osseous responses of any recorded group (Trinkaus et al., 1994). Jones and colleagues (1977) found that male tennis players had as much as 34.9% more bone in their playing arms as compared to their non-dominant arm. Similarly, females had up to 28.4% more bone in their dominant arms. Overall, these studies demonstrate that various skeletal asymmetries result from hand preference and differences in mechanical strain (i.e. stress placed on the bone as a result of movement, either with or without additional weight applied) placed on the dominant and non-dominant limbs. In this manner, it is possible to confidently use skeletal asymmetry as a proxy for handedness in past populations.

As skeletal remains from the recent past tend to be better preserved and more abundant than those from earlier periods, it is not surprising that many studies examining asymmetry in the upper limbs are based on populations dating to within the past 1000 years. If right-handedness is truly a characteristic that typifies humans, then evidence for this trait should be observable in these archaeological skeletal remains. The following summarizes the results of several studies which investigate handedness in past populations based on skeletal asymmetry.

Steele and Mays (1995) examined a large sample of skeletons from Wharram Percy, North Yorkshire, England. These remains were obtained from a medieval churchyard and date from the tenth to nineteenth century A.D., although the majority lived between the eleventh and sixteenth century. For the purpose of this investigation, Steele and Mays (1995) focussed on the maximum length of arm bones – humerus, radius,

and ulna. In general, the proportion of longer right to left elements was similar to modern distributions of asymmetries for hand/arm skill and strength. The results from combined humerus and radius length were perhaps the most reflective of modern handedness proportions, with 81% of individuals possessing longer right arms, while 16% had longer left limbs. The remaining 3% of individuals had arms that were the same length on both sides, perhaps suggestive of ambidexterity. Mays and colleagues (1999) also investigated the Wharram Percy skeletal collection to assess the evidence for handedness in the clavicle. This is particularly interesting not only because the clavicle is often overlooked in studies of handedness despite the fact that it serves as an anchor to many of the muscles used to move the arm, but also because previous work had determined the population to be predominantly right-handed (Steele & Mays, 1995). Unlike the bones of the arm, increased length in the clavicle is not necessarily associated with hand dominance. Rather, axial compression caused by mechanical loading acts to inhibit longitudinal growth leading to elements from the dominant side actually being shorter than their non-dominant counterparts. This trend is supported by evidence for clavicular length asymmetry being contralateral to humeral length asymmetry within individuals (Auerbach & Raxter, 2008). Therefore, it is not surprising that Mays and colleagues (1999) found that among both males and females the left clavicle tended to be longer than the right, an observation that both supports the work of Steele and Mays (1995) and the notion that populations in the past were right-handed.

Examination of soldiers from medieval Britain also provides important details about how handedness presents in skeletal remains and how the effects of habitual activity can confound results (Knüsel, 2000*b*; Rhodes & Knüsel, 2006). Analysis

conducted by Knüsel (2000*b*) of the skeletal remains recovered from the Battle of Towton (1461 A.D.) revealed that while the soldiers' humeri were bilaterally asymmetrical, this asymmetry varied depending on the measurement considered. Specifically, in the majority of individuals the proximal humerus was larger in the right element, while asymmetry of the distal humerus was more typical of left-handers. This has been corroborated with a cross-sectional analysis of the humeri of the population (Rhodes & Knüsel, 2006). Based on these results and what is known about medieval soldiers and warfare, it has been concluded that the variations in asymmetry witnessed in this population result from archery. Right-handed archers hold their bows with the left hand which, subsequently, can lead to architectural changes in the distal humerus but is not indicative of left-handedness. The confounding effect that unusual, repetitive movements can produce in the skeleton is an issue that must be kept in mind when attempting to identify handedness in the archaeological record.

Beyond the past 1000 years, skeletal evidence also points to a preponderance of right-handedness among humans. Analysis of 27 Neolithic skeletons from sites in the Middle Elbe-Saale region, which is now in Germany, revealed a right-sided dominance in 70% of individuals (Steele, 2000). The remaining individuals were divided equally between exhibiting left-sidedness and showing no difference between either side. Skeletal remains of *Homo sapiens* dating to the Mesolithic in northern Europe also demonstrate asymmetry consistent with right-handedness (Constandse-Westermann & Newell, 1989). Of 57 individuals, 43 had longer right arms, while the remaining 14 had longer left arms. These results suggest that right-handedness has been present at least since the Mesolithic.

Examination of older specimens, while few in number, indicates that skeletal evidence for handedness stretches back further. Churchill and Formicola (1997) have found strong support for behavioural lateralization in the early upper Palaeolithic in Europe. The burial discovered at Barma Grande, Italy, is believed to date to the Gravettian or EpiGravettian cultures of the region. Although three individuals were discovered in the burial, Churchill and Formicola's (1997) analysis focuses on an adult male, known as Barma Grande 2, who displays marked asymmetry of the upper limbs. Although skeletal material from both sides of the individual is remarkably robust, the researchers describe elements from the right side as hyper-robust. This is particularly evident in the humerus which exhibits dimensions well above those of other late Pleistocene males. Overall, asymmetry is more marked in diaphyseal rather than articular dimensions and, additionally, this asymmetry lessens as one moves distally from the upper arm to the forearm and wrist. These patterns suggest increased asymmetrical activity in adulthood rather than during development, and that this activity primarily focussed on the upper arm rather than the lower part of the limb. Similarly, it also points to more equal use of both forearms. This loading pattern is abnormal and would most easily be attributed to some kind of pathology which limited movement in the upper arm but did not affect the lower arm. Interestingly, while Churchill and Formicola (1997) were unable to definitively rule out pathology to the left arm which may have led to this pronounced asymmetry, there is no evidence for its presence. Therefore, this appears to represent a case of right-handedness in earlier modern human skeletal remains.

Analysis of Neandertal remains from the Late Pleistocene suggest that right-handedness was a trait characteristic of these archaic humans as well (Trinkaus et al.,

1994). Through examination of bilateral asymmetry in the humerus (diaphysis and articulations), Trinkaus, Churchill, and Ruff (1994) determined that Neandertals were differentially loading their upper limbs. In all cases, the right arm was more robust than the left, indicative of a right-hand preference.

The earliest evidence for handedness based solely on bilateral asymmetry of the upper limbs dates to the early Pleistocene, approximately 1.6 million years ago (Walker & Leakey, 1993). Recovered from the area around Lake Turkana, Kenya, the remains of a young male *Homo erectus*, known as the Nariokotome boy, demonstrate rugged muscle attachments on the right clavicle, and a longer right ulna compared to the left. This evidence suggests that right-handedness extends back to at least the early members of the genus *Homo*, although sample size is such that any conclusions must remain extremely tentative. In order to find signs of handedness during earlier periods of our evolutionary history, it is necessary to use alternate means of investigation.

Cranial Evidence of Handedness

Cranial features have also been used to identify handedness in the past. Brain-scan studies of individuals of known handedness have revealed some patterns in cerebral asymmetry associated with handedness (Steele, 2000). These include associations between hand preference and asymmetry of neocortical features such as the planum temporale (Steinmetz et al., 1991), the planum parietale (Jancke et al., 1994), and the Sylvian fissure (LeMay, 1976; Witelson & Kigar, 1992). Unfortunately, while these results may be able to offer valuable insight into the mechanisms underlying handedness, they are of little use to studies of past populations as dry skulls do not preserve evidence

of the aforementioned neocortical structures (with the possible exception of the Sylvian fissure; Steele, 2000). Therefore, it is necessary to consider grosser anatomical characteristics for evidence of asymmetry. Research in this area has been less successful in identifying cerebral asymmetry, although in females a clear right frontal petalia (impressions left on the inner surface of the cranium indicating an asymmetry of a lobe with respect to its hemispheric counterpart) and a greater left occipital width are positively associated with right-handedness (Steele, 2000). Although encouraging, this correlation is less useful when examining skeletons of unknown sex. Furthermore, it has been found that asymmetry patterns vary in some modern populations, most notably among Americans of African origin and individuals from South Africa (LeMay, 1992). Despite these drawbacks, some correlation does indeed exist between cerebral asymmetry and the presence of handedness and, therefore, it is relevant to compare the intra-cranial characteristics of modern humans to those of both non-human primates and our hominid ancestors.

A well-known study by Holloway and de la Coste-Lareymondie (1982) examined and compared the cranial endocasts of modern *Homo sapiens* to fossil hominids (*Australopithecus africanus*, *Australopithecus robustus*, *Homo erectus*, and Neandertals). Observation of intra-cranial features revealed that the tendency for left occipital and right frontal length and width asymmetry is a characteristic not only of modern humans, but is present in fossil hominids as well. Assuming that these asymmetry patterns characterize right-handedness, then it is possible that this trait existed in the australopithecines, as far back as 2 - 2.5 million years ago (Steele, 2000). Unfortunately, this study relied on visual inspection of asymmetry which the researchers admitted was a difficult task, particularly

in the small-brained australopithecines. As with many studies involving fossil hominid specimens, incomplete preservation was also problematic. Nevertheless, Holloway and de la Coste-Lareymondie (1982) conclude that intra-cranial asymmetry does not significantly differ between modern *Homo sapiens* and earlier hominids. Holloway and de la Coste-Lareymondie (1982) also found interesting results comparing modern human intra-cranial asymmetry to pongids (*Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, and *Pongo pygmaeus*). Overall, the researchers discovered a low incidence of both occipital width and frontal width asymmetry in the apes as compared to humans. This is particularly intriguing as occipital width asymmetry is the trait they found to be most significantly related to handedness. Of all the non-human primates observed, *Gorilla* demonstrated the greatest degree of occipital asymmetry, a result which is somewhat surprising given this species' greater phylogenetic distance from *Homo sapiens* as compared to *Pan*. The increased asymmetry, however, is still not within the range of modern *Homo sapiens*. Holloway and de la Coste-Lareymondie (1982) state that these results indicate a functional discontinuity between pongid and human brains, with the more asymmetrical human brain being correlated with the presence of handedness. As with the observation of hominid endocasts, it must be noted that great ape brains are approximately one-third the size of human brains and this necessarily makes visual identification of asymmetries difficult. In general though, many of the asymmetry patterns observed in humans are expressed in non-human primates, and it is possible that such features represent exaptation to hemispheric specialization in human evolution (Bruner, 2003). It has been suggested that cerebral asymmetry may have initially developed with symbolic or visuospatial integration acting as a selective force (Holloway

& de la Coste-Lareymondie, 1982). Furthermore, this asymmetry has been related to language and tool making and Bruner (2003) proposes that the basic asymmetry observed in non-human primates served as the basis for the significant hemispheric specialization present in humans.

Subsequent work by Holloway and colleagues (2003) has focussed on chimpanzee cerebral organization in an attempt to further the hypothesis that right-handedness extends back to our early fossil ancestors. They state that while fossil evidence clearly demonstrates that australopithecines did not possess the larger brains present in later hominid remains, it is not known if cerebral reorganization preceded this enlargement or developed afterwards. Furthermore, they note that the primary visual cortex (PVC) is a probable place for initial brain reorganization. Holloway and colleagues (2003) demonstrated that it is possible for cerebral reorganization to precede brain enlargement through the observation of two chimpanzees who exhibit PVC morphology similar to modern humans. If this hypothesis is correct and the basis for PVC reorganization is present in both *Pan* and *Homo*, then the basis for cerebral reorganization would most likely have been present in australopithecines as well, despite their relatively small brains. Such a finding corroborates the results from endocast studies described previously and, while it does not provide direct evidence for the notion that australopithecines were right-handed, it suggests that the cerebral organization associated with handedness was already in place at this point in hominid evolution. However, although handedness is related to cerebral asymmetry, this relationship is presently not well-understood. As Steele (2000) points out, the correlation between hand preference and intra-cranial asymmetry in modern humans is weak and makes it impossible to

estimate the proportion of left- and right-handers in past populations. Therefore, it seems unlikely that this avenue of research is a reliable means of advancing our understanding of handedness in human evolution, although it may be able to provide corroborating evidence for changes in cerebral organization and asymmetry which may be of some relevance to handedness. But as a proxy for handedness, this method falls short and any conclusions must remain tentative.

Handedness in Non-human Primates

It seems probable that handedness has a long history in the genus *Homo*, perhaps stretching back to the australopithecines or even farther. Subsequently, the next necessary step is to investigate the presence of handedness in our nearest living relatives, non-human primates. If right-handedness does indeed exist among these species this strongly suggests that the origins of handedness lie in a common ancestor. Traditionally, non-human primates were thought to exhibit a 50:50 ratio of right- to left-handedness, indicating that while individuals demonstrate consistent hand preference, population-level handedness does not exist (Warren, 1980). This assumption was initially challenged by MacNeilage and colleagues (1987) and subsequent research on laterality in primates has suggested that hand preference may not be as clear-cut as Warren (1980) proposed.

Westergaard and Suomi (1996) studied a captive group of capuchins for hand preference in stone artefact production and tool use. Results demonstrate that capuchins have a right preference for using stones as cutting implements and for striking stones against surfaces. This particular study is the first to observe a lateral bias in artefact production and the use of stone tools in a non-human population. It is worth noting that

these observations were carried out on a relatively small group – 14 for stone striking, and 6 for stone tool cutting. Therefore, it is necessary to demonstrate this preponderance for a right-sided preference in much larger populations before any definitive conclusions are drawn. However, supporting evidence can be found in studies of other non-human primates. O'Malley and McGrew (2006) observed a small group of captive-born orangutans for indications of hand preference across several tasks, including one-handed eating, making/modify a tool, and hand-fishing for raisins. Although the researchers found no evidence for either right- or left-handedness at a population level, they did note consistent preference among individual orangutans. Of particular note is the observation that significant hand preference emerged in relation to more manipulative tasks. This suggests that handedness may surface in response to more physically and cognitively demanding tasks, such as tool-use.

Unquestionably, the majority of non-human primate studies have focussed on chimpanzees, perhaps because they are the most closely related to humans. In general, they have demonstrated a much stronger preference for the right hand than any of the other great apes. There is some discrepancy, however, between captive and wild groups, with the most disturbing criticism centering on the use of artificial measures of hand preference in captive chimpanzees (Marchant & McGrew, 1996). Specifically, there is concern that these studies use only a few activities, such as using a stone tool to cut through an artificial barrier in order to obtain food, as measure of hand preference, and these are often tasks they would not normally perform. Additional concern comes from the possibility that close contact with humans has led to the mimicking of human hand preference (Hopkins et al., 2004). In order to establish a baseline of spontaneous,

everyday hand-use, Marchant and McGrew (1996) observed a group of wild chimpanzees in Gombe National Park, Tanzania. Results indicated that there were ten general categories of natural behaviour (not including tool use) that could be scored as either left- or right-handed. Interestingly, this group proved to be unlateralized in hand-use. Even at an individual level only a few chimpanzees showed mild hand preference across tasks. Sugiyama and colleagues (1993) also investigated hand preference in a group of wild chimpanzees living at Bossou, Republic of Guinea, West Africa. Contrary to the previous study, this project involved the observation of tool using behaviour in the form of nut cracking with a stone hammer. Also in contrast to the previous study, Sugiyama and colleagues (1993) found clear hand preference in hammer holding. They reported that all adults over 12 years of age always used one hand exclusively. Non-adults showed a strong side preference for hammer holding also, with only two of nine total individuals displaying ambidexterity. These results are consistent with what Boesch (1991) observed in wild chimpanzees, with adults being highly lateralized for nut-cracking. This suggests that complicated skills such as tool use may have led to the emergence of human handedness (Boesch, 1991; O'Malley & McGrew, 2006; Sugiyama et al., 1993). Although Sugiyama and colleagues' group proved more successful for demonstrating hand preference in chimpanzees, it still provides no evidence of population-level handedness, either right or left. Observations of wild chimpanzees by McGrew and Marchant (1992) also found no population-level handedness for termite fishing, although there was a slight trend toward left-sided preference.

The strongest indication for population-level right-handedness not just in chimpanzees, but in all of the great apes, comes from Hopkins and colleagues' (2004)

comparison of wild-caught to human-reared individuals in three separate colonies. This study is particularly valuable, not only because of the comparison between different rearing environments, but because it obtained results from over 450 individuals. Hopkins and colleagues (2004) point out that a downfall of many non-human primate studies is small sample size which makes it difficult to draw any statistically significant conclusions, including the presence of population-level handedness. Additionally, this project benefits from consistent methodological practices in data collection, an issue that the authors also believe may contribute to the weak evidence for population-level handedness reported in other studies. Rather than indiscriminately recording number of uses of the left and right hand, the researchers recorded the hand used in the first response to any given action so that it could be compared to total hand use. Overall, results indicate that while chimpanzees are predominantly right-handed, the ratio is only 2:1 of right- to left-handed individuals. Although this provides some insight into the evolution of handedness, it does not approach the level of right-handedness observed in human populations.

Based on the results of numerous studies, Hopkins (2006) has concluded that chimpanzees demonstrate population-level right-handedness while orangutans and gorillas do not, although it could be argued that studies of handedness for the latter two species have been rare compared to chimpanzees. Despite this potential drawback, there are several explanations for the apparent difference in hand preference between chimpanzees and the other great apes, including the possibility that the preponderance for right-handedness evolved relatively recently and, therefore, is specific only to *Pan* and *Homo*. The observed differences could also be caused by behavioural distinctions

between the various species, including locomotor patterns and foraging behaviour (Hopkins, 2006). For example, orangutans are much more arboreal than the other apes, often using one hand to forage while the other provides support. It is probable that this positional/postural behaviour has affected the expression of handedness among the great apes.

Explanations for Handedness in Humans

There are various possible explanations for the difference in distributions of right- and left-handedness between humans and non-human primates. It is possible that these differences are influenced by cultural systems unique to humans, as handedness in humans is often measured by tasks that do not exist among the great apes, such as writing or opening jars. Furthermore, there is cultural pressure to perform many of these tasks using the right hand. Although this may have some effect on comparisons between humans and the great apes, genetic factors appear to be the most likely candidates for explaining these variations. While the specific genes controlling handedness have yet to be definitively identified, recent work by Francks and colleagues (2007) suggests LRRTM1 is a candidate gene for the development of handedness and seems to play a role in brain asymmetry. It is possible that humans and great apes may have a common basis for handedness but the expression of this gene (or genes) is more prominent among humans (Hopkins, 2006). Similarly, Hopkins and Cantalupo (2004) have suggested that cerebral asymmetries in chimpanzees may be correlated with handedness. Corballis (1997) suggests that mutations occurred in the human genome following the split from *Pan*, and that this can account for the greater occurrence of right-handedness among

humans. Research by Williams and colleagues (2006) regarding the genetic mechanisms underlying the evolution of cerebral asymmetry support this idea. They propose that approximately 6 million years ago, about the time of the chimpanzee – hominid split, a translocation and subsequent duplication occurred in the *Protocadherin11X* gene which acted as a precursor to cerebral lateralization. Williams and colleagues (2006) also suggest that this duplication may have even led to the evolutionary split which is heralded by the rise of australopithecines. Furthermore, since the duplication there has been accelerated change in this gene and, as handedness has been attributed to lateralization of brain function (Annett, 1991; Corballis, 2002; White et al., 1994), this could account for the drastic difference in handedness proportions between chimpanzees and humans.

There are several genetic theories that attempt to account for the predominance of right-handedness in humans, the most notable of which is Annett's (2002) right shift theory. Annett (2002) hypothesises that cerebral asymmetry and handedness is controlled by one gene, which she calls the right shift gene. Additionally, this gene has two alleles, known as RS+ and RS-. The presence of the right shift factor in an individual gives an advantage to the speech related areas of the left cerebral hemisphere, hence, weakening the left hand and effectively causing right-handedness. As the right hemisphere is weakened, infants are more likely to use their left hemisphere in early phases of language learning. Humans who do not carry the right shift gene (RS - -) develop all of their lateral asymmetries by chance, just like non-human primates. The cost for absence of the right shift factor (RS+) is a risk of poor speech acquisition, a hypothesis which is supported by evidence for higher than normal rates of dyslexia and stuttering among left-handers (Geschwind & Behan, 1982; Tonnessen et al., 1993). In addition to this drawback, Annett

(2002) suggests that the right shift factor poses a serious risk of mutation (RS+a). While a normal gene works to impair the development of the right cerebral hemisphere, a mutant gene will impair one hemisphere randomly. Therefore, if it is paired with a RS- gene which does not impair either hemisphere, there is no problem. If, however, it is paired with a non-mutant RS+ gene there is a 50% chance that both hemispheres will be impaired, which could lead to schizophrenia and autism. Despite these hazards, the right shift gene would have provided a significant evolutionary advantage to humans by making language easier to acquire. Annett (2002) proposes that this gene evolved very early in hominid development, probably soon after divergence from the great apes, a view which is consistent with other studies regarding the development of handedness.

Annett's hypothesis, however, does not negate the possibility that handedness can be altered by certain pathological conditions. Investigations into the causal mechanisms underlying pathological left-handedness have been pursued by Satz and colleagues (1985), who integrated the disjointed information about the association between psychologically and intellectually disadvantaged groups and left-handedness. This has been appropriately named the Pathological Left-Handedness Syndrome (PLH) and, while it has been disregarded by some researchers who understandably do not want to risk negatively labelling left-handers, the basic premise remains valid. Essentially, pathological left-handedness suggests that the presence of left-handedness in various sub-groups represents the presence of an early brain injury that alters lateral development. This can serve to change hand dominance, transfer cerebral hemispheric control of speech, and redesign cerebral organization of visuospatial cognitive functions (Satz et al., 1985). The suite of symptoms can effectively be grouped together as a syndrome that

may be detected in individuals who: 1) are manifest left-handers 2) have a known or suspected cerebral injury. It is important to note that this hypothesis does not imply that all left-handedness results from pathology. The syndrome is only intended to refer to a small subset of the complete left-handed population, and acknowledges that the majority are assumed to be natural/genetic left-handers. Such reasoning follows what is known as the *two-type model* of left-handedness which maintains that there are two separate forms of left-handedness, one which is pathological and another that is not (Harris & Carlson, 1988). Additional research has found trends that support the conclusions reached by Satz and colleagues (1985). This has been especially useful in strengthening the hypothesis that early development (i.e. foetal and infant environment) plays an important role in handedness. Studies by O'Callaghan and colleagues (1993a, b) have identified a positive correlation between several factors and left-handedness. The authors concluded that extremely low birth weight (< 1000 grams), high neonatal risk (e.g. hyperbilirubinemia, mechanical ventilation), and a high incidence of minor physical anomalies (e.g. cleft palate) were significantly associated with left-handedness. While such a phenomenon may not have played a major role from an evolutionary perspective, it is something which needs to be considered when analysing infants who died prematurely or shortly after birth.

In the evolutionary development of handedness in humans, it seems that language as well as cerebral lateralization played a significant role. Corballis (2002) has advanced this hypothesis, suggesting that language initially arose from hand gestures, which is supported by Cantalupo and Hopkins (2003) who link asymmetry in the Broca's cap area of the brain in great apes to gestures and vocalizations. Gestural language could not fully develop in human ancestors, however, before bipedalism freed the hands from locomotor

duties. Once this was accomplished the hands could be used to make communicative gestures. Initially though, the hands were probably much more useful for tasks such as throwing and, eventually, making tools. The effect that tool-using behaviour can have on the expression of handedness has been discussed in relation to primates and it is possible that this practice also served to strengthen the manifestation of handedness in hominids as well (Bruner, 2003). However, before the advent of stone tools, early hominids may have used their hands for throwing, possibly as a defensive mechanism against predators. The precise timing and accuracy needed to perform this action likely contributed to increased cerebral development (Calvin, 1983).

Corballis (2002) proposes that hand gestures eventually came to be augmented with vocalizations. As a result, language started to become vocal rather than primarily gestural, which is supported by the fact that the same areas involved in the production of language are activated by either tongue or hand movements (Bruner, 2003). The lowering of the larynx was crucial in the development of vocal speech; this evolutionary change, however, is associated with a serious risk to human health (Annett, 2002). Lowering of the larynx means that breathing and swallowing must share the same passage which, subsequently, makes humans vulnerable to choking. Therefore, speech must represent a high degree of adaptive significance in human evolution (Corballis, 2002). It certainly has many advantages over gestural language, such as the ability to communicate in the dark. Based on this hypothesis, language is closely related to gesture. This can account for the tendency among humans for the neural centres controlling the preferred hand to be located in the same area as those that control articulate speech. If language was the

mechanism that led to the preponderance of right-handedness in *Homo*, this could explain why chimpanzees do not exhibit this trait to the same extreme as humans.

Handedness is a complex trait that appears to have deep evolutionary roots. The archaeological and fossil hominid record provides evidence suggesting that right-handedness may have been present since the advent of the genus *Homo*. Additional evidence provided by endocasts of hominid crania and observation of living non-human primates indicates that the potential for handedness likely arose sometime around the time of the chimpanzee-hominid bifurcation. It is unlikely, however, that early hominid populations, such as the australopithecines, demonstrated the same degree of right-handedness as modern humans as their hands had not been fully freed from locomotion (Tocheri et al., 2008). Similarly, while chimpanzees exhibit a propensity for right-handedness the proportion of right- to left-handers does not approach that of *Homo sapiens*. Genetic changes, possibly influenced by the advantages gained by language acquisition, may have continued after the hominid split from the great apes and subsequently led to the predominance of right-handedness observed in modern human populations.

Developmental Biology – Theoretical Constructs

Evolutionary developmental biology attempts to determine the ancestral relationship between organisms and how developmental processes evolved, including how phenotypic variation arises. Of particular relevance to the current study is the concept of morphological integration and modularity. This idea rests on the premise that organisms are composed of developmentally and anatomically distinct, semi-independent parts

(Hallgrímsson et al., 2002). Modularity is a key concept for understanding morphological integration, a feature that is primarily inferred from data regarding trait covariation (Klingenberg, 2008). A module can be described as a “complex of [biological] characters for which pleiotropic connections between the genes that affect it are stronger than those with other characters or character complexes” (Hallgrímsson et al., 2002 p.140). From an evolutionary perspective, it is disadvantageous for functionally unrelated characters to be selected for; integration then, allows for the cohesion of functional systems (Churchill, 1996). Integration is thus the result of phenotypic structures produced through interactions of biological processes (Klingenberg, 2008 p.116).

Based on the concepts of integration and modularity, it is possible to view the proximal humerus as part of a module, namely the shoulder girdle (clavicle, scapula, and humerus). Therefore, the development of the proximal portion of the humerus must be considered with respect to its relationship with the rest of the shoulder girdle and associated musculature. As such, the humerus did not evolve as a separate entity, but as part of a larger, integrated body plan, with changes in other areas of the body affecting the evolution of humeral morphology. Furthermore, although the humerus is a discrete element, the proximal and distal portions differ functionally. Subsequently, each end has been subject to different selective pressures. Differences between apes and humans with respect to distal humeral morphology are subtle but still apparent. In humans, the capitulum is anteriorly oriented, the olecranon fossa is shallow, and the development of the shape of the trochlea is fairly weak compared to apes. These differences have all been attributed to a loss of upper limb weight support in humans (Aiello & Dean, 1990; Wood & Richmond, 2000).

In the shoulder girdle, modern humans have laterally facing glenoids, relatively long clavicles, and a high degree of humeral torsion. Differences in the latter trait within modern humans have been noted between dominant and non-dominant sides, different populations, and males and females, suggesting a difference in habitual behaviours and activity levels (Larson, 2007). It has been proposed that the morphology of the modern shoulder girdle resulted from larger brain size and more complex tool technology, as the first major change in the hominin shoulder (scapula with a modern appearance) appears in early *Homo erectus*. It is also possible however, that this alteration resulted from the final abandonment of trees as places of refuge (Larson, 2007). Clavicular elongation represents the second major morphological change, which Larson (2007) suggests would have placed the scapula in a more dorsal position with the glenoid cavity facing laterally. Subsequently, this would have contributed to an increase in humeral torsion as well as a greater range of upper limb motion. Larson (2007) further proposes that throwing could have been a selective factor for the acquisition of greater shoulder mobility, especially posteriorly. Throwing objects was unquestionably an important factor that contributed to our survival as it would have provided a significant advantage in hunting as well as self-defense. Interestingly, Calvin (1983) has suggested that throwing may also have contributed to the rise of right-handedness. While fascinating to hypothesize, there is presently no solid evidence linking the evolution of right-handedness to the development of throwing ability.

Growth and Development in the Human Skeleton

As previously stated, it is uncertain whether the trend toward right-sided asymmetry is something that is present before or at birth or gradually appears throughout growth and development. The human skeleton is a complex system that is subject to continual development and change throughout an individual's lifetime. Although the alterations that bone undergoes during growth are unquestionably the greatest determinants of adult skeletal form, including robustness and bilateral asymmetry, development does not cease with physical maturity as biomechanical forces continue to affect bone throughout life, as will be described below. Additionally, growth and development are influenced by many factors, perhaps the most important of which are sex and physical activity. Therefore, these mediating influences must be considered in conjunction with skeletal development.

Pre-natal skeletal development

The development of the human skeleton is a highly complex process which begins early in embryonic growth. Although many of the processes that ultimately influence asymmetry and robusticity occur much later in development, early cellular and molecular processes establish the basis for skeletal form. Chondrogenesis represents the first stage of skeletal development and involves the creation of the cartilage anlagen, an intermediate form that eventually leads to endochondral ossification. This process includes the migration of mesenchymal cells from three embryonic tissues (Goldring, 2006). These cells are derived from the neural crest, paraxial mesoderm (somites), and lateral plate mesoderm. Each respective cell type goes on to form the bones of the craniofacial skeleton, axial skeleton, and limb skeleton. Genes pattern the distribution of

these cells into mesenchymal condensations, located at positions in the embryo where skeletal elements will form (Olson, 2000). Various patterning systems have been identified, of which fibroblast growth factor (FGF), hedgehog, bone morphogenic protein (BMP), and Wnt pathways are perhaps the most important for skeletogenesis (Goldring, 2006). Much of what is currently understood about gene functions in skeletal development derives from analysis of human bone disorders and experimental animal studies. For example, investigations involving mice demonstrate that a molecular pathway, known as the Wnt signalling system (the name of which is derived from a combination of Wg and INT genes), is important in the regulation of cell proliferation and differentiation during development. Hens and colleagues (2005) found that in the growing skeleton, Wnt signalling was active in chondrocytes, developing joints, intervertebral discs, osteoblasts, and osteocytes. In mature bone, however, the Wnt pathway is restricted to osteocytes and chondrocytes.

Once mesenchymal cells have moved to future skeletal locations, a process that is complete several days after conception, they differentiate into chondrocytes. In certain parts of the skeleton however, including parts of the skull and the clavicles, the mesenchymal cells differentiate directly into osteoblasts without the need for an intermediate cartilage anlagen (Karsenty, 1999). This process is known as intramembranous ossification. It is the first type of ossification to develop and, furthermore, it continues throughout life in the form of subperiosteal apposition. In general, intramembranous ossification results in dense compact or diploic bone, however, the process can be sub-divided into two distinct types – one which results in dermal bones and another which is responsible for the formation of perichondral bone. Scheuer

and Black (2004) point out that the distinction between types of intramembranous ossification is often overlooked by many researchers. The second main type of ossification is endochondral and it is more common than the intramembranous process previously described. Endochondral ossification is responsible not only for the longitudinal growth of long bones, but also for the formation of long bone epiphyses, aspects of the vertebral column, carpals, tarsals, and any element that has a large amount of cancellous bone. During this ossification process, mesenchymal cells differentiate into chondrocytes which go on to form the cartilage anlagen of future bones. Osteoblasts then form around the periphery and eventually invade the anlagen via cartilage canals. The cartilage calcifies and is subsequently replaced by bone and bone marrow. At this point osteoclast differentiation occurs and the balanced process of bone resorption and formation begins (Malina & Bouchard, 1991; Scheuer & Black, 2004).

After the primary centre of ossification forms, a region characterized by rapid growth develops between the epiphysis and diaphysis – this is known as the growth plate. It can best be described as discoid in shape, reflecting its role in longitudinal growth and diametric expansion of the diaphysis. The growth plate can subsequently be divided into functional zones. Scheuer and Black (2004) have defined these as the germinal zone, proliferative zone, zone of cartilage transformation, and zone of ossification, although these are not universal terms. The germinal zone is located closest to the epiphysis and is characterised by small, randomly distributed chondrocytes. Moving away from the epiphysis, the next area is the proliferative zone. In this area, chondrocytes become larger and are arranged in palisades which represent the sites of new cartilage and ensure continued longitudinal growth. Bordering the proliferative zone is the zone of cartilage

transformation where chondrocytes hypertrophy. This occurs before being replaced by bone in the zone of ossification. These processes commence *in utero* and continue throughout skeletal growth.

During development the skeleton increases in size and strength (Jee & Frost, 1992). Although much of this morphological change results from genetic and hormonal factors, mechanical influences play a significant role in development and the determination of skeletal form. For example, Ryan and Krovitz (2006) found that typical trabecular architecture in the femur did not begin to develop until about the age that a child learns to walk. However, it is unclear whether the presence of bilateral asymmetry *in utero* is primarily influenced by biomechanical factors or intrinsic genetic and hormonal characteristics, although results of Ryan and Krovitz's (2006) study seem to suggest that the latter factors may play more of a role than mechanical forces. Also, fluctuating asymmetry, which is directionally random departures from perfect symmetry (Leung et al., 2000), occurs in paired bones because of random genetic and environmental disturbances during morphogenesis. As development on each side of the skeleton results from local genetic influences, it is expected that at the population level the human skeleton should be symmetrical. On an individual level, however, fluctuating asymmetry is suggestive of developmental instabilities that can arise independently of handedness, a point which must be taken into account when using bilateral asymmetry as a proxy for handedness. Directional asymmetry can also result from innate factors leading to a side bias in skeletal asymmetry. This could include a process such as a left-right difference in blood oxygen level, which would potentially lead to unequal bone growth (Steele, 2000). Pande and Singh (1971) examined the muscles and bones from the

upper limbs of ten fetuses who did not reach full-term. Results indicate that in nine of the ten specimens, total muscle and bone weight was greater in the right limb. This is consistent with known proportions of right- to left-handers in modern human populations (Annett, 1985; Calvin, 1980; McManus, 2002), suggesting that skeletal evidence for this trait can be detected in foetal asymmetry. Bareggi and colleagues (1994) conducted a study using a more statistically robust sample of 58 aborted embryos and fetuses aged between 8 and 14 weeks. In almost all cases the right humerus, radius, and ulna proved to be longer than their left counterparts. Although it is possible that these asymmetries could result from genetic and hormonal factors, or local variations such as the oxygen differential mentioned above, Hepper and co-authors (1991) have also found that fetuses ranging in age from 15 weeks to term demonstrate a preference for right-handed thumb sucking. This finding demonstrates that lateralized motor control develops early and lends support to the notion that right-handedness may be present before birth.

The loading conditions in the embryo and fetus are poorly understood. What is known is that the initial contractile elements of the muscular system develop in the embryo at the same time as the primary ossification site, approximately 7 weeks *in utero* (Carter et al., 1987; Knüsel, 2000). At this point, tendons, ligaments, and muscles begin to influence the recently developed bone. Therefore, it is likely that loading of the cartilage anlage results from muscular activity of the embryo and fetus, although movement of the mother must also impart mechanical forces. Carter and colleagues (1987) investigated the effect of mechanical strain on chondroosseous development of the femur *in utero*. They discovered that strain energy density is the highest at the midshaft of the bone and, as ossification moves toward the epiphyses, the highest degree of strain

is immediately ahead of the ossification front, suggesting that mechanical forces are integral to skeletal development. However, other studies have produced results that challenge the notion that right-handedness is present before birth or early in development. For example, Steele and Mays (1995) found that among the archaeological population recovered from Wharram Percy, England, the left humerus tended to be longer in neonatal infants. If handedness is demonstrated *in utero* then mechanical influences should generate larger bones in the right arm. Bagnall and colleagues (1982) also found the left humerus to be longer in a large sample of foetuses aged 8 to 26 weeks. These studies cast doubt on the universality of right-sided directional asymmetry in the foetal skeleton. Steele (2000) points out, however, that it is best to make inferences from either full-term foetal skeletal remains or live full-term neonates as there is less possibility of pathological conditions affecting results.

Post-natal skeletal development

By the time a foetus reaches full-term the skeletal system has developed to a point where individual bones are recognizable compared to their adult counterparts, with the exception that many apophyses and epiphyses remain unfused. This fusion occurs systematically throughout growth and is often used to age skeletal individuals (Scheuer & Black, 2004). It should be noted, however, that there can be considerable variation in the timing of fusion among both individuals and populations. Additionally, this varies according to sex with females typically exhibiting fused epiphyses before males. For example, in an assessment of epiphyseal fusion in the distal tibia and fibula of European-, African-, and Mexican-Americans, Crowder and Austin (2005) discovered that complete

union varies by approximately 24 months in males and females. There was also a tendency for earlier fusion in the African-American and Mexican-American populations as compared to the European-American group. Such variations must be kept in mind when examining skeletal individuals, particularly as sex cannot be reliably determined in non-adult remains (White, 2000). This delay in fusion is also related to a delay in the adolescent growth spurt in males compared to females. Humphrey (1998) has indicated that the growth spurt typically occurs 2 years earlier in females, but this delay allows a longer period for growth in males. This difference can account for some of the dimorphism exhibited between the sexes, such as increased mean stature in males.

Following birth the relationship between skeletal form and various extrinsic and intrinsic factors becomes more straightforward. While the interplay between genetic/hormonal factors, specific conditions *in utero*, and biomechanical forces is unclear in embryonic and foetal development, the influence of movement and activity becomes much more pronounced after birth (Steele, 2000). However, it must be kept in mind that bone growth is also strongly influenced by environmental and hormonal factors. Developmental stability, also known as developmental homeostasis, refers to the ability of a biological organism to grow in a regular manner under a variety of environmental conditions. As such, environmental perturbations can disturb developmental homeostasis, resulting in bilateral asymmetry of the skeleton. Either directional or fluctuating asymmetry can be indicative of such a disturbance (Albert & Greene, 1999).

Medical conditions, including pulmonary insufficiency and paralysis, can work to differentially affect bones on either side of the body. Additionally, these childhood problems will be reflected in both diaphyseal and articular dimensions (Knüsel, 2000).

According to Frost's (1987) mechanostat theory described previously, hormonal fluctuations during growth, such as abnormal changes in estrogen level may also alter set-points for modelling and remodelling, resulting in either increasing or decreasing bone turnover rates. Nutritional intake plays a major role in determining skeletal form as well. Dietary protein, calcium, and vitamin D allow bones to optimally adjust to their mechanical environment. This is somewhat contrary to the notion that these nutrients directly contribute to increasing bone mass. Instead, they merely allow these gains to proceed in accordance with environmental demands. Therefore, children who are continually inactive due to pathological constraints, such as paralysis, will not develop normal bone mass simply through proper dietary supplements (Jee & Frost, 1992). It is clear then, that physical activity is a necessary component of skeletal growth and development.

In general, the shape of skeletal elements are well-suited to withstand mechanical strains. Jee and Frost (1992) provide an overview of long bone architecture that explains how their design affects the ability to accommodate physical activity and stresses. Growing bones possess two wide epiphyses that are located at either end and filled with thick trabeculae. Moving toward the middle of the bone are two flared metaphyseal growth plates, the specifics of which have been described previously. The final area is the diaphysis which can best be described as a relatively slender column of cortical bone that serves to join the metaphyses. This design can be explained from a biomechanical perspective. As it takes much more articular cartilage than bone to cope with mechanical loads, the wide ends of long bones reflect the need to accommodate large cartilage areas. Besides serving as the growth plate in developing bones, the metaphyses work to create a

smooth transition between the wide epiphyses and the narrow diaphysis. The flared shape that these areas exhibit maintains metaphyseal inwaisting as the bone grows and lengthens during development, preventing the creation of a 'trumpet' shape (Enlow, 1962). The diaphysis is also functional as the shaft of cortical bone works to resist compression and bending forces. Furthermore, as it grows longitudinally the shaft increases in diameter by means of subperiosteal apposition which preserves strength. Proportionally, however, the diaphyseal wall becomes thinner as endocortical bone resorption is balanced by apposition on the periosteal surface. Overall, the skeletal system is designed to maintain integrity throughout the growth process.

As stated previously, physical activity during growth is imperative for proper skeletal development. Furthermore, the mechanical strains to which bones are exposed during growth provide the basis of adult skeletal form. Several important studies have revealed how activity influences skeletal growth in children and adolescents. With regard to asymmetry in the upper limbs, observation of modern children demonstrates that hand preference tends to emerge between 18 and 24 months of age, usually in conjunction with the first use of two-syllable words, a finding which undermines the claims that handedness is reflected in the foetus (Butterworth & Hopkins, 1993; Hepper et., 1991; Ramsay, 1980). It has also been noted that until the age of approximately 8 years, hand preference fluctuates between left-handedness, bilaterality, and right-handedness. During this time, however, there is an increasing preference for the right hand (Corballis, 1983). These fluctuations in behavioural development seem to be reflected in the lack of consistent directional asymmetry among infants and young children. Steele and Mays (1995) examined the upper limb bones of non-adults from the medieval site of Wharram

Percy, England, in order to ascertain the degree of asymmetry between left and right sides. Compared with adults from the same skeletal population, the Wharram Percy non-adults exhibit less right-sided asymmetry. However, dimensions of the humerus indicate that, except in neonates, there is a rightward bias, with the number of longer right humeri exceeding longer left humeri in all non-adult age groups. This suggests that skeletal asymmetry resulting from handedness is not present at birth but gradually appears throughout development, which is consistent with behavioural evidence in children.

As children develop into adolescents there are certain changes that occur in the manner in which their bones respond to physical activity. Bass and colleagues (2002) investigated bone mineral content and humeral dimensions in competitive female tennis players to determine whether the effects of mechanical loading were dependent on maturational stage. Specifically, the researchers wanted to address the question of whether exercise in young individuals will promote periosteal expansion, while in mature individuals it will stimulate endocortical contraction. The individuals used in this study spanned the ages of 8 to 17, permitting comparisons between pre-, peri- and postpubertal females. Results show that growth exhibited as structural changes in the non-playing arm produced a 14% cortical area increase in the middle and distal humerus between the pre- and peripubertal years. This change occurred as a result of periosteal expansion rather than medullary contraction. Cortical area in the same regions of the humerus was about 20% greater in the postpubertal individuals than the peripubertal players, although medullary contraction was responsible for this feature in the distal section. With respect to asymmetry, bone mineral content and resistance to torsion was as much as 14% greater in the playing arm of prepubertal individuals. Interestingly, these features did not increase

further in the peri- or postpubertal players even though these individuals were subject to mechanical stress for a longer duration than the prepubertal players. Overall, mechanical strain imposed during the peri- and postpubertal period produced endocortical rather than periosteal apposition. Prior to puberty, endocortical resorption results in an enlarged medullary cavity that works to balance the cortical area increase created by periosteal apposition, which results in the bone maintaining integrity. As such, it is not only the type and magnitude of physical activity that is important in bone growth, but also the timing of mechanical loading. In Bass and colleagues' (2002) study, most structural changes occurred early in life as an adaptive response by the bones to maximize resistance to bending and minimize micro-damage from mechanical strain. Such fatigue induced micro-damage however, could actually be part of normal bone adaptation, with repair possibly being an important feature of remodelling throughout life (Martin et al, 1998). Depending on the type and duration of mechanical strain, the bone could adapt by depositing new bone, or in some cases this deposition could occur in an attempt to repair micro-damage (Rubin et al., 1995).

Overall, the conclusions reached in the above study are consistent with the idea that the most extreme osseous responses will be present in individuals who begin performing repetitive, strenuous tasks during childhood or early adolescence, before epiphyseal fusion. Continual loading after puberty only works to create medullary contraction which does not increase structural rigidity of the humerus (Bass et al., 2002). This may contradict the idea that handedness related asymmetries begin in utero, as movements associated with handedness do not seem to appear until later in development (Butterworth & Hopkins, 1993; Ramsay, 1980). Such observations have been noted in

other studies involving both tennis players and individuals engaged in manual labour before reaching physical maturity (Blackburn & Knüsel, 2006; Kannus et al., 1994). In general, tennis players represent a particularly interesting group for analysis as they have been found to exhibit the most asymmetrical osseous response of any group (Jones et al., 1977; Trinkaus et al., 1994). Jones and colleagues (1977) also found evidence that under similar loading conditions, males will experience slightly more exuberant bone growth than females, signalled by greater asymmetry between the playing and non-playing arms. Overall however, males and females adapt to mechanical loading in the same manner. Ruff (1992) used radiograph measurements of the mid-distal humeral diaphysis from 34 male and 12 female professional tennis players to investigate mechanisms of bone adaptation. These individuals ranged in age from 14 to 39 years and had between 8 and 28 years of experience playing tennis. Similar to Bass and colleagues' (2000) study, Ruff (1992) found an increase in total area, cortical area, and polar second moments of area (i.e. the ability to resist bending as averaged over all planes) in the playing compared to the non-playing arm. Not surprisingly, this was coupled with an overall decrease in medullary area. As with the previous study, Ruff (1992) also discovered that individuals who began playing in mid-late adolescence or early in adulthood had below average increases in total area, cortical area, and polar second moments of area. Endocortical contraction, however, was normal or above average in these individuals compared to those who began playing at young ages. Not only does this support the idea that postpubertal individuals respond to mechanical strain through medullary contraction rather than periosteal apposition but, unlike the previous investigation, Ruff's (1992) work demonstrates that this is true in both males and females. Therefore, the endocortical

response to mechanical loading may be due to increased levels of steroid hormones present from puberty through to the third and fourth decade of life. Although these hormones would not change the mechanical nature of bone, they could alter set-points and raise the minimum effective strain required to produce change (Frost, 1987).

Skeletal development following physical maturity

The preceding discussion has established that bone morphology is highly influenced by activity. Mechanical strains serve to elicit osseous responses that are directly related to the magnitude of force and the frequency and direction of loading (Burr & Martin, 1992; Martin, 2000; Martin et al., 1998; Turner, 1999). As illustrated in the examples of tennis players, repetitive movements promote the formation of bone. This increased mechanical strain promotes modelling and bone growth while simultaneously inhibiting remodelling, or cellular turnover. Therefore, skeletal dimensions are increased in order to accommodate greater mechanical strain and resist failure. Furthermore, abnormal patterns and directions of loading tend to produce more pronounced osseous responses compared to typical mechanical strains. If a reduction in loading is experienced, however, this can subsequently lead to bone loss. When the skeleton senses reduced mechanical strain, resulting from immobilization for example, remodelling is activated so that resorptive activity exceeds osseous formation. This process is evidenced by less cortical bone, a smaller cross-sectional area, and enlarged medullary canal. Overall, this reduces bone rigidity and resistance to fracture (Bloomfield, 2001; Knüsel, 2000*a*).

As bones are in their most malleable state early in life, the most significant effect on skeletal form occurs before physical maturity. This is true of both diaphyseal

dimensions and articular dimensions. However, diaphyseal dimensions remain susceptible to loading throughout life (Ruff, 1988; Ruff et al., 2006). Conversely, once epiphyseal fusion occurs, articular surfaces lose most of their plasticity and ability to transform their external dimensions in response to mechanical stress. Instead, it is hypothesized that articulations respond to mechanical forces by altering the subchondral architecture (Ruff, 1991). Therefore, in adult skeletons articular dimensions tend to reflect physical activity during growth rather than loading during adulthood (Knüsel, 2000). As most individuals are right-handed, it is not surprising that articular dimensions in the upper limbs tend to exhibit bilateral asymmetry favouring the right side (Plochocki, 2004).

Lieberman and colleagues (2001) have investigated the effects of mechanical loading and body mass on articular surface areas using an experimental approach. A group of male sheep was exercised on a treadmill for a 90 day period and subsequently euthanized in order to directly observe limb bone articulations. In order to compare age-related changes in articular surfaces, the sheep were divided into three categories – juveniles, sub-adults, and adults. Additionally, the exercised animals were compared to an unexercised control group so that genetic/hormonal factors could be accounted for. Among the juvenile sample, articular surfaces were somewhat larger in the exercised compared to the control group, although this difference never reached statistical significance. A similar trend was observed in the adult sample with slightly larger articular surfaces in the exercised group. The sub-adult sample was the group that exhibited the only deviation from this trend, with exercised animals demonstrating smaller articular dimensions than the control group. Diaphyseal dimensions were also

examined and, as predicted, they exhibited the mechanically-induced changes typical of this skeletal region; changes in cross-sectional properties were noted, with exercised sheep displaying increased resistance to bending forces (i.e. higher second moments of area). Also as predicted, these changes were most pronounced in the juvenile group. Overall, results suggest that the effects of mechanical loading on articular surfaces are complex and not easily interpreted. Although caution must be used when extending results from animal models to humans, this study calls into question the assumption that joint articulations are reflective of mechanical loads experienced during growth. However, the diaphyses of long bones are much more susceptible to biomechanical influences throughout an individual's lifetime and, therefore, are more reflective of these forces around the time of death. Additionally, it suggests that diaphyseal dimensions rather than articular surfaces may be a better target for analyses of handedness in skeletal remains as they are more reflective of mechanical loading (Plochocki et al., 2006).

Sex differences in adult skeletal development

To this point males and females have followed very similar patterns in skeletal growth and development, although there is a delay in epiphyseal fusion and the adolescent growth spurt among males (Humphrey, 1998). While these variations may be at least partially responsible for the increased potential for robusticity and asymmetry in males, the underlying mechanisms that affect these traits are the same in both males and females. Perhaps the most striking difference in bone development between the sexes occurs later in life as a result of the menopause in women. Osteoporosis is a condition that is typified by loss of bone mass and micro-architectural deterioration of osseous tissue. These

symptoms result in an overall weakening of the skeletal system which can subsequently lead to fractures. This condition primarily affects post-menopausal women because of hormonal changes, although lifestyle factors are also believed to affect the occurrence of osteoporosis and the degree of osseous deterioration present (Mays et al., 1998). Because of its pathological significance in modern populations there have been numerous studies devoted to this topic, using both living individuals and skeletal samples from archaeological populations (Beck et al., 1993; Mays, 1996; Mays et al., 1998; Sanchis-Moysi, 2004; Taaffe et al., 1994).

Beck and colleagues (1993) examined age-related structural changes in the femoral necks of over 1000 females ranging in age from 18 to 89. Only females were included in this study as previous work by Beck and colleagues (1992) found that while increasing age results in bone mineral density (total amount of bone mineral per unit of bone) decreases in both sexes, only females experience a loss of bone rigidity. Males, however, exhibit compensatory restructuring of femoral neck architecture which counteracts age-related bone loss. Results from the present study confirm that this compensatory growth is almost purely a male phenomenon. Both younger and older females demonstrate a significant decrease in bone mineral density, but after the age of 50 this decline accelerates by 2.5 times. Furthermore, after 50 years of age bone rigidity significantly declines. In younger females, the loss of bone density seems to be offset by slight increases in femoral neck width, but this trend disappears in older women. The lack of restructuring in post-menopausal women results in substantial increases in shear and tensile stresses in the femoral neck. Ultimately, this leads to inflated fracture rates among

older women. Prior to the age of 50, however, women and men show similar changes in bone mineral density and geometric properties.

One of the primary questions that researchers have addressed is the potential that exercise has for offsetting the effects of age-related bone loss. It has been demonstrated that physical activity is important for generating bone mass but the ability of this process to counteract osteoporosis remains unclear, perhaps due to the presence of confounding intrinsic and extrinsic factors. Sanchis-Moysi and colleagues (2004) point out that while bone mineral density is a trait largely under genetic control, nutrition, hormonal fluctuations, and exposure to drugs and toxins can also influence bone metabolism. Additionally, some studies have suggested that intense weight bearing exercise in post-menopausal individuals can attenuate bone loss at some skeletal locations. Taaffe and colleagues (1994) found that in both young and elderly women, hand preference was positively correlated with higher levels of bone mineral density in upper limb bones. This suggests that the effects of mechanical loading throughout an individual's lifetime are retained, at least to some extent, in old age. In a similar study, Sanchis-Moysi and co-authors (2004) examined a group of recreational tennis players to determine if post-menopausal women retained increased bone mineral density and bone mineral content (amount of bone mineral as hydroxyapatite within a measured region) in their dominant arms. These individuals were subsequently compared to a control group of post-menopausal women who had always experienced an inactive lifestyle. Unlike Taaffe and colleagues' (1994) work, the tennis players did not exhibit increased bone mineral density, perhaps because they had not started playing until approximately the third decade of life. However, they did demonstrate increased bone mineral content in their

dominant arm compared to their non-dominant arm, a trait that was not present in the inactive control group. These results suggest that exercise can increase bone size and mass in post-menopausal women, although commencing activity early in life may provide additional benefits and work to more effectively offset bone loss.

As osteoporosis is commonly encountered in modern populations, particularly European groups, it is important to determine if this pathological bone loss results from factors associated with contemporary lifestyles. As osteoporosis has been linked to smoking and alcohol consumption, it is possible that the prevalence of this condition was much smaller in past populations. To investigate this question, Mays (1996) and Mays and colleagues (1998) observed the skeletal remains from the medieval village of Wharram Percy for evidence of bone loss. Respectively, these studies examined cortical bone loss in metacarpals, and bone mineral density and cortical bone loss in femora from the above mentioned skeletal population. Both of these studies indicated that bone loss was present in the Wharram Percy females but was not significant among males. Most importantly, this condition was found to be present in a similar degree as witnessed in modern European societies, strongly suggesting that bone loss is not merely a lifestyle-related problem. It also calls into question the hypothesis that increased activity can prevent bone loss, as the females from Wharram Percy would likely have had a much more physically strenuous lifestyle than most modern women. In the context of the present study, this points to the need for considering bone loss as a factor potentially affecting bilateral asymmetry among older females.

Overall, the human skeleton is a complex structure that is highly susceptible to a variety of intrinsic and extrinsic forces. While genetic and hormonal factors lay the

foundation for skeletal form, mechanical stresses ultimately act to produce bones that are well-adapted to accommodate strain without failure. Provided that pathological or environmental stress does not result in severe developmental instability, bones of the upper limb should exhibit a right-sided asymmetry consistent with hand preference. Furthermore, as the adult skeleton still retains the ability to alter its form, it is appropriate to consider growth and development as a process that does not necessarily cease with physical maturity. Activity continues to affect the form of skeletal elements, although periosteal apposition is replaced by endocortical contraction, the impact of which is considerably less than during early development. Finally, bone mass gradually diminishes with increasing age, a trend that is especially pronounced in post-menopausal women. Although the severity of this condition can potentially be attenuated through continued physical activity, it does not seem possible to eliminate bone loss entirely.

Morphometrics and Asymmetry

Traditionally, studies of size, shape, and asymmetry exhibited in the human skeleton have employed simple metric techniques. Linear measurements tend to provide sufficient data to recognize differences in form. The following example illustrates the potential that traditional methods have to identify asymmetry in the skeleton.

Stirland (1993) examined the skeletal remains of soldiers from Henry VIII's flagship, the *Mary Rose*, for evidence of humeral asymmetry. Although the *Mary Rose* sank over 450 years ago, these remains were particularly well-preserved due to the anaerobic environment. As Stirland (1993) was confident that these individuals were archers she paid particular attention to the proximal humerus. Previous work has shown

that archery is correlated with *os acromiale* (non-fusion of the acromion process of the scapula) so, presumably, this practice significantly affects the shoulder, although research has demonstrated that it also results in differential asymmetry of the humerus (Knüsel, 2000b; Stirland, 1984). Sliding callipers and an osteometric board were used to measure the maximum length, proximal and distal breadths, head diameter, and maximum and minimum midshaft diameters. Additional measurements of the proximal humerus included the horizontal width of the greater and lesser tubercles. These measurements were chosen as muscles of the rotator cuff insert in this area. All measurements were standardized by dividing the left side by the right side, producing a ratio that is free from individual size variations. A sign test was applied to assess these measurements for statistically significant asymmetry between right and left sides. Results indicate that only one measurement, the horizontal dimension of the greater tubercle, demonstrates significant bilateral asymmetry. Furthermore, it is the left elements that tend to be larger, an observation that Stirland (1993) interprets as being consistent with archery. This is similar to what was discovered among the Towton soldiers, who also exhibited left-sidedness, particularly in the distal portion of the humerus (Knüsel, 2000b). Humeral asymmetry in the *Mary Rose* soldiers was compared with a contemporary skeletal population recovered from a poor parish church graveyard in Norwich, England. These individuals also exhibited a left-sided asymmetry for the horizontal dimension of the greater tubercle, although not to the same degree as observed in the *Mary Rose* sample. Stirland (1993) concedes that some of the Norwich men would likely have practiced archery also. However, the *Mary Rose* soldiers would have been professionals which can account for the greater asymmetry in this group.

Studies such as Stirland's (1993) demonstrate that traditional methods can reveal important insights into asymmetry of the human skeleton, although projects relying on linear measurements necessarily rely on the personal choices of each individual researcher and can introduce some degree of bias. However many of these issues are dealt with through the implementation of checks, such as inter- and intra-observer error tests.

In another study of asymmetry, Pfeiffer (1980) examined humeri excavated from the Kleinburg Ossuary in Ontario. Although individual paired elements were not identified, the size and shape of right and left were compared according to eight discrete measurements – maximum length, physiological length, maximum and minimum midshaft diameter, maximum and minimum head diameter, epicondylar breadth, and lower articular breadth. Pfeiffer (1980) states that these measurements were chosen because they represent a thorough approximation of size and shape over the entire surface of the humerus. While these measurements are typically used in studies of asymmetry, there is still the possibility that other features, perhaps more difficult to identify from visual inspection, could yield important information regarding the expression of this trait in the humerus.

Geometric Morphometrics

In recent years more complex methods of morphometric analysis have become common. Morphometrics can be described as the quantitative characterization, analysis, and comparison of form (Roth & Mercer, 2000). Although traditional analyses that rely on simple linear measurements remain effective for some problems, more robust

morphometric methods hold greater potential for delving into deeper problems related to biological shape change. Morphometrics goes beyond traditional shape analysis by gaining information not only on chords (linear distances), outlines, and angles, but on the relative positions of landmarks as well. Essentially, this field represents a sub-discipline of statistics that integrates tools from geometry, computer graphics, and biometrics (Bookstein, 1997). It focuses on the analysis of shape and continuous shape variation in geometrical objects through the use of digital data and multivariate statistics. The digital data can be obtained through various means, such as laser or CT scanning (both medical and non-medical, such as micro CT and industrial CT). This data can subsequently be analysed using computer software, much of which has been developed during the past decade. Data can then be compared to a standard shape, often obtained as an average of all shapes in a given data set (i.e. all right humeri from a skeletal population). Bilateral asymmetry can also be assessed by comparing the shape of right and left skeletal elements. Conclusions can subsequently be drawn regarding variations in shape between individuals and within the population. There are various methods for conducting morphometric analysis and, in general, these can be divided into techniques that use landmark data and those that use outlines.

Bookstein (1991) identifies four main principles/themes that characterize morphometric analysis, at least as they apply to landmark-based techniques (outline techniques will be considered later). With that in mind, it is not surprising that Bookstein's (1991) first principle states that the most effective way to analyse many biological shapes is through the identification of landmark points. These points are denoted by Cartesian coordinates and are theoretically homologous across all specimens

in a data set. Furthermore, the use of homologous landmarks dictates the explanations resulting from analysis. For example, changes in shape can be described as landmarks being moved apart or pulled together. The second principle refers to the fact that the shapes created by configurations of landmarks reduce to multiple vectors of shape coordinates. These shape coordinates are in pairs representing one landmark. Bookstein's (1991) third principle states that all landmark data can be subjected to biometric investigation through the use of multivariate statistical analyses. In this manner it is possible not only to identify variations in shape related to certain factors, but also to pinpoint the nature of that shape change. This is contrary to earlier morphometrics used for taxonomy that posed questions about "similarity" and "common ancestry". Such enquiries are not appropriate for modern morphometric techniques. The final principle relates to the form that answers take in morphometric analysis. Although this may not apply to all types of analyses, Bookstein (1991) recommends that results not be presented as traditional statistical tabulations but, rather, as geometric diagrams superimposed over a representation of the typical form. This is often done because, as Richtsmeier and colleagues (2002) point out, a diagram depicting the relative location of points does not convey a lot of information to most people. Therefore, the superimposed outline provides a context for landmark-based results. These graphical outputs set modern morphometric methods apart from traditional metric analyses which rely on reporting the statistical significance of various discrete measurements of skeletal features, and do not generally capture enough information to reconstruct the spatial relationships among structures. In contrast, robust morphometric methods retain sufficient geometric information that

results can be mapped back into physical space. As such, these visual representations are one of the main benefits of geometric morphometrics (Slice, 2005).

Euclidean distance matrix analysis (EDMA) of shape difference is a relatively recent addition to geometric morphometrics. This method offers an alternative to popular superimposition methods, many of which suffer from subjectivity. As Lele (1991) states, superimposition analyses can be scientifically dangerous as it is possible to support almost any hypothesis by choosing the appropriate loss functions. Deformation-based approaches can also be dangerous as they involve the arbitrary choice of a smoothing or homology function that can affect results (Lele & Richtsmeier, 1995). EDMA does not depend on arbitrary coordinate systems in order to describe size and shape. Similarly, size and shape are not altered because of the imposition of nuisance parameters, such as rotation and translation (Cole & Richtsmeier, 1998). Therefore, this method employs the use of invariant forms. Although EDMA was developed more recently than other morphometric methods, it is perhaps the most similar to traditional methods as it relies on linear distance data. Like other morphometric techniques, this information is obtained by digitizing data from specimens and assigning landmarks. However, rather than focussing on the landmarks specifically, EDMA concentrates on the linear distances between landmarks. In order to calculate the matrix containing all linear distances, researchers can either compute the mean location of landmarks with the use of generalized Procrustes analysis, or determine the Euclidean distances between all pairs of landmarks. Necessarily then, comparisons between specimens analyse the distances connecting landmark pairs in one form to the corresponding distances in another form. The use of distances rather than coordinate data eliminates many assumptions that other methods

must account for, such as rules of superimposition or minimum bending energy (Richtsmeier et al., 2002).

This linear based method also avoids the assumptions that are associated with the graphic display of results. Richtsmeier and colleagues (2002) explain that the lack of visually appealing graphics has led to considerable critique of linear-based methods. This seems justified as easily interpretable graphic output is one of the primary advantages of geometric morphometrics. However, as many of the biological interpretations resulting from other morphometric analyses rely on questionable assumptions, the inferences drawn from their graphics are of little value. Instead, Cole and Richtsmeier (1998) state that it is necessary to develop graphics which draw on the advantages of the coordinate system invariance that characterizes EDMA. Richtsmeier and co-authors (2002) describe new software that provides graphical output depicting various degrees of difference for the linear distances. Another method of graphic representation has been presented that allows influential landmarks to be quickly identified (Cole & Richtsmeier, 1998). Influential landmarks can be described as those that significantly affect differences in shape according to whatever factor is being analysed, such as growth patterns or asymmetry. Identifying and focussing on these landmarks could also serve to streamline EDMA, a possibility that has been suggested by some researchers (Richtsmeier et al., 2002). In this manner, it would be possible to only consider the most influential pairs of landmarks rather than all linear distances. The adoption of such a practice, however, may serve to undermine what is otherwise a method virtually free of assumptions and arbitrary decisions.

Although EDMA certainly demonstrates some advantages over other morphometric models, it is not without problems as well. Coward and McConathy (1996) applied several morphometric methods to facial landmark data to assess type I error rates. Increases in these error rates can result in researchers believing that differences between comparative forms exist when they actually do not. These tests were applied to a case where some assumptions were knowingly violated and only a few landmarks were used for analysis. EDMA demonstrated inflated type I error rates, tending to be too liberal with small samples. This problem held true when analysing both 2D and 3D data, but was less significant in the 2D sample. A similar problem was discovered by Rohlf (2003) when investigating mean square error and bias in estimates of mean shape. Unlike the results for the generalized Procrustes method described previously, EDMA produced the largest errors. Rohlf's (2003) test involved the use of triangles, and it also demonstrated that EDMA has a pattern of bias for isosceles triangles where it produces a form with one side much shorter than the other two. This naturally calls into question the accuracy of other shapes analysed by this method. It can be argued, however, that the simplistic models of error are not representative of data-sets in the real world and subsequently lack validity (Slice, 2005).

Richtsmeier and colleagues (2005) have applied EDMA to the study of asymmetry in order to provide an alternative to the commonly used Procrustes methods. The drawbacks of these methods have been discussed previously, but generally center around the arbitrary choice of superimposition criteria used. In this manner, the location of maximum difference can be shifted from one biological location to another or, alternatively, spread the changes at one location to nearby, unaffected locations. Rather

than risk the inaccuracy of results from such an analysis, Richtsmeier and colleagues (2005) propose using the matrix of interlandmark distances typical of EDMA to investigate asymmetry. This is accomplished in a manner similar to that used in traditional methods that focus on linear distances. For each individual in a sample, a form matrix is calculated that consists of all unique interlandmark distances, and all bilaterally occurring linear distances are then paired. Asymmetry is defined as $L-R$; if $L-R=0$ then the individual is symmetric. Asymmetric individuals will have $L-R>0$ or $L-R<0$, and this will vary depending on whether the left or right side is larger. The mean of the sample necessarily measures directional asymmetry. A bootstrap-based algorithm is then applied to determine if directional asymmetry is significant. If it is found to be significant for one or more linear distance pairs then Richtsmeier and co-authors (2005) state that the researcher must decide if a biological interpretation of directional asymmetry should be included in the analysis. In studies that focus on the presence of fluctuating asymmetry, perhaps as it relates to developmental instability, directional asymmetry may only complicate analysis. However, in other studies, such as those focussed on handedness, directional asymmetry may be of primary importance. This method, although quite similar to traditional techniques, can accommodate a more thorough investigation of linear distances which in turn allows for a more robust analysis of asymmetry in biological forms.

While landmark-based morphometric methods offer many advantages over traditional metric analyses, it must be acknowledged that there are certain things that cannot be known about the specimens being studied. Richtsmeier and colleagues (2002) point out several important things that must be considered in morphometric studies. First,

population parameters are only based on a sample and, subsequently, true population parameters cannot ever be known. This is the same problem faced by all statistical analyses. However, the operations of translation, rotation, and reflection transform all specimens into a uniform coordinate system, making it falsely appear that variation can be accurately estimated. Second, the portion of the shape that is represented necessarily relies on the researcher's choice of landmarks and usually reflects the questions being addressed. As the number of landmarks used must be limited in some way, the whole shape of a specimen is never known, which is similar to limitations of traditional measurements. Finally, there are notable problems with the use of coordinate systems. In order to make shape comparisons, most landmark-based systems depend on superimposition in an arbitrary coordinate system or on randomly defined deformation or loss functions (Cole & Richtsmeier, 1998). The lack of a common system among forms means that differences between specimens cannot be realistically measured (Richtsmeier et al., 2002).

Outline-based Approaches

Although landmark data are the most commonly used, it is not necessarily appropriate for all studies as it overlooks curves and the space between landmarks. In cases where these characteristics of morphology are of interest, then outline-based approaches may be more appropriate (Richtsmeier et al. 2002). However, MacLeod (1999) has asserted that neither landmark nor outline data can fully explain morphology if used in isolation and, therefore, the hard distinctions drawn between the two should be eliminated.

Fourier Shape Analysis

Hammer and Harper (2006) provide an overview of Fourier analysis. This method can be divided into two types – polar (radial) Fourier shape analysis and elliptic Fourier analysis, both of which work with the two-dimensional coordinates produced from the digital outline of a closed shape. For polar Fourier analysis a central point is identified which is typically the centroid of the shape. Vectors from the centroid project outwards to the perimeter of the shape, and the lengths of these vectors describe the outline in polar coordinates. Hammer and Harper (2006) report several problems with this method, including the arbitrary choice of center point and the tendency for the radial vector to cross the shape more than once in complicated outlines. As such, the polar method is generally considered less sophisticated than more modern methods and is not commonly used in current studies. The elliptic Fourier technique however, is one of the most commonly used methods of outline analysis. This method avoids the problems associated with the polar Fourier technique by employing Cartesian rather than polar coordinates. This makes elliptical Fourier analysis better equipped to deal with complicated shapes. Although outline methods can certainly prove effective in cases where the use of landmark data is inappropriate, such as to trace an outline curve, critics of Fourier analysis claim that the coefficients used in this technique provide no information about homology or the biological processes underlying shape modification (Bookstein, 1991). This opinion is exercised despite the fact that important distinctions between geometrical and biological homology are regularly confused in landmark analyses (MacLeod, 1999). In order to infuse landmark philosophy into outline analysis, Bookstein (1997) has attempted to combine Procrustes superimposition and thin-plate splines to create a new

method for evaluating curved outlines. While this and similar techniques have yet to be successfully integrated into outline analysis, they represent a positive step towards incorporating these two morphometric approaches.

Elliptic Fourier analysis has been used in several studies to successfully examine asymmetry in biological forms. For example, Sforza and colleagues (1998) investigated asymmetrical differences between human footprints using this method. The outlines of adult feet were obtained using a podograph and x, y coordinates were assigned. EFA was then used to examine intra-subject asymmetry in footprint shape and size. Results of this analysis revealed that on average, females tended to be more asymmetrical than males. The current study will use a similar technique to examine bilateral asymmetry in humeral cross-sections by using 2D translations of 3D data.

Eigenshape Analysis

Along with Elliptic Fourier analysis, Eigenshape analysis is among one of the most common techniques used to deal with outline data. Like Fourier analysis, this method reduces outline shape to several parameters which can then be subjected to multivariate analysis. However, while Fourier analysis data goes through a transformation stage, Eigenshape analysis is based directly on raw outlines (Hammer & Harper, 2006). This is one of the primary benefits of Eigenshape analysis. It is also useful for producing graphics that have a direct and natural correspondence to the analysed specimens. As such, the graphical outputs of this method are both meaningful and easily interpreted. Additionally, extended Eigenshape allows for the analysis of open curves rather than merely closed ones (MacLeod, 1999). Although the periphery of objects represents one of

the most commonly analysed closed curves, open curves may be of analytical interest for numerous reasons. MacLeod (1999) describes this technique as being useful for structures such as blood vessels, which are truly open curves. From the perspective of physical anthropology, however, issues of preservation may make this method useful. For example, observation of vertebral foramina in an archaeological population may necessitate the use of open curve analysis as it is likely that in many specimens the total outline of this trait will not be preserved. Extended Eigenshape analysis also represents an attempt to bridge the gap between landmark and outline methods by using landmarks to improve biological correspondence of outlines along their entire length. This method, however, retains summaries of shape trends that are distinct from those used in landmark-based analyses, with the latter being primarily employed to evaluate biological hypotheses. MacLeod (1999) asserts that extended Eigenshape can still approach these biological problems, particularly through the use of graphics, as discussed above. He cautions though, that care must be taken not to extend biological interpretations beyond the aspects of shape that are actually measured. Also, it must be kept in mind that it is not shape per se that is being measured, but the covariances that occur in aspects of shape change and biological processes (MacLeod, 1999). This caution holds true whether an investigation focuses on outline methods or landmark-based techniques. Finally, Eigenshape analysis requires a common starting point be set for each specimen which can subsequently introduce error. For this reason, Elliptic Fourier Analysis is the method employed in the present study as the reliability of consistently finding the same starting point is questionable, particularly in younger individuals.

Conclusions

The deep evolutionary roots of handedness are well-established, based on both non-human primate and hominid fossil evidence. Although it is still unclear exactly when or why this trait arose, handedness is a distinctly human phenomenon, with the majority of individuals being right-handed. Behaviourally, hand preference seems to emerge early in childhood, generally before the age of five. Skeletally, it is possible to examine this trait by using bilateral asymmetry in the upper limb bones as a proxy for handedness. As osteological tissue is highly malleable, particularly early in life, the habitual use of one arm more than the other results in hypertrophy of the dominant limb.

The methods used in traditional analyses of shape variation in biological specimens are valuable tools and, therefore, will be used in the current study. However, they fail to provide the same level of precision as more robust morphometric techniques. The distances and angles calculated in traditional methods cannot successfully encode all geometric information about biological specimens. Failure to record this geometry means that traditional techniques provide a less comprehensive assessment of shape variability. Furthermore, these methods risk neglecting important geometric relationships as they rely solely on the researcher's choice of measurements. Geometric morphometrics has greatly reduced the potential for overlooking areas of shape variation. For these reasons, modern morphometric techniques offer the potential for more robust and thorough investigations into shape variation in biological structures. With regard to the development of asymmetry in the humerus, geometric morphometrics will allow for a more thorough investigation of shape changes that are not detectable by traditional methods. Overall, the use of 3D data will allow for more precise analyses of humeral size and morphological

asymmetry, thereby contributing to the understanding of how handedness presents and develops in the skeleton.

Chapter 3 - Materials and Methods

Archaeological Skeletal Samples

The development of humeral asymmetry is something that can only be reliably assessed using a wide range of skeletal samples, rather than one specific population. This eliminates the possibility of population-specific variables affecting the overall results. A total of 12 archaeological skeletal populations were used in this study, most of which are of British origin. Although the majority of individuals were non-adults (less than 18 years) a small sample of adult individuals was studied for comparative purposes. The bulk of the skeletal populations (i.e. archaeological sites) examined are curated at the University of Bradford, although more than half of the total sample of individuals originates from other sources, including the University of Sheffield, the English Heritage Centre for Archaeology, and the Canadian Museum of Civilization. Sites containing large numbers of non-adults were favoured, and individuals included in this study were required to have both humeri relatively well-preserved and to be free of obvious pathological alterations. Discrepancies in total number excavated and sample size (Table 3.1) can primarily be accounted for by archaeological preservation. First, except in rare instances, non-adults only make up a small portion of a total skeletal sample. Often, children are not included in formal cemetery burials and may be disposed of elsewhere (Rega, 1997). There is also differential preservation of their skeletal remains due to a lower bone mineral content, and the small size of infant and child skeletal remains can make recovery during excavation difficult (Chamberlain, 2000). Therefore, obtaining samples with both humeri sufficiently intact to perform analyses can be difficult. Second, even in adults, preservation can be problematic, often with an individual only being

represented by a small portion of fragmented remains. Finally, the low number of adults sampled in this work results from the fact that this research focuses on non-adults. While a small portion of adults was sampled, an attempt was made to limit the number to approximately 20% of the total non-adult sample so as not to overwhelm the main focus of this work. Additionally, the inclusion of all adults was not feasible due to time and budgetary constraints. In general, the adults were chosen randomly with no preference for age or sex.

Table 3.1: Distribution of total sample according to site

Site	Approximate Date	Period	Total Excavated	Total Adult Sample	Total Non-adult Sample
Raunds	900-1100 A.D.	Medieval	363	10	42
Box Lane	unknown	Medieval	121	6	11
Blackfriars	1246-1539 A.D.	Medieval	172	6	11
Hereford	900-1791 A.D.	Medieval	1400	10	30
Chichester	1100-1650 A.D.	Medieval	351	11	40
Wolverhampton	1800-1900 A.D.	Industrial	152	10	18
Baldock	100 B.C. – 350 A.D.	Romano-British	139	4	3
Kingsholm	300-400 A.D.	Romano-British	48	3	4
Blackgate	700-1168 A.D.	Medieval	821	4	60
Wharram Percy	1000-1300 A.D.	Medieval	687	14	105
Ancaster	200-300 A.D.	Romano-British	327	6	31
Native Point	1400-1903 A.D.	n/a	778	5	37
Total			5359	89	392

Raunds Furnells – University of Bradford

A large collection of skeletal remains were examined from the rural Anglo-Saxon churchyard of Raunds Furnells, Northamptonshire, England. Excavations between 1977 and 1985 yielded a total of 363 individuals (170 non-adults), 52 of which were examined in this study. It is believed that the total number recovered is close to the actual number originally interred as erosion of the graveyard was minimal. These burials are all dated to

between the tenth and early twelfth century, after which time the church was converted to a manor house. Infant mortality at Raunds is relatively low for a pre-industrial population (20%), but the care spent on infant burial, including the provision of stone cists, grave covers, and coffins, may reflect the importance of their proper burial, and there is no indication of any other methods of disposal. The treatment at death of infants and children varies by population, but at Raunds it appears to have been carefully undertaken in relation to other burials in the same population. This could result from a high level of respect given to children in this group, and a reflection of the loss of potential adult members of a community. The church at Raunds has been described as an obscure rural parish. As such, the majority of the associated adult and older adolescent population would have been involved in an agricultural lifestyle, presumably engaging in a large variety of physical tasks (Boddington, 1996). This physical activity is reflected in a high incidence of degenerative joint disease, particularly in the vertebrae of adults (Powell, 1996).

Box Lane, Pontefract – University of Bradford

A small sample of skeletal material, 17 individuals in total, was obtained from the Box Lane, Pontefract collection. Excavation of this West Yorkshire site yielded over 59 inhumations and fragments of 62 additional individuals. This medieval cemetery is notable for the small number of children's remains and virtual absence of infants and neonates, suggesting that individuals under a certain age, perhaps who were unbaptised, were buried elsewhere. It is also possible that infant skeletons did not survive well, but this seems unlikely given the soil conditions of the site. The Box Lane site contains a

high number of mature adults (46+ years) and, therefore, it is not surprising that degenerative joint disease was common. Many individuals demonstrated a high incidence of inflammatory lesions and Schmorl's nodes suggesting that this was a hard-working rural community. The incidence of postcranial fractures was higher in the Box Lane population than other contemporary sites, which also supports the notion of a vigorous life (Lee, 1989).

Blackfriars, Gloucester – University of Bradford

A sample of 17 individuals was examined from the Blackfriars site. This site dates to the medieval period and represents the cemetery associated with the Gloucester Dominican Friary. Ground penetrating radar indicated that the cemetery may have contained up to 2000 burials, of which 129 discrete individuals and 43 partial skeletons were excavated. Burials at the Friary commenced in 1246 and ceased in 1539 although the presence of females and non-adults indicates it was not merely the Friary residents who received burial in this cemetery, but the larger community as well. Forty percent of individuals from Blackfriars were non-adult, which is a fairly typical child mortality rate for this period (Weiss, 1973). Overall, there is a lack of stress indicators which suggests this population had an adequate diet and were not overly plagued by childhood infections. Furthermore, the lack of osteoarthritic changes in the shoulders and hips, as well as an absence of long bone fractures, suggests this was not an agricultural population. There are, however, a high proportion of older adults combined with a large number of severe pathological lesions, such as those consistent with syphilis. This suggests that the friary may have also served as a hospital to the surrounding community (Wiggins et al., 1993).

Hereford Cathedral – University of Bradford

The city of Hereford is located several kilometres east of the Welsh border, on the river Wye. There is little evidence for prehistoric or Roman settlement in Hereford, although there are Iron Age hill forts and Roman settlements in the surrounding area. While it is possible that a Roman settlement could have existed at Hereford, the large majority of evidence points to the origin of the city occurring during the Saxon period. The skeletal remains from Hereford Cathedral cemetery cover a vast amount of time, spanning from the Late Saxon to Post-Medieval period, between 900AD and 1791AD, and by 1143AD the cathedral had gained burial rights of all city and suburb parishes, as well as some parishes lying outside the city walls (Stone & Appleton-Fox, 1996).

Excavation revealed approximately 1200 individuals from the cemetery, including an estimated 200 individuals from 3 mass graves which are believed to be the result of the Black Death in the mid-fourteenth century (Stone & Appleton-Fox, 1996). A total of 40 individuals were examined, all of which originated from the cemetery proper, not the plague pits. It should be noted that only a portion of this collection was available for access, resulting in a larger than normal discrepancy between the total number excavated and the number sampled. This skeletal collection represents the citizens of the city of Hereford, initial observation of which suggests a relatively healthy population with good nutrition, based on a lack of skeletal pathology. A general trend of decreasing robusticity from the Saxon to Post-Medieval period has also been observed (Stone & Appleton-Fox, 1996), perhaps indicating a change in physical activity. There is a scarcity of infant burials at Hereford (about 30 in total), which suggests that there may have been a discrete

area for children. It is also possible that infants and still-born babies could have been interred in disused burial grounds to avoid paying fees (Stone & Appleton-Fox, 1996).

Chichester – University of Bradford

The Medieval hospital of St. James and St. Mary Magdalene was located approximately half a mile outside the Roman walls of Chichester, West Sussex (Magilton & Lee, 1989). The cemetery associated with this site was in use from the early 12th century to the mid 17th century and represents the largest British skeletal sample from a documented leprosarium. The hospital was originally founded for 8 leper brethren and, not surprisingly, the oldest area of the cemetery consists primarily of males, approximately half of whom exhibit leprosy changes. It is probable that the majority of these individuals represent the hospital's leper population, their caretakers, and benefactors. Around 1540 A.D. women and children were admitted, and by 1594 the hospital was essentially transformed into an almshouse which provided care and shelter (Lee, 2001). The portion of the cemetery associated with the almshouse phase has a more normal distribution of individuals, with males, females, and non-adults represented. Excavation of the cemetery recovered the skeletal remains of 351 individuals, 51 of which are included in the present study. Magilton and Lee (1989) propose that this skeletal sample may have had a very physically active lifestyle as a portion likely represent both individuals who tended the land and farms of the leprosy inmates, as well as less infirm inmates who would have provided domestic and agricultural labour for the hospital. Although the severely leprosy individuals would not have been able to care for themselves or be fit enough to work

(Magilton & Lee, 1989), steps were taken not to include these individuals in the present study. Rather, the individuals chosen focus on the non-pathological skeletons.

Wolverhampton – University of Bradford

The Wolverhampton collection is comprised of 152 individuals excavated from the cemetery of St. Peter's Collegiate Church, Wolverhampton, West Midlands. Of that total, 28 individuals are included in the current study. Wolverhampton, like many English towns, grew enormously during the 19th century. Much of Wolverhampton's growth was fuelled by a nearby coalfield with limestone and iron ore. As such, a large number of individuals, both adults and children, would have been employed in the mines or in occupations related to the iron industry. During the 1800's, as mechanisation increased, the economy changed from small industrial units to large factories. With this growth, social conditions continued to worsen and the town was described as "disgustingly filthy" (Arabaolaza et al., 2006). Of the individuals excavated from St. Peter's church cemetery 42% died before twenty years of age, and 76% of non-adults died before the age of five. Overall, the burials from Wolverhampton represent an urban, industrial population where people suffered from bad health, child mortality was high, and living and working conditions were both poor and dangerous (Arabaolaza et al., 2006).

Baldock – University of Bradford

A small number of individuals (n=7) were examined from the Romano-British cross-roads site of Baldock, Hertfordshire. In total, 139 discrete burials plus many groups and disarticulated remains were excavated, primarily from a ditched enclosure. The majority

of burials date to the second half of the 4th century AD, although two individuals come from the Late Iron Age, around the 1st century BC, one of whom is included in the present study. Of the excavated individuals, there were slightly more females than males, and fifteen non-adults among the collection (Roberts, 1988).

Kingsholm – University of Bradford

The Kingsholm site represents a Romano-British cemetery dating to the 4th century AD and located within the city of Gloucester. Excavation revealed between 48 and 50 individuals, most of whom were adults. Due to the paucity of non-adult remains, as well as preservation issues, 7 individuals are included in the present work. These individuals derive from an urban context which is situated within a settled agricultural landscape (Roberts et al., 2004). Overall, health in Roman Britain is believed to have been good; there is little osteological evidence to suggest major dietary elements were missing, and stature has been shown to increase from the earlier Iron Age period. In towns hygiene and sanitation were also good during this time, with the development of clean water systems, sewage disposal, and the construction of bathhouses. Joint disease and trauma, however, are fairly common. These conditions most likely result from a heavy workload and interpersonal violence, the latter of which was common during the Roman period (Roberts & Cox, 2003).

Blackgate – University of Sheffield

The Blackgate cemetery, located in Newcastle upon Tyne, lies upon the ruins of a Roman fort, abandoned in the late 4th or early 5th century. Excavation yielded 821 individuals and

it is believed that burials most likely commenced in the 8th century and continued until 1168. It is uncertain which settlement(s) the cemetery served, or whether these individuals derived from urban or rural centres (Nolan, 1998). However, a high incidence of osteoarthritis and Schmorl's nodes suggests that much of this population participated in some form of heavy activity (Boulter & Rega, 1993). Use of the cemetery was interrupted in 1080 when a Norman castle was built on the site. Afterwards, individuals continued to be interred inside the area enclosed by the castle and these burials likely represent the castle garrison and their families (Nolan, 1998). The current study focuses on a relatively large sample of 64 individuals from this site.

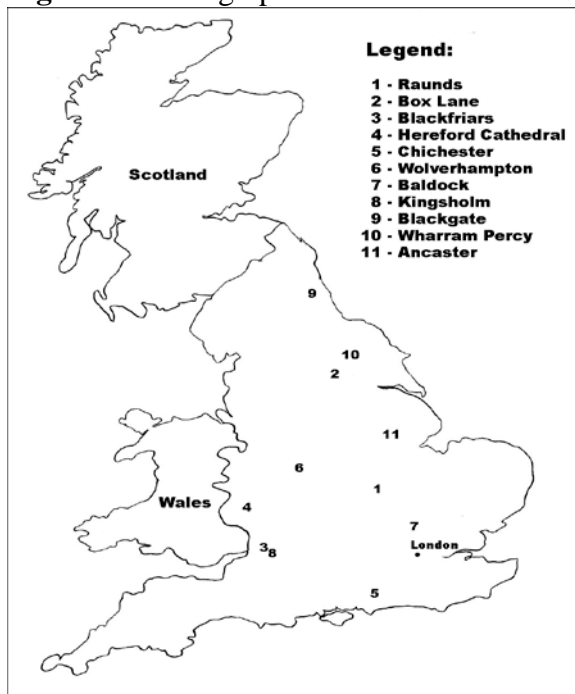
Wharram Percy – English Heritage Centre for Archaeology

Wharram Percy is a deserted village in North Yorkshire. In excavations running from 1950 to 1990 a total of 687 burials were recovered from the churchyard, 119 of which will be considered here. These burials date from the mid-tenth to the nineteenth century AD, but the majority are medieval (eleventh-fourteenth century). Infant mortality was fairly modest among this group with approximately 15% of individuals not surviving their first year. There is also a lack of evidence for iron deficiency in infants which suggests prematurity or low birth weight was not a significant problem in this population. However, growth in children drops behind their modern counterparts after the age of one year, suggesting poorer nutrition in medieval times. Despite this, about 40% of individuals were aged over 50 years, a respectable proportion for a rural, peasant population (Mays, 2007).

Ancaster – English Heritage Centre for Archaeology

The site of Ancaster, located in Lincolnshire, represents a small defended settlement dating to the late Roman period (3rd-4th century AD) (Mays & Faerman, 2001). Excavations at the cemetery yielded 327 individuals, a quarter of which were non-adult. Of these, 37 individuals were examined in the present study. Overall, health and nutritional status was good apart from joint disease and dental caries. Cox (1989) describes this population as experiencing a rough and tumble life, based on the presence of fractures and periostitis. Additionally, robust muscle attachment sites in the upper limbs of males suggest this group participated in hard physical labour (Cox, 1989). Although changes in the proportion of infant death between the Roman and subsequent medieval period in Britain has led to the hypothesis that infanticide may have been practiced (Mays, 1993), DNA results of the sex of neonates and infants suggest that this may not have been the case at Ancaster (Mays & Faerman, 2001).

Figure 3.1: Geographic distribution of British archaeological sites



Summary of British Sites:

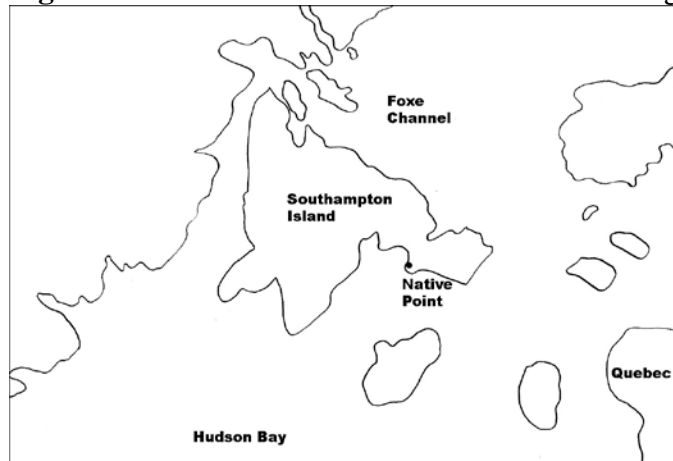
The skeletal samples originating from Britain span a large period of time, from approximately the 1st century B.C. to the 19th century A.D.. Over this span of time, however, lifestyle and activities would have changed little and agriculture would have been central to subsistence. Most of the sample dates to the Romano-British and Medieval periods, however, the individuals from Wolverhampton date to the Industrial period in England. Therefore, this population represents a shift in lifestyle which is not witnessed among the earlier groups. While it is not possible to know with certainty the exact occupations of the individuals represented in these samples, overall many would have been engaged in rather homogeneous activities centered around an agricultural subsistence and, most probably, would have been part of the lower classes.

North American Skeletal Sample:*Native Point – Canadian Museum of Civilization*

A sample of Sadlermiut skeletal remains from the Native Point site (Southampton Island, Nunavut) was analysed in addition to the British collections. This is a particularly useful collection as it has an unusually high number of well-preserved infant skeletons (Holland, 2007), and can serve as the basis for a valuable comparison across cultures and ancestral groups. The Sadlermiut are thought to have occupied Native Point for approximately 500 years between the early 1400's and 1903 when the population went extinct after being exposed to an epidemic from a Scottish whaling vessel. Therefore, the individuals considered here could represent both pre- and post-contact populations (Merbs, 1983). The origins of the Sadlermiut remain somewhat mysterious and it is unclear whether they descended from Thule or Dorset peoples, although this may be complicated by their

isolation on Southampton Island (Hayes, et al. 2005; Rowley 1994). What is known about them suggests they relied on the use of the kayak, and they were considered excellent whalers (Comer 1910; Mathiassen 1927). Recent work on the Native Point skeletal collection by Holland (2007) suggests female infanticide may have been practiced among the Sadlermiut, something which was common among other past Inuit groups (Balicki 1967). The implications of these results are important for the current study as they negate the possibility that the Native Point infants died from a condition which may have affected upper limb asymmetry (Left Hander Syndrome) (O’Callaghan et al., 1993a; O’Callaghan et al., 1993b; Satz et al., 1985).

Figure 3.2: Location of the Native Point archaeological site, Nunavut



Methods

In all instances, age and sex data were obtained from existing skeletal reports compiled by previous researchers. Each skeletal age was subsequently assigned to an age category according to the Bradford system (Table 3.2). This system was chosen for several reasons, including that previous work has been performed using the age categories which facilitates comparison. Additionally, and more fundamentally, this system divides the

non-adults (less than 18) into sufficient categories to allow for meaningful analysis in terms of what is understood about when handedness appears in children. It is important to consider the behavioural implications of age categories. For example, if ages are grouped into large categories (eg. 1-6 years) then we lose the ability to meaningfully discuss behavioural tendencies, such as those associated with a toddler or adolescent, that could affect skeletal asymmetry. Conversely, if ages are sub-divided too thoroughly (eg. 2-3 years; 4-5 years) age estimates become less reliable. In summary, the age categories below (Table 3.2) will allow for meaningful age-related behaviour to be considered, while maintaining reliability in the actual ages assigned.

Table 3.2: Age categories – following initial analysis, categories 8, 9, 10, and 11 were collapsed to create one adult age category

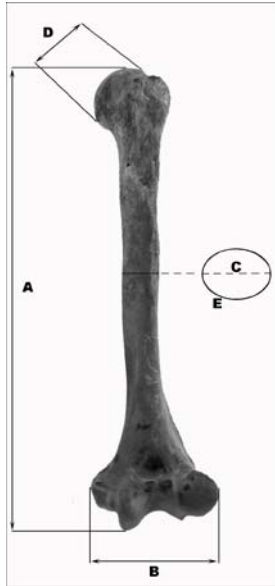
Age Category	Age Range	n
1. Foetus	under 40 weeks	20
2. Neonate	birth – 1 month	25
3. Infant	1 – 12 months	61
4. Juvenile 1	1 – 4 years	76
5. Juvenile 2	5 – 8 years	81
6. Juvenile 3	9 – 12 years	58
7. Adolescent	13 – 17 years	45
8. Young adult	18 – 25 years	32
9. Young middle adult	26 - 35 years	23
10. Old middle adult	36 – 45 years	10
11. Mature adult	46+	24

Prior to inclusion in this study, each individual pair of humeri was examined for evidence of pathology, such as fractures or periostitis (new bone growth), as these conditions could affect asymmetry. Any individuals with signs of pathology were not considered in this study. In addition to pathological issues, lack of completeness and

sporadic poor preservation did not allow all individuals to be included. As four measurements in non-adults and five in adults were considered it was necessary for at least one of these characteristics to be measurable in both the left and right element.

Whenever possible, five measurements were acquired for each adult humerus (Fig. 3.3). Maximum length was taken to the nearest millimetre, by means of a standard osteometric board according to Brothwell's (1981) definition. In order to take maximum length the most proximal and most distal areas had to be intact. Dial callipers were used to obtain the epicondylar breadth to the nearest 0.1 millimetre by measuring from the furthest protruding point on the lateral epicondyle to the equivalent point on the medial epicondyle (Buikstra & Ubelaker, 1994). Maximum midshaft diameter and head diameter were also taken with dial callipers to the nearest 0.1 millimetre. Midshaft diameter was obtained by dividing the total length of the element in two and rotating the dial callipers until the maximum measurement was established. In cases of poor preservation, total length was estimated. The diameter of the head was taken as a vertical measurement from the most superior and inferior points of the articular margin (Buikstra & Ubelaker, 1994). Finally, midshaft circumference was measured at the same point as midshaft diameter and was obtained either by wrapping a soft tape measure horizontally around the diaphysis, or by wrapping a string around the diaphysis and then measuring on an osteometric board. Non-adult measurements were obtained in the same manner as the adults, however, head diameter was omitted from this sample as the unfused proximal epiphysis of the non-adult humerus suffers from very poor preservation.

Figure 3.3: Humerus measurements – A, maximum length; B, epicondylar breadth; C, midshaft diameter; D, head diameter; E, midshaft circumference



Calculation of Asymmetry

In each individual, asymmetry was standardized by means of the following equation (Steele & Mays, 1995):

$$\text{standardized asymmetry} = \frac{R - L}{(R + L)/2} \times 100$$

where R is the right measurement and L is the left measurement. The standardization of asymmetry scores serves to provide a measure of both the direction and degree of asymmetry expressed in each individual case. Absolute asymmetry was also calculated, simply removing the negative sign in cases where the left element was larger than the right. This allows magnitude of asymmetry to be observed irrespective of direction.

Statistical Analysis

All measurement data were analysed using SPSS 15. Standardized and absolute asymmetry results were tested for a normal distribution using the Shapiro-Wilk test of

normality, which indicated a non-normal distribution for all measurements except standardized head diameter (Table 3.3). As such, most statistical analyses were performed using non-parametric tests. However, many similar studies have used parametric statistics and, therefore, these analyses were conducted as well, in order to make the results more easily comparable. Descriptive statistics were first used to observe any general trends in mean and median asymmetry in the British samples. The Sadlermiut data was tested separately in order to avoid the inclusion of any confounding factors resulting from population differences. One way ANOVA (parametric) and Kruskal-Wallis (non-parametric) tests were performed for each measurement to determine if there is a significant difference between different age groups. The same tests were used to observe any population differences in asymmetry (i.e. between the British and North American samples). All data was tested for homogeneity of variances; Bonferroni post hoc tests were applied when equal variances were assumed, and Tamhane's T2 was used when equal variances were not assumed. Additionally, one-tailed *t*-tests (parametric) and Mann-Whitney U-tests were performed to establish whether there is a significant difference in asymmetry between different time periods (i.e. industrial and pre-industrial) and between males and females. As sex was not assessed for the majority of non-adult skeletons, the latter tests necessarily focus primarily on the adult portion of the sample.

Table 3.3: Results of Shapiro-Wilk test for normality among asymmetry results

Measurements	df	Standardized asymmetry		Absolute asymmetry	
		Statistic	p	Statistic	p
Length	243	0.938	0.000	0.830	0.000
Midshaft Diameter	412	0.909	0.000	0.770	0.000
Midshaft Circumference	411	0.971	0.000	0.889	0.000
Epicondylar Breadth	116	0.935	0.000	0.812	0.000
Head Diameter	44	0.982	0.710	0.878	0.000

Repeatability of Measurements

The repeatability of measurements was estimated through the re-measurement of five randomly selected individuals. Standardized asymmetry was then calculated for the new measurements. Therefore, all repeatability calculations were based on asymmetry rather than raw measurements in order to account for effects of size differences between individuals. Measurement error was subsequently calculated by determining the square root of the sum of squared differences between the first and second measurement, divided by twice the sample size (Steele & Mays, 1995; Knapp, 1992). The results indicate that in all cases the measurement error is smaller than the overall sample standard deviation (Table 3.4).

Table 3.4: Results of Intra-observer error test for all measurements

Measurement	S_m	S
Length	0.059	0.325
Midshaft diameter	0.208	1.071
Midshaft circumference	0.645	0.945
Epicondylar breadth	0.020	0.639
Head diameter	0.052	0.524

S_m is the measurement error
S is the sample standard deviation

3D Data

Morphometric data from the Bradford and Sheffield samples were captured using a Polhemus hand-held, laser scanner. Digital scans were not taken of the individuals from Wharram Percy, Ancaster, or Native Point and, therefore, it should be kept in mind that all subsequent results from the 3D data do not include these populations.

The 3D shape and geometry of the skeletal material was acquired using the Polhemus Fastscan handheld 3D scanner. The scanner uses a laser, camera and motion

tracking system to accurately record a 3D point-set of the original object surface. The laser and range-finding camera are contained in a portable handheld wand. A fan of laser light is emitted from the wand as the user scans the object's surface using a motion similar to spray painting. The range finding optics calculate the distance from the object to the scanner and records the position as a point in 3D-space. The motion tracking system establishes these points relative to the transmitter through a low frequency magnetic field generated by the transmitter. As such, the Polhemus Fastscan has the ability to scan objects with accurate six degrees of freedom (X,Y,Z, Azimuth, Elevation and Roll). Since the motion tracking system is based on a field generated from the transmitter, accuracy depends on wand-object range in relation to the transmitter. The scanner provides a number of advantages for scanning skeletal material. The handheld wand allows for the manipulation of the data acquisition device to suit the variable size, orientation and surface quality of the object. Laser intensity can also be adjusted on the wand, so differences in surface quality to be compensated for (Hoppa, pers. comm.).

Humeri of younger individuals were mounted upright in modelling clay which allowed all sides of the element to be captured in one image. The heavier humeri of adults and adolescents were placed in a cup filled with mustard seed, which also allowed all sides to be captured but unfortunately obscured the distal epiphysis. Image processing of the scan data was undertaken using RapidForm software by Inus Technology Inc. Multiple sweeps of objects were registered to create 3D models of each skeletal element. The Polhemus tracks the point cloud data for each sweep separately, but all data are triangulated according to the same zero point. Therefore, each model is created from a single scanning session and the process of registration serves to reduce the redundancy of

multiple sweeps. In general, the post-processing of 3D models follows a set pattern of tasks: registration of multiple scans (views) for a single element, simplification of 3D point cloud, and detailing and cleaning of the final 3D model to remove noise and ensure the model is as accurate as possible. Midshaft was visually estimated for each humerus (the details of which are discussed below), and if image quality was deemed suitable a circumference was obtained, a cross-section of the diaphyseal shape taken, and x y coordinates exported for further analysis. In each individual, right cross-sections were “flipped” along the z x axis to allow for direct comparison to the left element. Subsequently, 2D coordinates were obtained of circumferential outlines allowing for shape analysis.

Repeatability of Cross-Section Data Collection

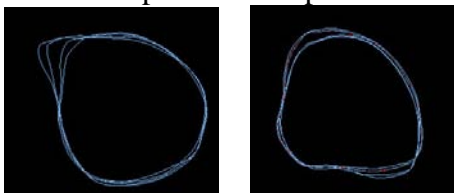
In order to assess the repeatability of estimating the placement of these cross-sections, an intraobserver error test was performed. A sample of 18 individuals was chosen to represent all stages of development. In each case, midshaft, followed by distal and proximal cross-sections were estimated five times. Their position on the X axis was recorded, as was the circumference. The repeatability of both the circumference and positional (X axis) data were analyzed by calculating the average difference between the summed differences of each measurement and the mean (White, 2000). Results indicate that while the mean difference in positional repeatability varies by as much as 13.4%, this has very little effect on the circumference (Table 3.4). Although the distal cross-section was assessed more consistently than the proximal, shape changes in the distal portion can lead to significant variability between even closely-spaced cross-sections (Figure 3.5).

Conversely, the proximal diaphysis does not experience such drastic shape variations. Therefore, in further analyses the proximal position was determined first (relative to the midshaft). The distance between the midshaft and distal cross-section can then be calculated and the proximal cross-section can be placed the same distance from the midshaft. This technique can also help ensure that the position of cross-sections is comparable between left and right elements.

Table 3.5: Average variation in repeatability of positional and circumference data in 3D models

Cross-section	Circumference	X axis	n
Midshaft	0.3%	13.4%	18
Distal	0.6%	3.6%	18
Proximal	0.9%	6.0%	18

Figure 3.4: Overlaid distal (left) and proximal (right) cross-sections demonstrating shape differences between repeated attempts.



Effects of Repairing Holes

In many instances, the 3D models contained holes in the surface which would not allow for complete cross-sections to be taken. The reasons for this problem are unclear, although a more detailed discussion of the issues encountered in this research can be found in Chapter 5. In order to salvage as much data as possible, a method of repairing the holes was devised and a test to ensure this did not affect “true” circumference was performed. Five humeri of individuals from age categories 3, 4, 5, 6, and 10 were used to assess the effects of filling holes in 3D models. Cross-sections were taken and

circumferences were obtained for each intact image, then a hole was created by deleting a portion of the surface where the cross-section was located (Figure 3.5). The RapidForm fill tool was then used to repair the surface and make a cross-section possible. Circumferences between original and filled images were compared by calculating the square root of the sum of squared differences between the first and second measurement, divided by twice the sample size (Steele & Mays, 1995; Knapp, 1992). Results indicate a measurement error of 0.06mm which is very small compared to the mean difference between left and right circumference measurements (0.89mm). Therefore, filling holes in data does not appear to have a significant effect on circumference. Shape also does not appear to be altered based on visual inspection of overlaid cross-sections (Figure 3.6).

Figure 3.5: Original 3D model with cross-section (left) and image with a portion of the surface intentionally deleted (right)

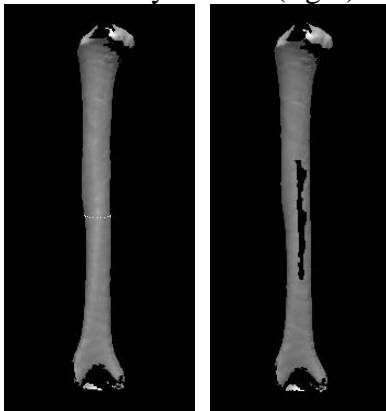
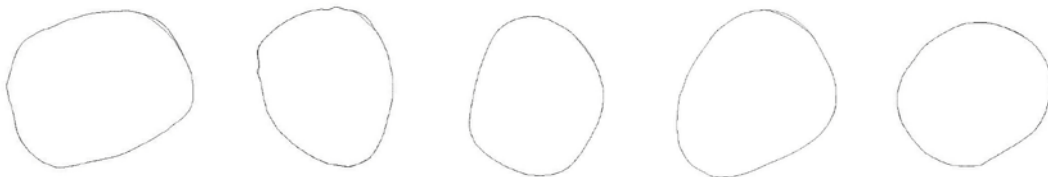


Figure 3.6: Original cross-sections overlaid with repaired cross-sections, demonstrating a lack of shape change as a result of repairing holes



Shape Analysis

All shape data obtained from cross-sections was analysed using PAST 1.51 (Hammer et al., 2001). As age categories 5 and 6 (5-8 years and 9-12 years respectively) were determined to be a key transitional period in the development of bilateral asymmetry, they were the focus of geometric morphometric analysis. Furthermore, as PAST 1.51 (Hammer et al., 2001) requires the same number of coordinates for each case, and the number of coordinates must be less than the number of cases, it was necessary to limit the analysis to individuals of similar age as this factor is size, and therefore, age dependent. As such, age categories 5 and 6 were determined to be the only ones that met the necessary criteria and were viable for analysis. Coordinate data from midshaft cross-sections were used to generate Elliptic Fourier coefficients which are normalized for position and size. To determine whether the shapes from different age categories, or from the left and right side in the same age category, differed significantly from each other a multivariate analysis of variance (MANOVA) was performed using the Fourier coefficients. Canonical variates analysis (CVA) was also performed using the above coefficients in order to provide a visual representation of similarities and differences among the left and right elements and between ages. The purpose of CVA is to project a multivariate down to two or more dimensions in a manner that maximizes separation between groups (Hammer & Harper, 2006). As such, CVA is used as an ordination procedure to display how groups are configured in a way that emphasizes the differences that exist between groups, in this case the differences between left and right sides in 5-8 and 9-12 year olds, and of left humeri between the two age groups.

Hypotheses

This work will test several hypotheses regarding the presence of bilateral asymmetry in the humerus of anatomically modern human populations.

1) The primary hypothesis will test when a preference for right-handedness (as inferred from right-sided asymmetry) appears during growth and development. Based on behavioural evidence for handedness, right-sided asymmetry should appear shortly after 2 years of age (Butterworth & Hopkins, 1993; Hepper et., 1991; Ramsay, 1980), but may be preceded by either left-sidedness or symmetry.

2) A secondary hypothesis proposes that bilateral asymmetry results from behaviourally-related mechanical strain in the skeleton. That is, environmental factors play a larger role than genetic determinants in asymmetry.

3) Males will exhibit stronger bilateral asymmetry than females, as the male skeleton has been shown to be more strongly affected by mechanical strain (Jones et al., 1977).

4) As activities would have changed throughout time, particularly during the Industrial Revolution, patterns in bilateral asymmetry will similarly change over time. As individuals living in urban settings during the 18th and 19th centuries had reduced workloads compared to their earlier counterparts (Auerbach & Ruff, 2006; Ruff, 1987) the individuals from Wolverhampton should exhibit less asymmetry than the other skeletal populations.

5) The Sadlermiut will exhibit different patterns of bilateral asymmetry than the British populations due to differences in lifestyle. However, this difference should be more marked in the adults and older adolescents as changes in lifestyle and activity patterns would be more pronounced in this group as compared to infants and children.

6) Patterns of bilateral asymmetry in infants and children will be the same between the Sadlermiut and British populations indicating that a) humeral asymmetry develops according to the same mechanisms between populations and b) pathological left-handedness is not a confounding factor in the study of archaeological populations as it has been suggested that many of the Sadlermiut infants died as a result of infanticide (Holland, 2007).

Chapter 4 - Results

Traditional Measurements:

A total of 481 skeletal individuals were used in this study; bilateral measurements were obtained in a smaller portion of the sample, with maximum midshaft diameter and midshaft circumference providing the most data, and head diameter providing the fewest measurements (Table 4.1). An analysis of asymmetry distribution indicates that epicondylar breadth has the strongest trend toward left-sidedness while maximum length most closely resembles known handedness proportions in modern populations with 16.2% left-sided and 82.8% right-sided (Table 4.2). Overall, this suggests that length may be the best predictor of handedness.

Table 4.1: Total number of measurements obtained from both North American and British samples (N = number of individuals)

Measurement	British (N)	North American (N)	Total
Maximum Length	243	29	272
Max. Midshaft Diameter	413	42	455
Midshaft Circumference	412	42	454
Epicondylar Breadth	116	19	135
Head Diameter	44	5	49

Table 4.2: Distribution of left and right-sided asymmetry for all individuals across all age categories

Measurement	Left (N)	Percent	Right (N)	Percent
Maximum Length	44	16.2%	228	82.8%
Max. Midshaft Diameter	126	27.7%	329	72.3%
Midshaft Circumference	90	19.8%	364	80.2%
Epicondylar Breadth	46	34.1%	89	65.9%
Head Diameter	15	30.6%	34	69.4%

Analysis of variance (ANOVA) tests were performed for all measurements in order to determine if there was a difference in mean standardized and absolute asymmetry between the adult age categories. In all cases there was no significant difference between any of the adult ages and, therefore, data was collapsed over this

variable. As such, all subsequent analyses consider individuals 18 years of age and older as one age category.

Analysis of mean standardized asymmetry for each measurement by age category yielded results which indicate a trend from left-sided to right-sided asymmetry throughout growth and development (Table 4.3, Figure 4.1). For both length and midshaft circumference, a left-sided dominance is present in foetal and neonate remains, while the epicondylar breadth remains left-dominant until 12 months of age. With regard to median standardized asymmetry, all measurements commence as symmetrical and gradually change to right-sided throughout growth, with the exception of the epicondylar breadth which is left-sided in the foetal skeletal and remains as such until 1-12 months (Table 4.3, Figure 4.2). Of the four measurements taken on non-adults, only the midshaft diameter does not exhibit left-sidedness in any age category. An analysis of variance (ANOVA) test indicates that the difference in mean standardized asymmetry between ages is statistically significant for all measurements except midshaft diameter, while a Kruskal-Wallis test indicates a significant difference for length only (Table 4.4). Additionally, post-hoc tests indicate that these significant differences exist between the younger and older age categories (i.e. age categories 1, 2, 3 vs. age categories 6, 7, 8), although there is some variation by measurement (appendix).

Table 4.3: Mean and median standardized asymmetry of traditional measurements for all individuals for factor = age (N = number of individuals; negative means indicate left-sidedness)

Age Category		Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth
Foetus	Mean	-0.07271	0.25990	-0.63510	-0.19010
	Median	0.00000	0.00000	0.00000	-0.08400
	N	17	20	20	10
	Stand. Dev.	0.336591	1.946707	1.432428	0.671618
Birth-1 month	Mean	-0.10650	0.15655	-0.19600	-0.69780
	Median	0.00000	0.26700	0.00000	-0.28100
	N	10	22	22	5
	Stand. Dev.	0.172095	0.928437	0.760745	1.346602
1-12 months	Mean	0.06500	0.04336	0.02639	-0.58350
	Median	0.00000	0.00000	0.00000	-0.58350
	N	6	39	38	2
	Stand. Dev.	0.188612	0.999988	0.965891	0.543765
1-4 yrs	Mean	0.05515	0.36910	0.40636	0.02483
	Median	0.00000	0.39100	0.35000	0.02250
	N	40	73	73	6
	Stand. Dev.	0.174409	0.951792	0.928094	0.566491
5-8 yrs	Mean	0.15066	0.54506	0.33933	0.26300
	Median	0.14700	0.45900	0.34000	0.21300
	N	58	79	79	13
	Stand. Dev.	0.271519	0.883247	0.873132	0.505796
9-12 yrs	Mean	0.19643	0.17554	0.37381	0.38150
	Median	0.25600	0.31400	0.49500	0.46550
	N	35	57	57	16
	Stand. Dev.	0.325365	1.407519	0.764051	0.506548
13-17 yrs	Mean	0.45680	0.56540	0.65348	0.17479
	Median	0.38000	0.63300	0.87350	0.13500
	N	20	40	40	14
	Stand. Dev.	0.484600	0.839445	0.832600	0.511205
Adult 18+	Mean	0.31883	0.57384	0.65283	0.10398
	Median	0.31700	0.50950	0.67350	0.21950
	N	59	82	82	50
	Stand. Dev.	0.283536	0.852814	0.790563	0.583760

Figure 4.1: Mean standardized asymmetry of traditional measurements for all individuals for factor = age

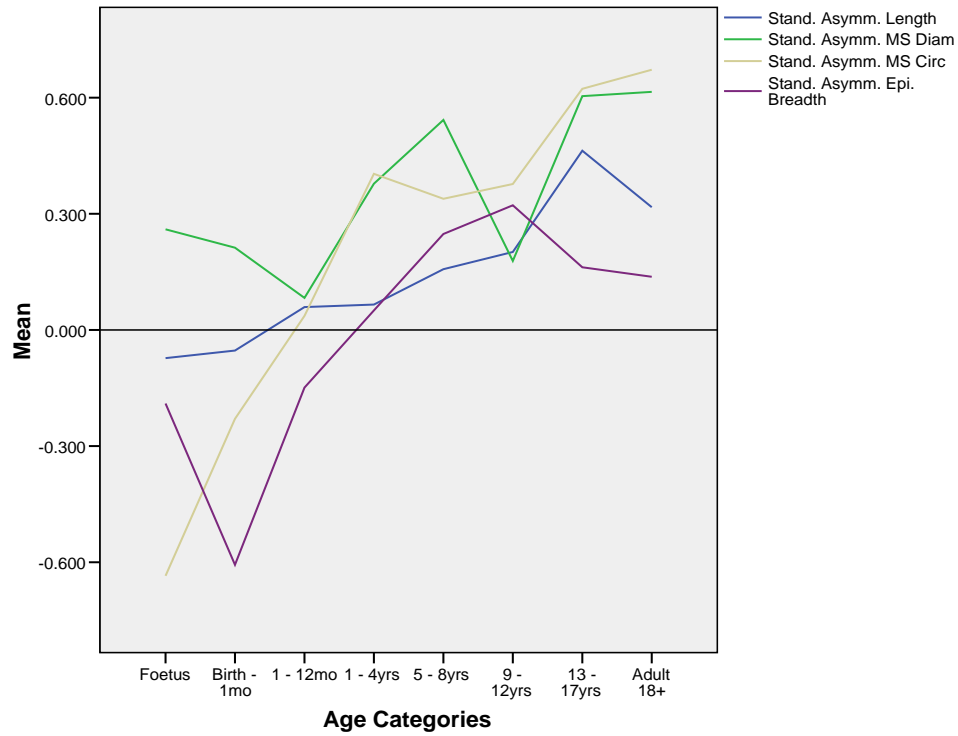


Figure 4.2: Median standardized asymmetry of traditional measurements for all individuals for factor = age

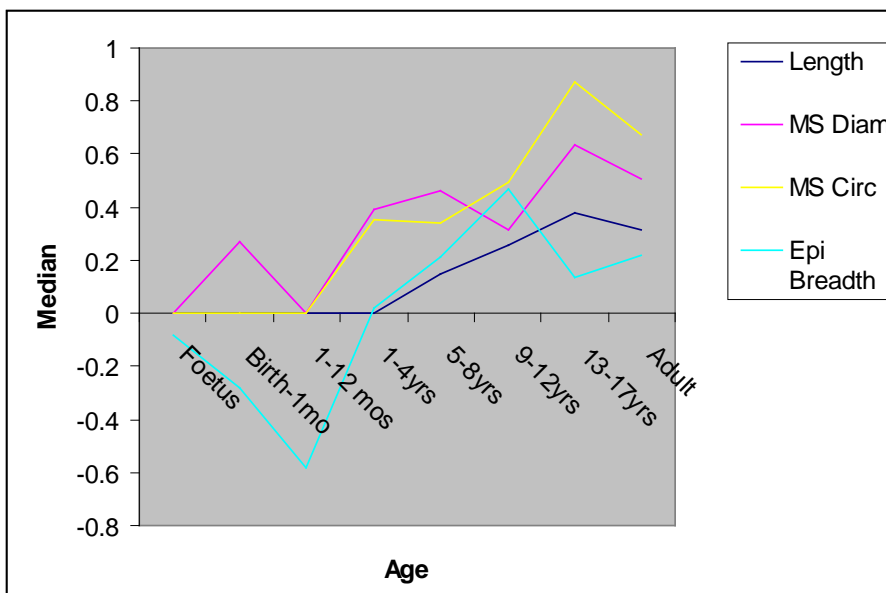


Table 4.4: Results of ANOVA and Kruskal-Wallis – Standardized asymmetry of traditional measurements for all individuals for factor = age

Measurement	ANOVA			Kruskal-Wallis		
	df	F	p	df	Chi-square	p
Length	242	8.859	0.000	7	16.612	0.020
Midshaft Diameter	411	1.893	0.069	7	8.947	0.256
Midshaft Circumference	410	7.509	0.000	7	5.674	0.578
Epicondylar Breadth	115	2.561	0.018	7	10.668	0.154

Absolute asymmetry, that is, non-directional asymmetry, was examined in addition to directional asymmetry. These analyses were performed because, although not directly related to handedness *per se*, absolute asymmetry can reveal trends that may be reflective of activity patterns. In turn, these can then be used to help understand what types of activities a population was engaging in and provide a more complete picture of bilateral asymmetry. Observation of trends in absolute asymmetry between age categories does not indicate any clear trends during growth and development (Table 4.5, Figure 4.3), which is corroborated by no significant ANOVA results for most measurements (Table 4.6), although post-hoc tests do reveal a significant difference between the first and third age categories for midshaft diameter (appendix). Results do reveal a statistically significant difference in age categories for length and midshaft circumference asymmetry indicating these traits may be subject to different influences than the other measurements. Similar to the standardized asymmetry results, post hoc tests for length indicate that there is generally a difference between the younger and older age categories (i.e. age categories 2 vs. 8 and 4 vs. 6, 8). Post hoc tests for the remaining measurements however, including midshaft circumference, do not indicate any between-group differences (appendix). Results of a Kruskal-Wallis test for median values indicate no significant differences between age categories for any measurement (Table 4.6, Figure 4.4).

Table 4.5: Mean absolute asymmetry of traditional measurements for all individuals for factor = age (N = number of individuals)

Age Category		Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth
Foetus	Mean	0.21871	1.36380	1.07240	0.48390
	Median	0.00000	1.04900	1.19150	0.38750
	N	17	20	20	10
	Stand. Dev.	0.260938	1.379467	1.125105	0.480673
Birth-1 month	Mean	0.10650	0.70391	0.52436	0.88460
	Median	0.00000	0.49650	0.30850	0.46700
	N	10	22	22	5
	Stand. Dev.	0.172095	0.607113	0.575264	1.201601
1-12 months	Mean	0.12700	0.76654	0.67582	0.58350
	Median	0.09300	0.61600	0.65900	0.58350
	N	6	39	38	2
	Stand. Dev.	0.145910	0.631556	0.681608	0.543765
1-4 yrs	Mean	0.13845	0.74551	0.69219	0.36117
	Median	0.17450	0.55800	0.66700	0.29250
	N	40	73	73	6
	Stand. Dev.	0.117806	0.687859	0.736881	0.406352
5-8 yrs	Mean	0.23627	0.78061	0.67178	0.40715
	Median	0.16700	0.62800	0.60200	0.37700
	N	56	79	79	13
	Stand. Dev.	0.199991	0.681079	0.649538	0.388811
9-12 yrs	Mean	0.33580	0.81032	0.64693	0.53300
	Median	0.33400	0.59800	0.53200	0.49850
	N	35	57	57	16
	Stand. Dev.	0.171765	1.146496	0.547731	0.329859
13-17 yrs	Mean	0.45680	0.83320	0.90415	0.38236
	Median	0.38000	0.75200	0.90900	0.26950
	N	20	40	40	14
	Stand. Dev.	0.484600	0.566144	0.522123	0.369848
Adult 18+	Mean	0.35385	0.79304	0.85022	0.45862
	Median	0.33100	0.66250	0.74050	0.36500
	N	59	82	82	50
	Stand. Dev.	0.237553	0.651137	0.569771	0.370383

Figure 4.3: Mean absolute asymmetry of traditional measurements for all individuals for factor = age

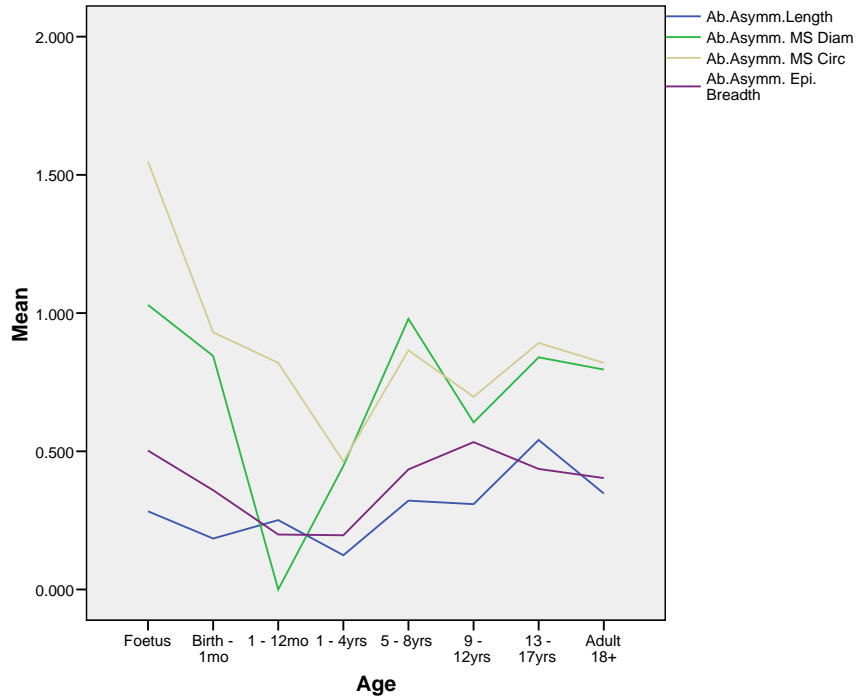


Figure 4.4: Median absolute asymmetry of traditional measurements for all individuals for factor = age

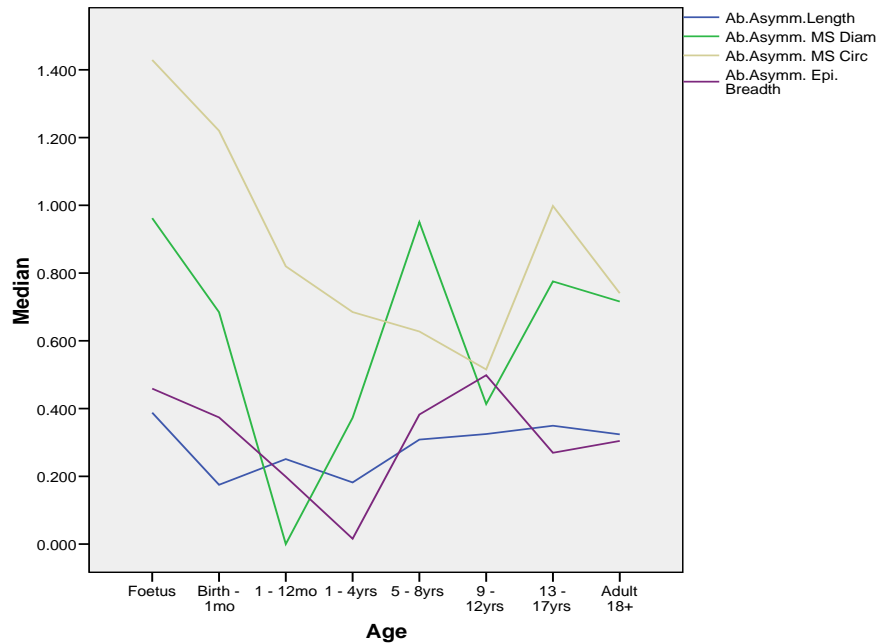


Table 4.6: Results of ANOVA and Kruskal-Wallis test for factor = age – Absolute asymmetry of traditional measurements for all individuals

Measurement	ANOVA			Kruskal-Wallis		
	df	F	p	df	Chi-square	p
Length	242	6.366	0.000	7	5.080	0.650
Midshaft Diameter	411	1.588	0.137	7	5.078	0.650
Midshaft Circumference	410	2.148	0.038	7	7.418	0.387
Epicondylar Breadth	115	0.875	0.529	7	4.989	0.661

Steele and Mays (1995), yielded results similar to those found here. However, as Steele and Mays (1995) sample population (Wharram Percy) was also included in the present study, additional tests were performed to determine if the Wharram Percy data is influencing the results (Table 4.7). Results indicate that omitting the individuals from Wharram Percy does have a minor affect on the trends noted above, most notably with regard to mean length asymmetry. Rather than moving from left to right-sidedness, length remains right-sided throughout growth. It is worth noting though, that this right-sidedness is very weak in the first two age categories, barely differing from symmetry. Results of an ANOVA reveal that all measurements differ significantly across age categories (Table 4.8, appendix), consistent with what was found in the pooled data. A Kruskal-Wallis test also provides significant results except for median epicondylar breadth asymmetry, while asymmetry in the pooled data was non-significantly different other than for median length. Overall, the inclusion of the Wharram Percy data does not appear to affect the overall results, especially with regard to creating increased left-sidedness in the youngest age categories. Rather, Wharram Percy more likely strengthens a trend that is present in the remaining data but which is difficult to detect due to small sample sizes in the youngest age categories.

Table 4.7: Standardized asymmetry for factor = age, without Wharram Percy data included

Age Category		Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth
Foetus	Mean	0.00600	-0.57225	-0.77562	0.00067
	Median	0.00000	-0.49650	0.00000	0.31100
	N	4	8	8	3
	Stand. Dev.	0.311979	1.444223	1.747974	0.541849
Birth-1 month	Mean	0.00975	0.17083	-0.26322	-1.27533
	Median	0.00000	0.22000	0.00000	-0.68900
	N	4	18	18	3
	Stand. Dev.	0.332913	1.129875	0.651457	1.505705
1-12 months	Mean	0.52400	0.08564	0.02338	-0.14275
	Median	0.00000	0.00000	0.00000	0.00000
	N	20	59	58	8
	Stand. Dev.	0.226420	1.033320	0.960070	0.367028
1-4 yrs	Mean	0.07247	0.47047	0.40355	0.05029
	Median	0.00000	0.41350	0.17500	0.04500
	N	19	58	58	7
	Stand. Dev.	0.140077	0.997370	0.810250	0.521499
5-8 yrs	Mean	0.20741	0.38690	0.41608	0.31067
	Median	0.15350	0.35500	0.36650	0.15600
	N	22	52	52	9
	Stand. Dev.	0.288988	0.873197	0.728558	0.552874
9-12 yrs	Mean	0.25667	0.17013	0.45737	-0.07457
	Median	0.27950	0.41950	0.49750	-0.23500
	N	18	40	40	7
	Stand. Dev.	0.283031	1.637678	0.764702	0.488814
13-17 yrs	Mean	0.51406	0.60755	0.55662	0.16660
	Median	0.38800	0.69700	0.76200	0.07900
	N	16	42	42	15
	Stand. Dev.	0.525203	0.842461	0.788243	0.494986
Adult 18+	Mean	0.30912	0.58807	0.67823	0.15902
	Median	0.30300	0.50950	0.67350	0.21900
	N	51	74	74	41
	Stand. Dev.	0.279420	0.884342	0.797136	0.623666

Table 4.8: Results of ANOVA and Kruskal-Wallis test for factor = age comparing standardized asymmetry for each measurement (Wharram Percy data omitted)

Measurement	ANOVA			Kruskal-Wallis		
	df	F	p	df	Chi-square	p
Length	153	4.982	0.000	7	32.258	0.000
Midshaft Diameter	350	2.631	0.012	7	19.872	0.006
Midshaft Circumference	349	6.841	0.000	7	43.576	0.000
Epicondylar Breadth	92	2.758	0.012	7	10.172	0.179

An independent samples t-test and a Mann-Whitney U-test were performed to compare both the mean and median standardized asymmetry between the Sadlermiut (Native Point) and British skeletal populations. With regard to standardized asymmetry, there were no significant differences between the two groups for any measurements (Tables 4.9, 4.10; Figures 4.5, 4.6). A Mann-Whitney U-test and a t-test were performed on the absolute asymmetry data and results indicate that there is a significant difference in midshaft circumference and epicondylar breadth between the British and Sadlermiut populations with the British being more asymmetrical (Tables 4.11, 4.12; Figures 4.7, 4.8).

Table 4.9: Standardized asymmetry - Results of t-test for factor = population

Measurement	Population	N	Mean	Stand. Dev.	df	t	p
Length	British	244	0.17923	0.324983	27	0.110	0.912
	Sadlermiut	29	0.17234	0.247728	0		
Midshaft Diameter	British	412	0.38661	1.014360	45	-0.599	0.550
	Sadlermiut	42	0.48948	1.014360	2		
Midshaft Circumference	British	411	0.34413	0.935609	45	0.797	0.426
	Sadlermiut	42	0.22440	0.843974	1		
Epicondylar Breadth	British	116	0.09277	0.638653	13	-0.155	0.878
	Sadlermiut	19	0.10905	0.377530	3		
Head Diameter	British	44	0.19175	0.524286	47	-0.193	0.847
	Sadlermiut	5	0.23800	0.249911			

Table 4.10: Standardized asymmetry - Results of Mann-Whitney U – test for factor = population

Measurement	Population	N	Median	Mann-Whitney U	Z	p
Length	British	244	0.17800	3440.500	-0.209	0.835
	Sadlermiut	29	0.25600			
Midshaft Diameter	British	412	0.35800	8548.500	-0.128	0.898
	Sadlermiut	42	0.32550			
Midshaft Circumference	British	411	0.40300	7706.500	-1.154	0.248
	Sadlermiut	42	0.00000			
Epicondylar Breadth	British	116	0.11050	1029.000	-0.462	0.644
	Sadlermiut	19	0.07700			
Head Diameter	British	44	0.17400	104.500	-0.182	0.856
	Sadlermiut	5	0.06200			

Figure 4.5: Mean standardized asymmetry of traditional measurements for all individuals for factor = population

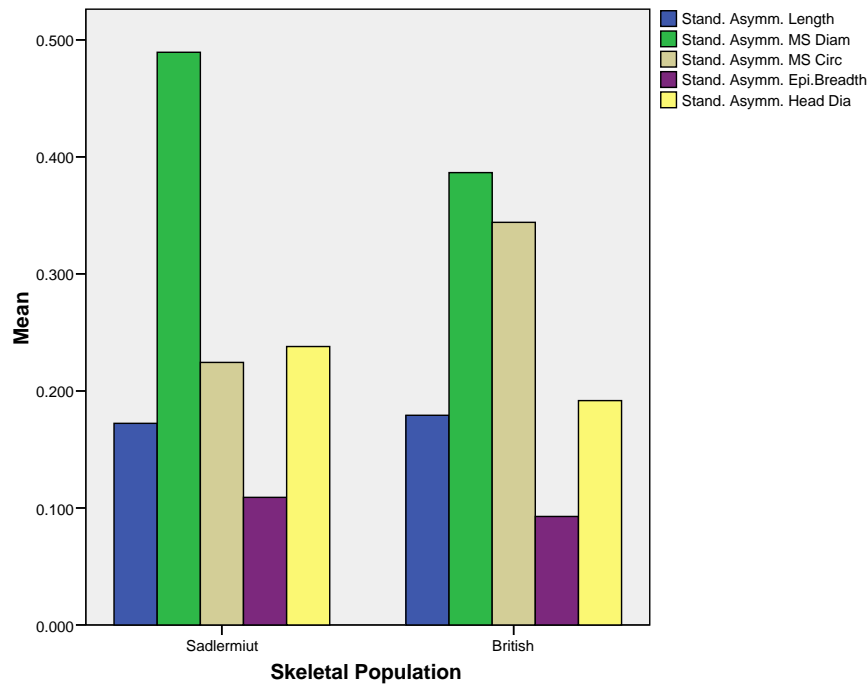


Figure 4.6: Median standardized asymmetry of traditional measurements for all individuals for factor = population

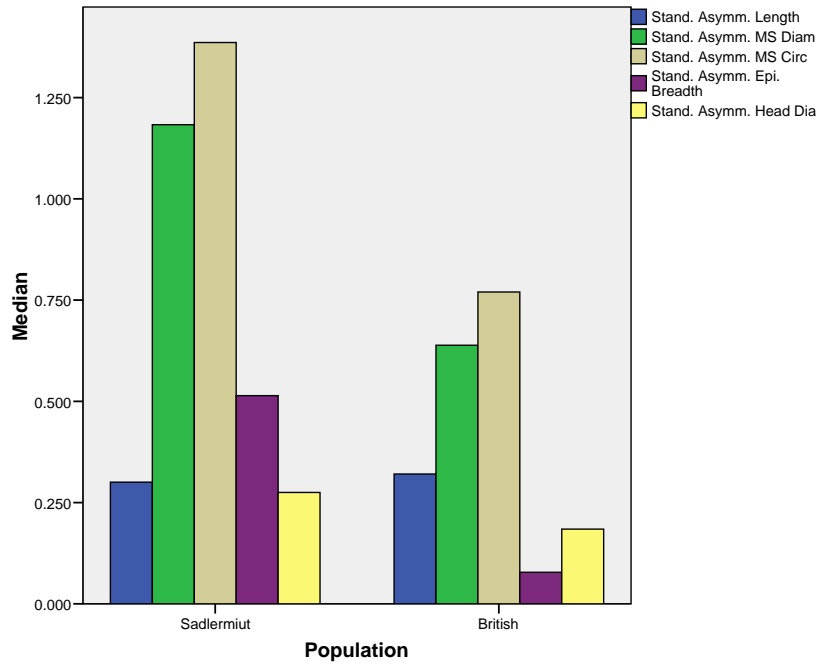


Table 4.11: Absolute asymmetry - Results of t-test for factor = population

Measurement	Population	N	Mean	Stand. Dev.	df	t	p																																												
Length	British	244	0.27193	0.252226	270	0.697	0.487																																												
	Sadlermiut	29	0.23828	0.182564				Midshaft Diameter	British	412	0.80896	0.790185	452	0.299	0.765	Sadlermiut	42	0.77062	0.816100	Midshaft Circumference	British	411	0.74387	0.662860	451	-0.042	0.967	Sadlermiut	42	0.75417	0.678630	Epicondylar Breadth	British	116	0.47156	0.438469	133	2.200	0.030	Sadlermiut	19	0.24126	0.306007	Head Diameter	British	44	0.42608	0.355117	47	1.084	0.284
Midshaft Diameter	British	412	0.80896	0.790185	452	0.299	0.765																																												
	Sadlermiut	42	0.77062	0.816100				Midshaft Circumference	British	411	0.74387	0.662860	451	-0.042	0.967	Sadlermiut	42	0.75417	0.678630	Epicondylar Breadth	British	116	0.47156	0.438469	133	2.200	0.030	Sadlermiut	19	0.24126	0.306007	Head Diameter	British	44	0.42608	0.355117	47	1.084	0.284	Sadlermiut	5	0.24580	0.338617								
Midshaft Circumference	British	411	0.74387	0.662860	451	-0.042	0.967																																												
	Sadlermiut	42	0.75417	0.678630				Epicondylar Breadth	British	116	0.47156	0.438469	133	2.200	0.030	Sadlermiut	19	0.24126	0.306007	Head Diameter	British	44	0.42608	0.355117	47	1.084	0.284	Sadlermiut	5	0.24580	0.338617																				
Epicondylar Breadth	British	116	0.47156	0.438469	133	2.200	0.030																																												
	Sadlermiut	19	0.24126	0.306007				Head Diameter	British	44	0.42608	0.355117	47	1.084	0.284	Sadlermiut	5	0.24580	0.338617																																
Head Diameter	British	44	0.42608	0.355117	47	1.084	0.284																																												
	Sadlermiut	5	0.24580	0.338617																																															

Table 4.12: Absolute asymmetry - Results of Mann-Whitney U-test for factor = population

Measurement	Population	N	Median	Mann-Whitney U	Z	p
Length	British	244	0.22900	3384.500	-0.349	0.727
	Sadlermiut	29	0.29200			
Midshaft Diameter	British	412	0.62950	7906.500	-0.921	0.357
	Sadlermiut	42	0.46850			
Midshaft Circumference	British	411	0.64900	6857.000	-2.215	0.027
	Sadlermiut	42	0.00000			
Epicondylar Breadth	British	116	0.38950	625.500	-3.015	0.003
	Sadlermiut	19	0.15100			
Head Diameter	British	44	0.34950	65.500	-1.470	.142
	Sadlermiut	5	0.00000			

Figure 4.7: Mean absolute asymmetry measurements of traditional measurements for all individuals for factor = population

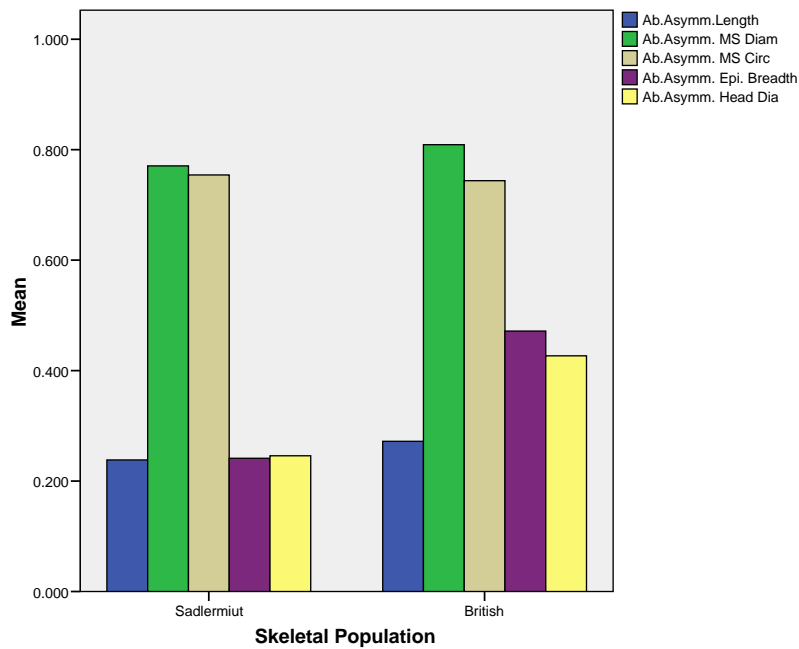
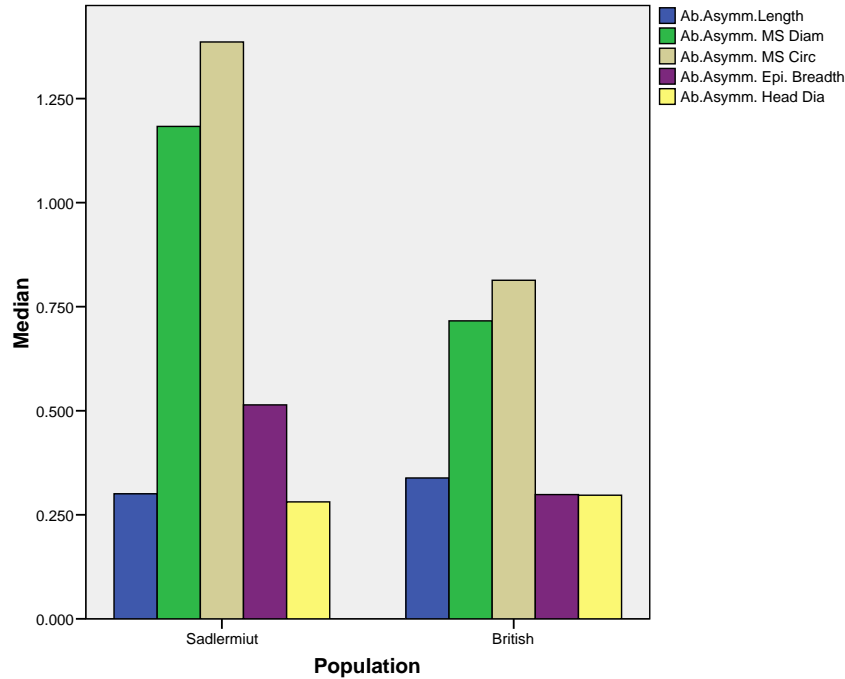


Figure 4.8: Median absolute asymmetry measurements of traditional measurements for all individuals for factor = population



Although many of the age categories in the Native Point data contain very small sample sizes, observation of this population independent of the British data offered a comparison based on cultural and genetic differences. Asymmetry for length and midshaft diameter among the Sadlermiut remains consistently right-sided which is unlike what was observed in the British sample (Table 4.13). In the pooled British and Native Point sample, a trend was noted from left to right-handed, with individuals up to one month of age exhibiting left-sided asymmetry. However, in the Native Point population the foetal age category is not represented and the neonate data only encompasses two and three individuals for each respective measurement. The midshaft circumference and epicondylar breadth were consistent with the British sample, exhibiting left-sided asymmetry in the neonate and 3-12 month age categories. With regard to absolute

asymmetry, no trends were noted between age categories, consistent with what was observed in the British data (Table 4.14).

Table 4.13: Mean standardized asymmetry of Native Point population for factor = age (N = number of individuals; negative means indicate left-sidedness)

Age Category	Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth
Birth-1 month	0.21368	0.62291	-0.47619	-0.15106
N	2	3	3	1
Stand. Dev.	0.302182	1.834182	0.824786	-
1-12 months	0.05681	0.15290	0.05334	-0.02477
N	16	22	22	7
Stand. Dev.	0.236198	1.064056	0.942003	0.165445
1-4 yrs	0.27613	0.82990	0.32680	0.20325
N	2	3	3	1
Stand. Dev.	0.27894	0.919922	0.566030	-
5-8 yrs	0.33016	0.44170	0.31646	0.14993
N	2	2	2	2
Stand. Dev.	0.257088	0.624653	0.447536	0.008253
9-12 yrs	0.37783	0.33333	0.56180	-0.63114
N	1	1	1	1
Stand. Dev.	-	-	-	-
13-17 yrs	0.58824	0.91221	0.37790	0.10113
N	1	5	5	3
Stand. Dev.	-	0.648012	0.518070	0.124154
Adult 18+	0.29673	1.17668	0.93607	0.55518
N	5	6	6	4
Stand. Dev.	0.188953	0.503292	0.609445	0.523284

Table 4.14: Mean absolute asymmetry of Native Point population for factor = age (N = number of individuals)

Age Category	Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth
Birth-1 month	0.21350	1.20367	0.47633	0.15100
N	2	3	3	1
Stand. Dev.	0.302182	1.834182	0.824786	-
1-12 months	0.17631	0.61036	0.53386	0.11057
N	16	22	22	7
Stand. Dev.	0.236198	1.064056	0.942003	0.165445
1-4 yrs	0.27600	0.82967	0.32667	0.20300
N	2	3	3	1
Stand. Dev.	0.027894	0.919922	0.566030	-
5-8 yrs	0.33000	0.44150	0.31650	0.15000
N	2	2	2	2
Stand. Dev.	0.257088	0.624653	0.447536	0.008253
9-12 yrs	0.37800	0.33300	0.56200	0.63100
N	1	1	1	1
Stand. Dev.	-	-	-	-
13-17 yrs	0.58800	0.91200	0.37780	0.10133
N	1	5	5	3
Stand. Dev.	-	0.648012	0.518070	0.124154
Adult 18+	0.29680	1.17700	0.93617	0.55525
N	5	6	6	4
Stand. Dev.	0.188953	0.503292	0.609445	0.523284

The British population was further subdivided according to time period, to create the categories “Pre-industrial” and “Industrial.” The Industrial period was represented by Wolverhampton while the remainder of sites fell into the Pre-industrial category. An examination of trends in standardized asymmetry reveals that the Industrial population is more strongly right-sided for all measurements except head diameter. Similarly, absolute asymmetry is more pronounced among the Industrial group for all measurements except head diameter (Tables 4.15 & 4.18; Figures 4.9 & 4.10). Although a t-test for standardized asymmetry did not reveal any differences between the pre-industrial and industrial groups, a Mann-Whitney U-test revealed a significant difference between populations for midshaft circumference (Tables 4.16, 4.17). A t-test and a Mann-Whitney

U-test, however, do not indicate any significant differences for absolute asymmetry (Tables 4.19, 4.20). As clear patterns are visible, it is possible that the lack of significant results is due to small sample sizes among the Industrial sample.

Table 4.15: Mean and median standardized asymmetry of all individuals from British populations for factor = time period

Period		Measurement				
		Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth	Head Diameter
Pre-industrial	Mean	0.17372	0.37835	0.32623	0.06961	0.20761
	Median	0.17550	0.35450	0.40000	0.11000	0.18400
	N	232	386	385	109	41
	Stand. Dev.	0.322074	1.059669	0.919130	0.622109	0.537968
Industrial	Mean	0.29555	0.50931	0.60919	0.45329	-0.02500
	Median	0.23800	0.50600	0.61700	0.23500	-0.09600
	N	11	26	26	7	3
	Stand. Dev.	0.379552	1.159188	1.140990	0.830618	0.214502

Figure 4.9: Mean standardized asymmetry of all individuals from British sites for factor = time period

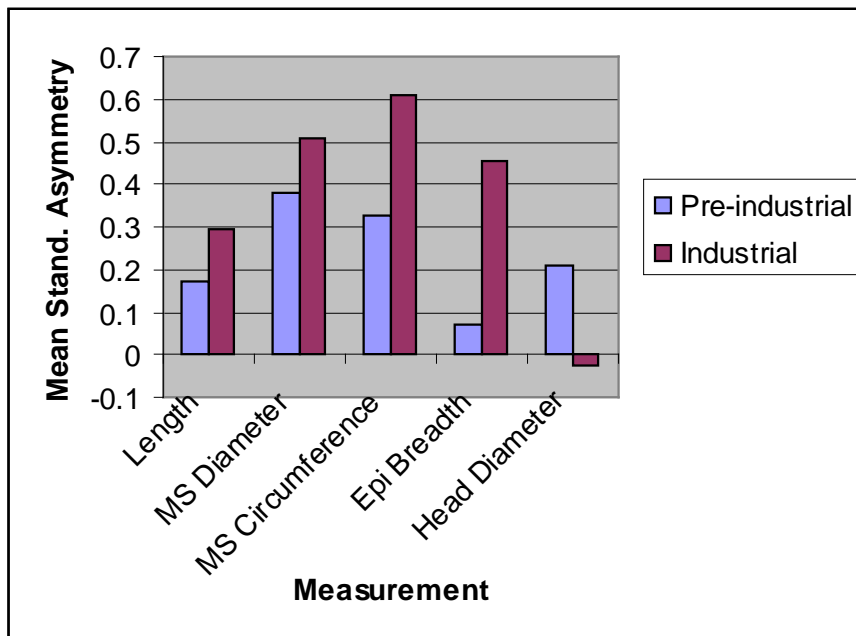


Figure 4.10: Median standardized asymmetry of all individuals from British sites for factor = time period

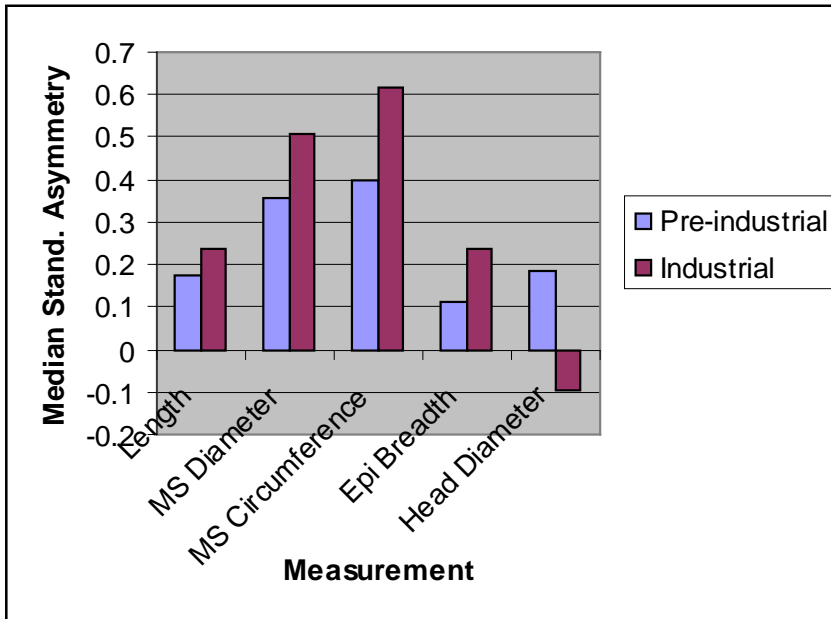


Table 4.16: Standardized asymmetry for all individuals from British sites - Results of t-test for factor = time period

Measurement	df	t	p
Length	241	-1.216	0.225
Midshaft Diameter	410	-0.606	0.545
Midshaft Circumference	409	-1.495	0.136
Epicondylar Breadth	114	-1.550	0.124
Head Diameter	42	0.738	0.465

Table 4.17: Standardized asymmetry of all individuals from British sites - Results of Mann-Whitney U-test for factor = time period

Measurement	Population	Mann-Whitney U	Z	p
Length	Pre-industrial	1083.500	-0.925	0.355
	Industrial			
Midshaft Diameter	Pre-industrial	1611.500	-1.639	0.101
	Industrial			
Midshaft Circumference	Pre-industrial	1361.500	-2.874	0.004
	Industrial			
Epicondylar Breadth	Pre-industrial	458.500	-0.959	0.338
	Industrial			

Table 4.18: Mean and median absolute asymmetry of all individuals from British sites for factor = time period

Period		Measurement				
		Length	Midshaft Diameter	Midshaft Circumference	Epicondylar Breadth	Head Diameter
Pre-industrial	Mean	0.26667	0.79490	0.72718	0.46134	0.44566
	Median	0.22500	0.61950	0.63300	0.39100	0.41800
	N	232	386	385	109	41
	Stand. Dev.	0.250253	0.792836	0.647527	0.420839	0.360572
Industrial	Mean	0.38300	1.01769	0.96388	0.63071	0.16900
	Median	0.32500	0.92250	0.92600	0.37600	0.19500
	N	11	26	26	7	3
	Stand. Dev.	0.280685	0.732366	0.849460	0.438469	0.355117

Figure 4.11: Mean absolute asymmetry measurements of all individuals from British sites for factor = time period

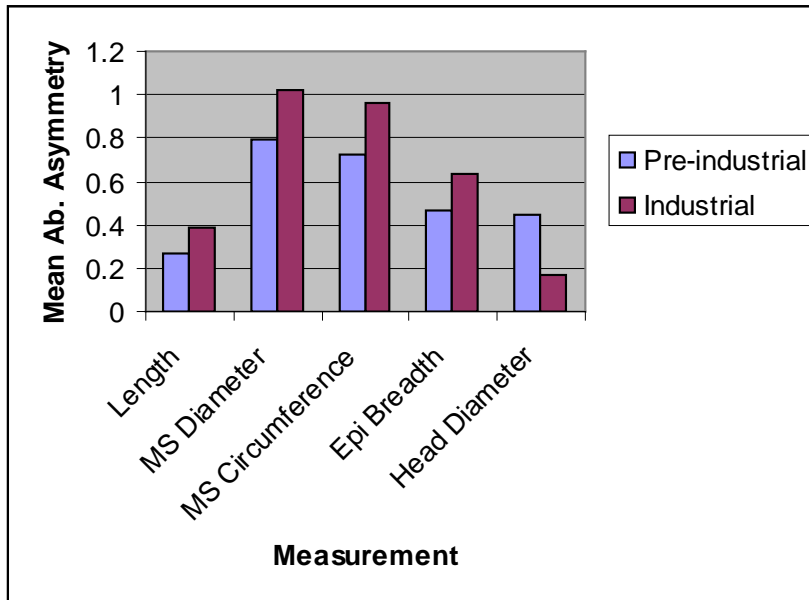


Figure 4.12: Median absolute asymmetry measurements of all individuals from British sites for factor = time period

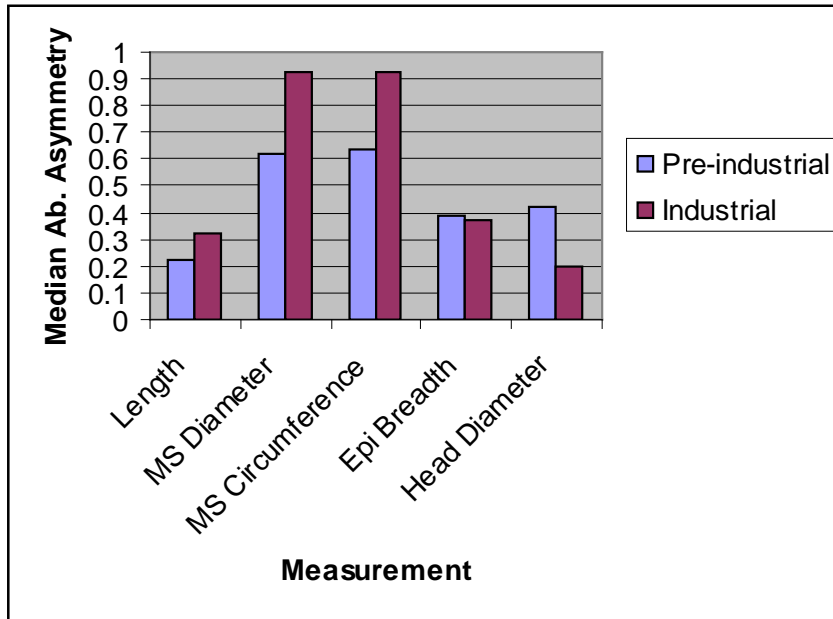


Table 4.19: Mean absolute asymmetry of all individuals from British sites - Results of t-test for factor = time period

Measurement	df	t	p
Length	241	-1.499	0.135
Midshaft Diameter	410	-1.393	0.164
Midshaft Circumference	409	-1.766	0.078
Epicondylar Breadth	114	-0.991	0.324
Head Diameter	42	1.314	0.196

Table 4.20: Median absolute asymmetry for all individuals from British sites - Results of Mann-Whitney U-test for factor = time period

Measurement	Population	Mann-Whitney U	Z	p
Length	Pre-industrial	922.500	-1.561	0.118
	Industrial			
Midshaft Diameter	Pre-industrial	3938.500	-1.837	0.066
	Industrial			
Midshaft Circumference	Pre-industrial	4212.000	-1.361	0.173
	Industrial			
Epicondylar Breadth	Pre-industrial	365.500	-0.186	0.853
	Industrial			
Head Diameter	Pre-industrial	34.000	-1.280	0.200
	Industrial			

The final factor that was observed was differences in standardized and absolute asymmetry between males and females. In order to reduce the possibility of any confounding factors from age affecting results, all individuals below the age category of 13-17 years were eliminated from analysis. This age category was chosen for several reasons, including the knowledge that sex can be reliably determined in the skeleton once puberty is reached. Also, from a biomechanical perspective, adolescents are likely to have been involved in similar activities as adults. This hypothesis is supported by results outlined above, indicating that the 13-17 year age category exhibits similar asymmetry to adults. A Mann-Whitney U-test and an independent samples t-test indicate there is a significant difference between males and females for standardized asymmetry of midshaft circumference (Tables 4.21, 4.22; Figures 4.13, 4.14). Similarly, a t-test indicates significant differences between males and females were observed for absolute asymmetry of both midshaft diameter and midshaft circumference (Table 4.24; Figure 4.16). A Mann-Whitney U-test for median data also reveals a significant difference between sexes for midshaft circumference (Table 4.23) with males being more asymmetrical than females (Figure 4.15).

Table 4.21: Standardized asymmetry of individuals older than 13 years - Results of a Mann-Whitney U-test for factor = sex

Measurement	Sex	N	Median	Mann-Whitney U	z	p
Length	Male	38	0.30650	454.000	-1.013	0.311
	Female	28	0.35350			
Midshaft Diameter	Male	57	0.64100	860.000	-1.694	0.090
	Female	38	0.33900			
Midshaft Circumference	Male	57	0.88500	683.000	-3.039	0.002
	Female	38	0.41650			
Epicondylar Breadth	Male	34	0.08550	299.500	-0.996	0.319
	Female	21	0.24400			

Table 4.22: Standardized asymmetry of individuals older than 13 years - Results of t-test for factor = sex

Measurement	Sex	N	Mean	Stand. Dev.	df	t	p
Length	Male	38	0.35442	0.424821	64	-0.151	0.880
	Female	28	0.36861	0.296515			
Midshaft Diameter	Male	57	0.66456	0.901272	93	1.728	0.087
	Female	38	0.37018	0.658714			
Midshaft Circumference	Male	57	0.80926	0.873330	93	2.755	0.007
	Female	38	0.40750	0.547510			
Epicondylar Breadth	Male	34	0.03626	0.664026	53	-0.852	0.398
	Female	21	0.17600	0.444963			
Head Diameter	Male	27	0.24470	0.487803	42	0.841	0.405
	Female	17	0.10765	0.582932			

Figure 4.13: Median standardized asymmetry measurements of individuals older than 13 years divided for factor = sex

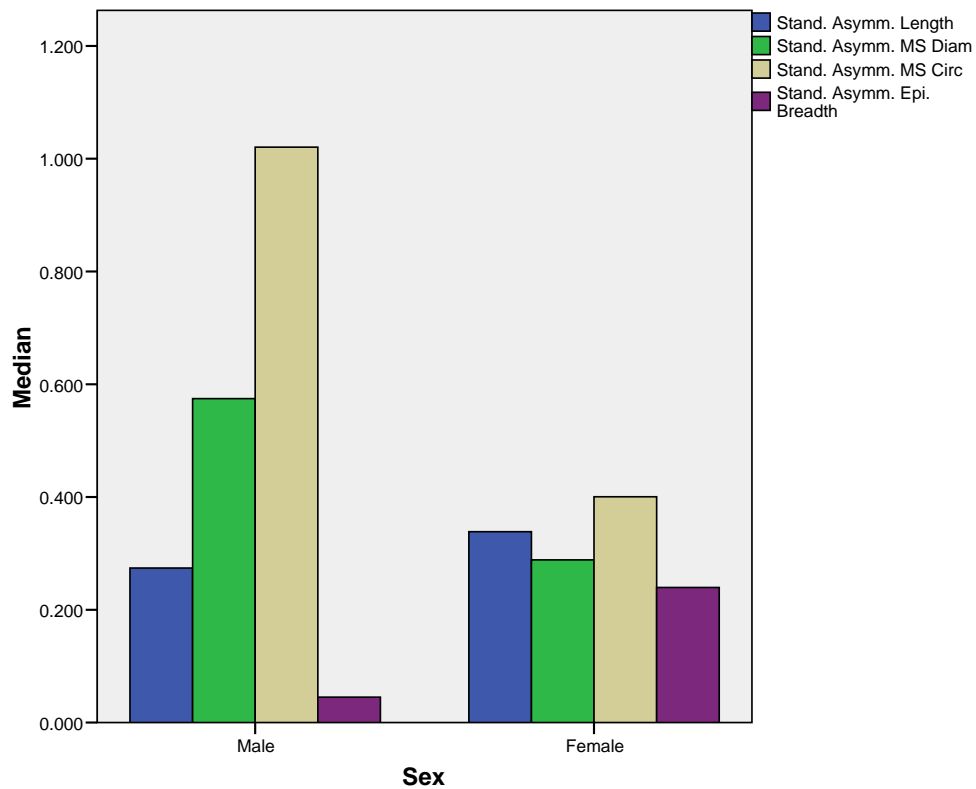


Figure 4.14: Mean standardized asymmetry measurements of individuals older than 13 years for factor = sex

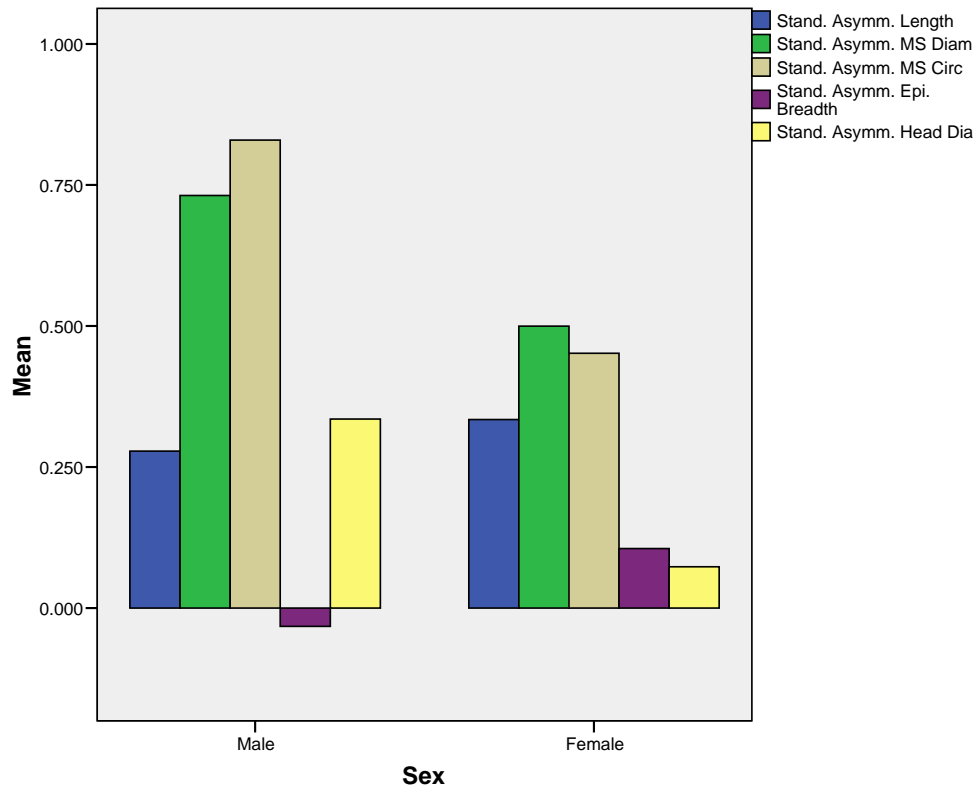


Table 4.23: Median absolute asymmetry of individuals older than 13 years - Results of Mann-Whitney U-test for factor = sex

Measurement	Sex	N	Median	Mann-Whitney U	z	p
Length	Male	38	0.31050	426.500	-1.370	0.171
	Female	28	0.37800			
Midshaft Diameter	Male	57	0.71500	858.500	-1.750	0.088
	Female	38	0.47500			
Midshaft Circumference	Male	57	1.02000	555.000	-4.012	0.000
	Female	38	0.43850			
Epicondylar Breadth	Male	34	0.36500	315.000	-0.728	0.467
	Female	21	0.35200			
Head Diameter	Male	27	0.44500	197.000	-0.783	0.433
	Female	17	0.26800			

Table 4.24: Mean absolute asymmetry of individuals older than 13 years - Results of t-test for factor = sex

Measurement	Sex	N	Mean	Stand. Dev.	df	t	p
Length	Male	38	0.37489	0.406372	64	-0.467	0.642
	Female	28	0.41461	0.224853			
Midshaft Diameter	Male	57	0.87775	0.691092	93	2.424	0.017
	Female	38	0.58997	0.466012			
Midshaft Circumference	Male	57	1.04354	0.566460	93	4.983	0.000
	Female	38	0.54818	0.402099			
Epicondylar Breadth	Male	34	0.50185	0.427549	53	1.132	0.263
	Female	21	0.38314	0.276367			
Head Diameter	Male	27	0.44263	0.310931	42	0.369	0.714
	Female	17	0.40165	0.425111			

Figure 4.15: Median absolute asymmetry measurements of individuals older than 13 years for factor = sex

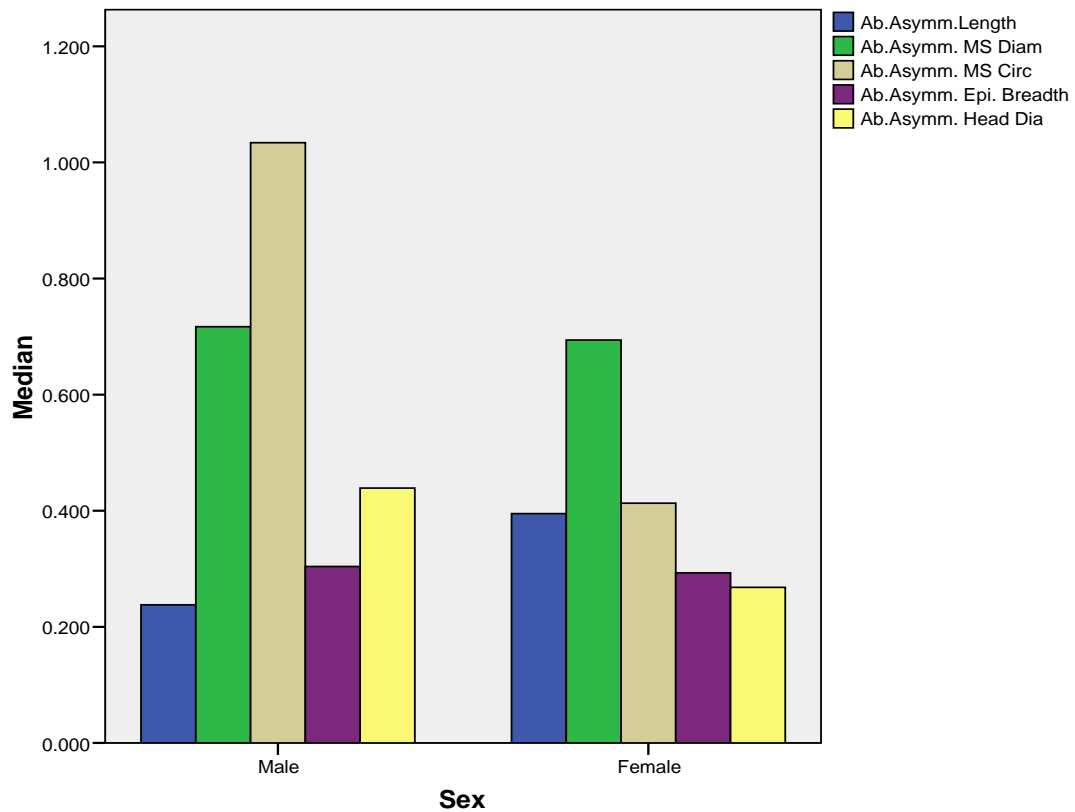
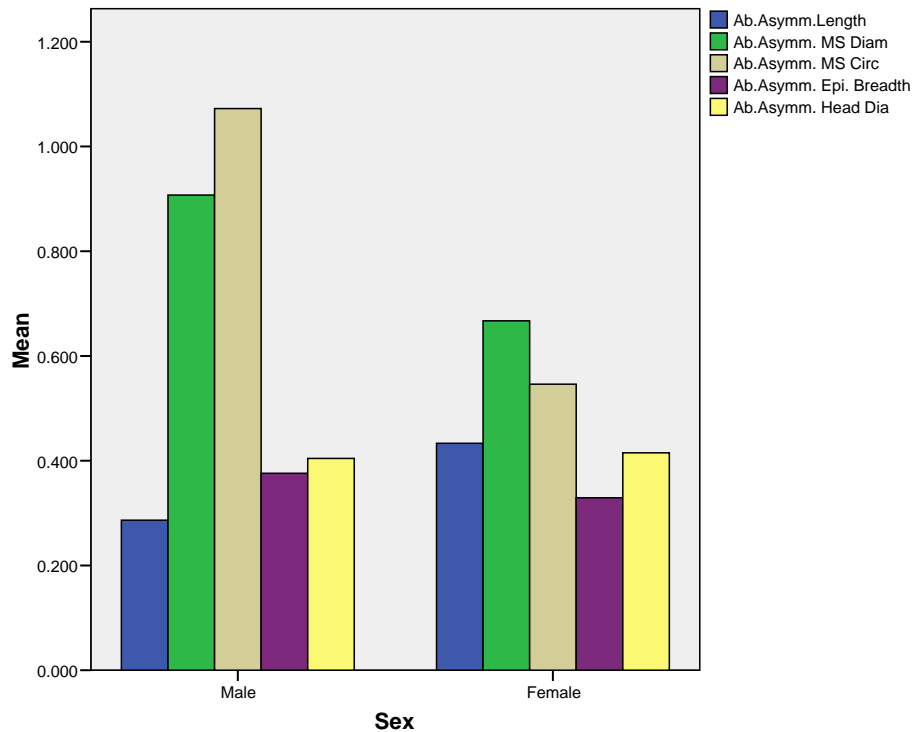


Figure 4.16: Mean absolute asymmetry measurements of individuals older than 13 years for factor = sex



3D Data:

Similar analyses were performed on the 191 2D circumference measurements obtained from the 3D data. Observation of standardized asymmetry trends reveals a tendency for left-sidedness between birth and 5-8 years of age (Table 4.25; Figures 4.17 & 4.18). Kruskal-Wallis and ANOVA results indicate that there is a significant difference between age categories for both standardized and absolute asymmetry measurements (Tables 4.26, 4.27). While post-hoc tests for standardized asymmetry indicate that significant differences exist between 5-8 year olds and the oldest two age categories, with the exception of a difference between the foetus and neonate categories, there are no specific inter-age differences for absolute asymmetry (appendix). As with the traditional measurements, the sample was divided according to time period. Results of a Mann-Whitney U-test and an independent samples t-test were not found to be significant

although the industrial population did exhibit stronger asymmetry than the pre-industrial group (Tables 4.28 - 4.30; Figures 4.21 & 4.22). Finally, t-tests comparing males and females reveal a significant difference for absolute but not standardized asymmetry, contrary to what was found in analyses of the traditional measurements (Table 4.31 – 4.33; Figures 4.23 & 4.24).

Table 4.25: Asymmetry of 3D circumference data for factor = age (N = number of individuals; negative means indicate left-sidedness)

Age Category	N	Standardized Asymmetry			Mean Absolute Asymmetry		
		Mean	Stand. Dev.	Median	Mean	Stand. Dev.	Median
Foetus	2	2.03055	0.475968	2.03055	2.03050	0.475883	2.03050
Birth -1 month	5	-1.80271	1.677101	-2.32558	2.02300	1.326815	2.32600
1-12 months	17	-0.27535	1.956177	-0.71206	1.43324	1.313061	0.99600
1-4 yrs	24	-0.21227	1.844266	-0.09914	1.50596	1.040239	1.55950
5-8 yrs	28	-0.40782	1.448874	-0.14797	1.18204	0.907090	1.13750
9-12 yrs	29	0.27609	1.189772	0.31944	0.86186	0.851737	0.70800
13-17 yrs	31	1.01004	1.278518	1.31166	1.44326	0.732476	1.49600
Adult 18+	55	0.75240	1.148156	0.64647	1.08656	0.832078	0.86100

Figure 4.17: Mean standardized asymmetry of 3D circumference data for factor = age

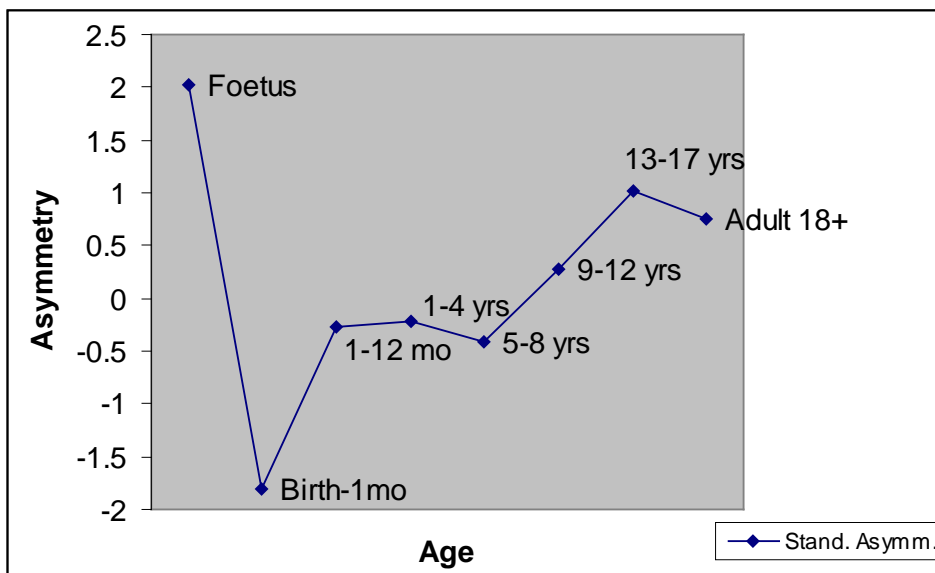


Figure 4.18: Median standardized asymmetry of 3D circumference data for factor = age

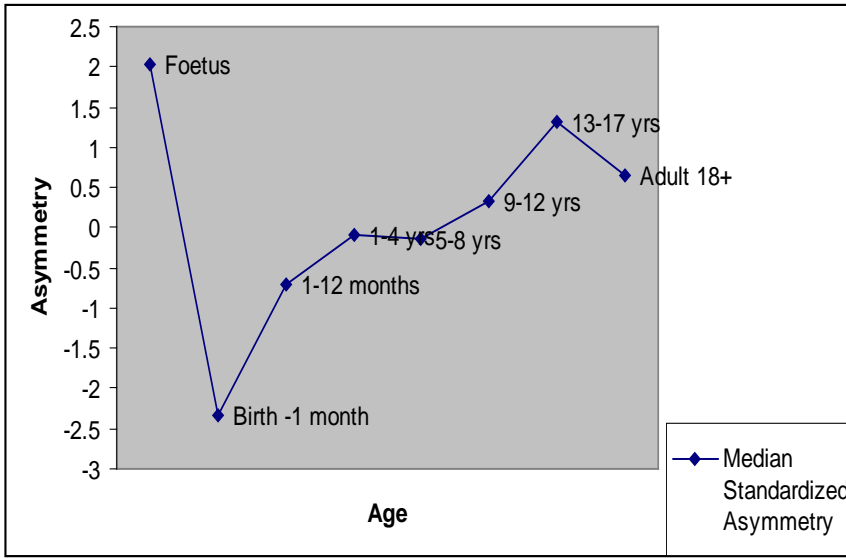


Figure 4.19: Mean absolute asymmetry of 3D circumference data divided for factor = age

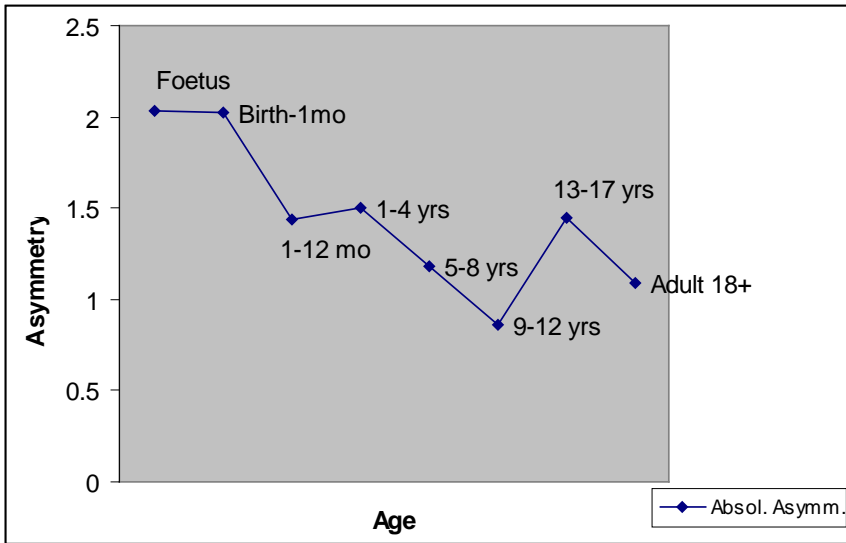


Figure 4.20: Median absolute asymmetry of 3D circumference data for factor = age

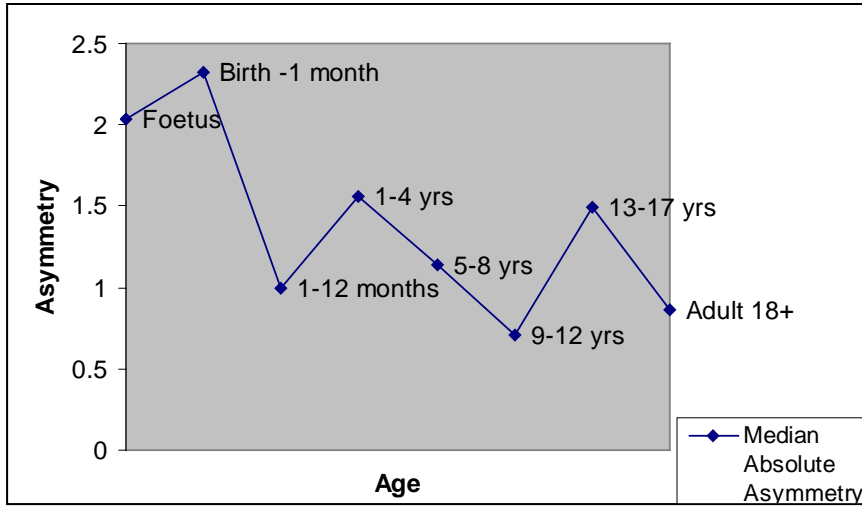


Table 4.26: Results of Kruskal-Wallis test – 3D circumference asymmetry for factor = age

	df	Chi-square	p
Standardized asymmetry	7	35.928	0.000
Absolute asymmetry	7	17.059	0.017

Table 4.27: Results of ANOVA – 3D circumference asymmetry for factor = age

	df	F	p
Standardized asymmetry	190	5.756	0.000
Absolute asymmetry	190	2.260	0.031

Table 4.28: Asymmetry of 3D circumference data for factor = time period

Time period	N	Standardized asymmetry			Absolute Asymmetry		
		Mean	Stand. Dev.	Median	Mean	Stand. Dev.	Median
Pre-industrial	175	0.22696	1.467179	0.42609	1.19691	0.873878	1.09200
Industrial	16	0.92723	2.107793	0.67530	1.73863	1.461455	1.41250

Figure 4.21: Mean and median standardized asymmetry of 3D circumference data for factor = time period

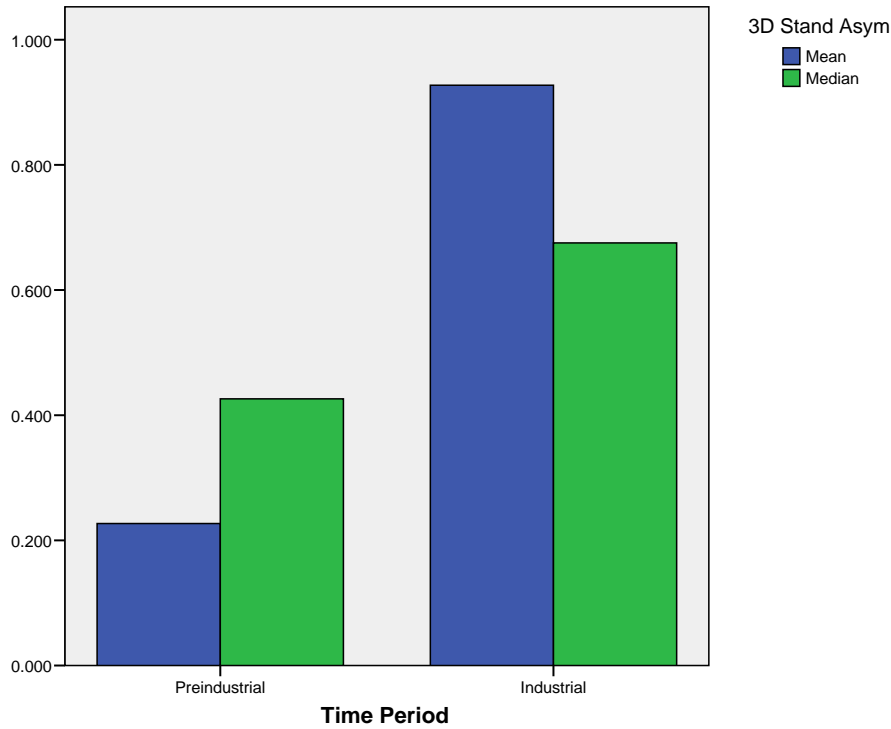


Figure 4.22: Mean and median absolute asymmetry of 3D circumference data for factor = time period

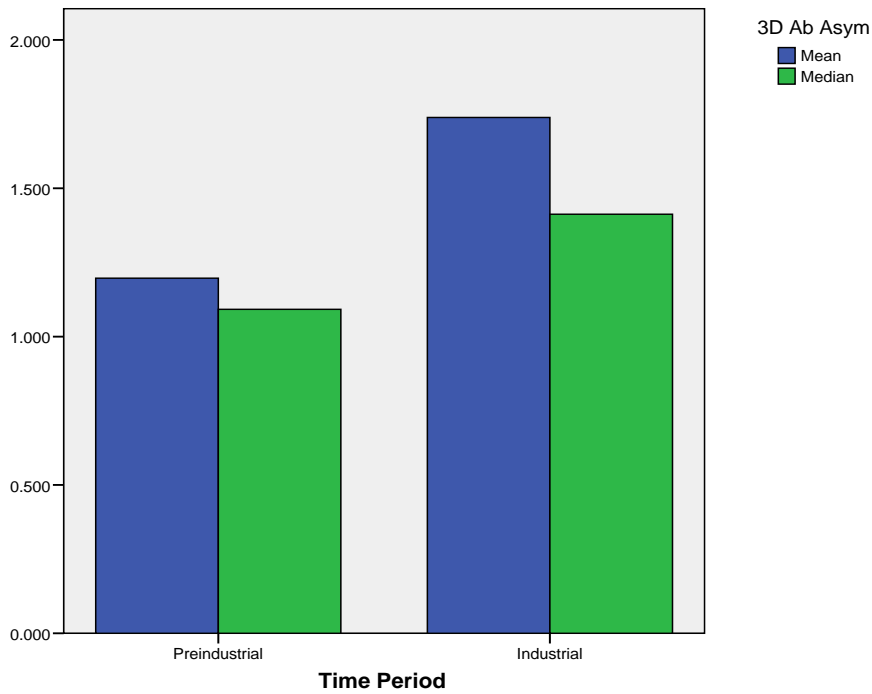


Table 4.29: 3D circumference asymmetry - Results of Mann-Whitney U-test for factor = time period

	Mann-Whitney U	Z	p
Standardized asymmetry	1029.000	-1.755	0.079
Absolute asymmetry	1013.500	-1.829	0.067

Table 4.30: 3D circumference asymmetry - Results of t-test for factor = time period

	df	t	p
Standardized Asymmetry	189	-1.300	0.211
Absolute asymmetry	189	-1.459	0.164

Table 4.31: Asymmetry of 3D circumference data for factor = sex

Sex	N	Standardized asymmetry			Absolute Asymmetry		
		Mean	Stand. Dev.	Median	Mean	Stand. Dev.	Median
Male	38	0.82266	1.320345	1.05533	1.34034	0.770336	1.23050
Female	25	0.50962	0.956012	0.39742	0.73240	0.791051	0.46000

Table 4.32: 3D circumference asymmetry of individuals above the age of 13 years - Results of Mann-Whitney U-test for factor = sex

	Mann-Whitney U	Z	p
Standardized asymmetry	367.000	-1.518	0.129
Absolute asymmetry	294.000	-2.543	0.011

Table 4.33: 3D circumference asymmetry of individuals above the age of 13 years - Results of t-test for factor = sex

	df	t	p
Standardized asymmetry	61	1.021	0.311
Absolute asymmetry	61	3.032	0.004

Figure 4.23: Standardized asymmetry trends according to 3D circumference data for factor = sex

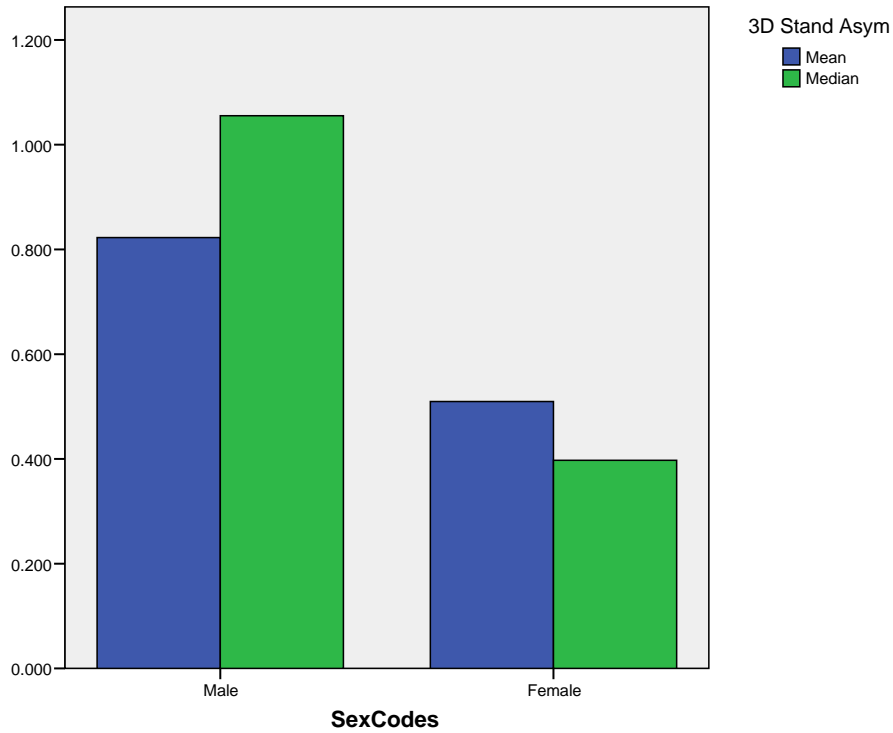
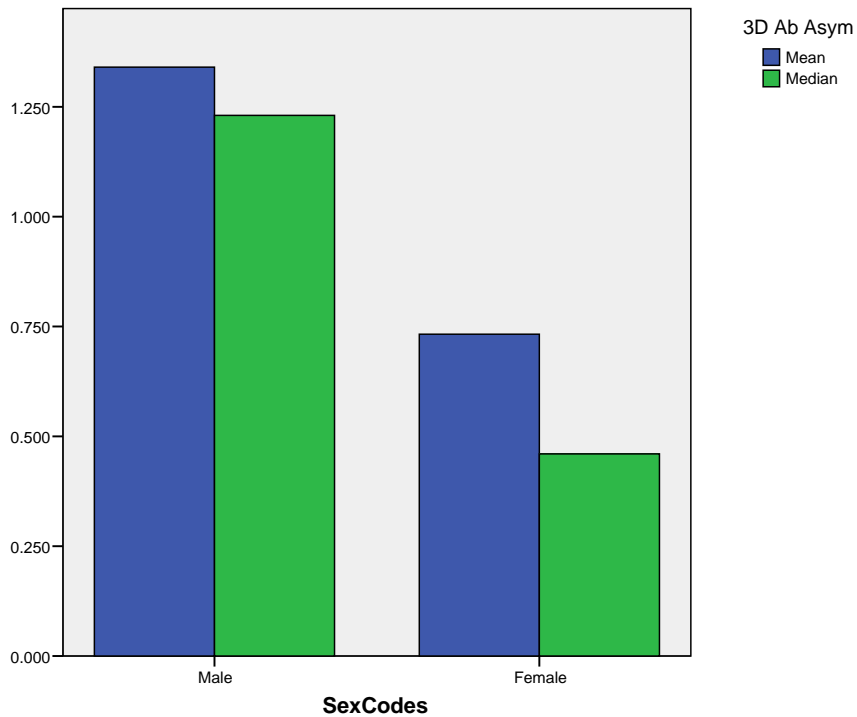


Figure 4.24: Asymmetry trends according to 3D circumference data for factor = sex



Shape Analysis:

The protocol constraints of PAST 1.51 (Hammer et al., 2001) discussed in Chapter 3 did not allow for shape analysis of all 191 midshaft cross-sections. However, a smaller comparison of asymmetry within the 5 to 8 (n = 26) and 9 to 12 (n = 28) year olds was performed. It was hypothesized that there would be a shape difference between left and right sides due to differential usage. Further shape differences were predicted between the two age groups based on the results outlined above; specifically that the differences between the left and right side undergo a transition to predominantly right-sidedness after the age of eight. Results of Multiple Analysis of Variance (MANOVA) tests reveal that in both cases there is no significant difference in shape between left and right sides (Figures 4.25 – 4.28; Table 4.34). Further analysis demonstrated no significant difference in shape of left humeri between the two age groups (Figures 4.29 & 4.30; Table 4.34). However, comparison of right humeri between the two age categories revealed that there is a significant difference in shape (Figures 4.31 & 4.32; Table 4.34).

Figure 4.25: CVA (Canonical Variates Analysis) plot of shape asymmetry in 5-8 year olds – grouped scatter plot of left and right sides demonstrating considerable overlap between the shape of the two groups.

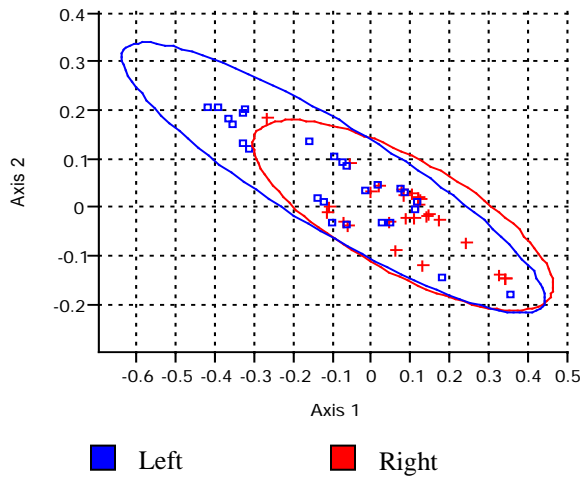


Figure 4.26: Shape outlines of left (blue) and right (red) elements for all 5-8 year olds as determined by plotting coordinates in PAST 1.51. The anomalous blue outline represents an outlier.

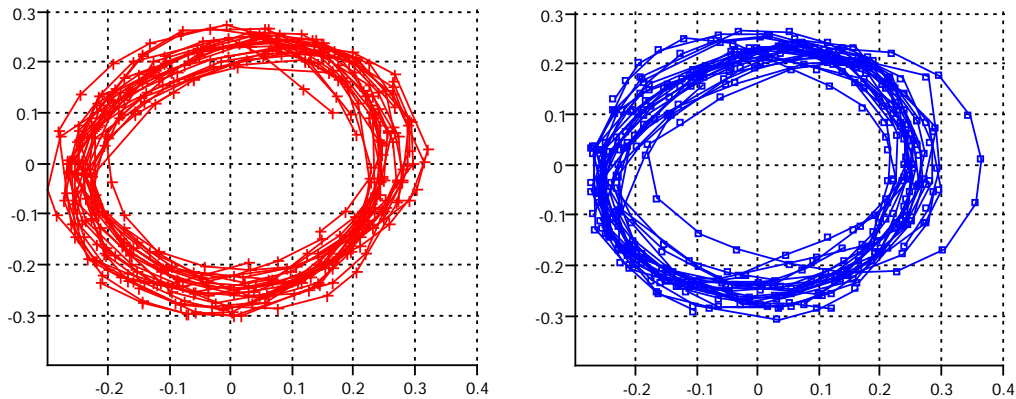


Figure 4.27: CVA (Canonical Variates Analysis) of shape asymmetry in 9-12 year olds – grouped scatter plot demonstrating considerable overlap between left and right sides.

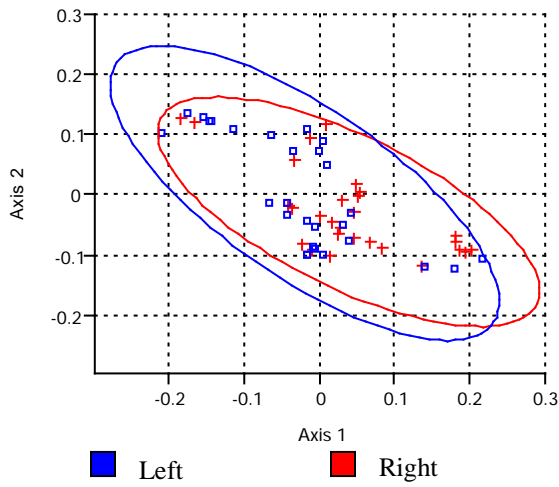


Figure 4.28: Shape outlines of left (blue) and right (red) elements for all 9-12 year olds as determined by plotting coordinates in PAST 1.51.

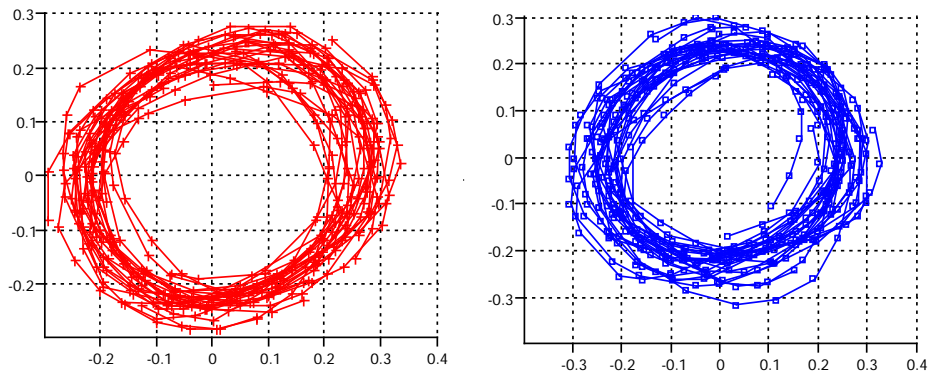


Figure 4.29: CVA (Canonical Variates Analysis) plot of shape variation between 5-8 and 9-12 year olds – scatter plot of left sides demonstrating almost complete overlap between the two groups.

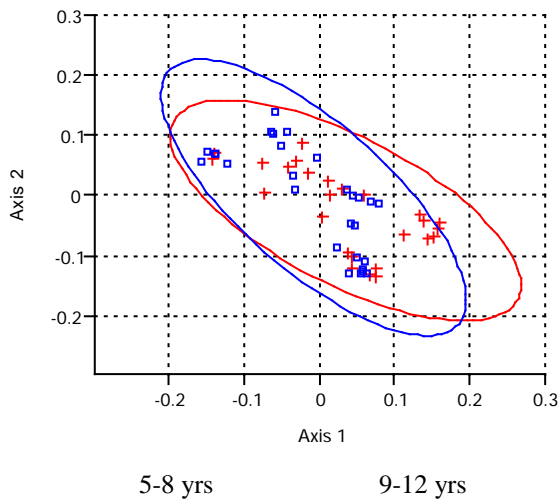


Figure 4.30: Shape outlines of 5-8 (red) and 9-12 (blue) year olds as determined by plotting coordinates in PAST 1.51.

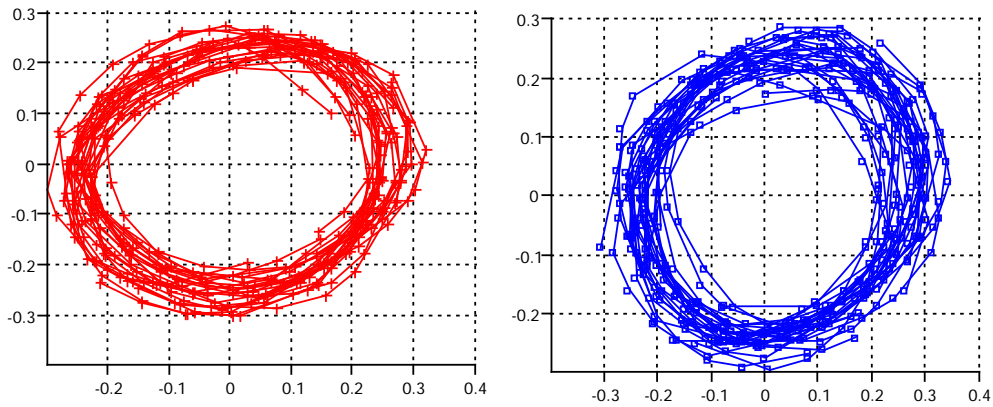


Figure 4.31: CVA (Canonical Variates Analysis) plot of shape variation between 5-8 and 9-12 year olds – scatter plot of right sides demonstrating almost complete overlap between the two groups.

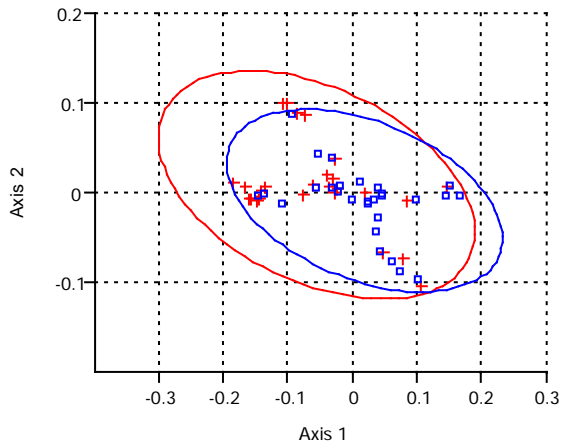


Figure 4.32: Shape outlines of 5-8 (red) and 9-12 (blue) year olds as determined by plotting coordinates in PAST 1.51.

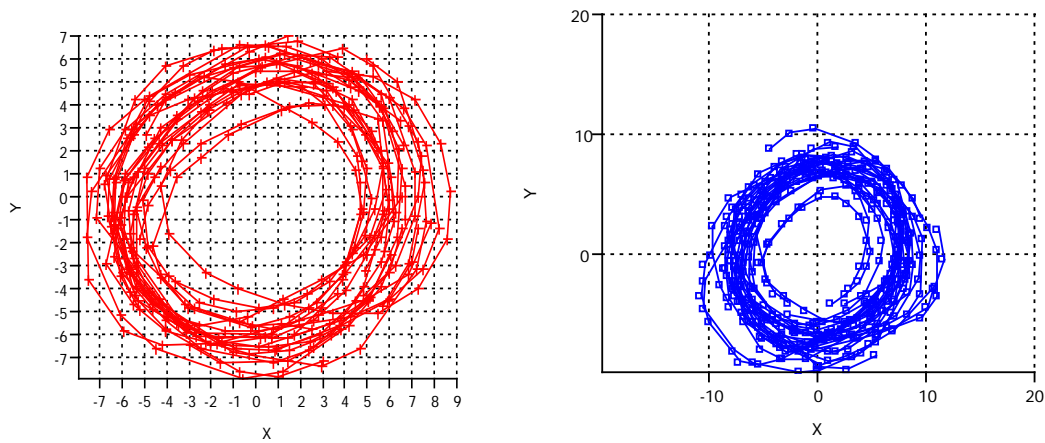


Table 4.34: Results of MANOVA tests for humeral shape variation

	Wilk's Lambda	df1	df2	F	p
5-8yrs Right vs Left	0.2380	40	11	0.8803	0.6394
9-12yrs Right vs Left	0.2273	40	15	1.275	0.3135
5-8 vs 9-12yrs Left	0.2423	40	13	1.016	0.5168
5-8 vs 9-12yrs Right	0.1205	40	13	2.372	0.0471

In summary, traditional and 3D (translated as 2D circumference) asymmetry data were tested for differences throughout growth and development, according to population, and based on sex. All of these tests revealed significant differences for some aspect of asymmetry, indicating that various factors are involved in producing this skeletal trait.

Chapter 5 - Discussion

The purpose of this project is to expand our understanding of hand preference, by applying both traditional metric and geometric morphometric techniques to help answer when bilateral asymmetry, and by proxy, handedness, appears in skeletal growth and development. It builds upon results from Blackburn (2004) which examined the correlation between hand preference and bilateral asymmetry of the epicondylar breadth of the humerus in a living population. Comparative examination of an archaeological population from Anglo-Saxon Britain revealed interesting insights into how lifestyle and physical activity can affect skeletal asymmetry. This work demonstrated that the upper limbs of modern North Americans are more asymmetrical than rural Anglo-Saxons, a result that suggests the archaeological population was engaged in ambidextrous activities, perhaps as a result of an agricultural lifestyle.

Although the development of behavioural handedness has been observed in children (Butterworth & Hopkins, 1993; Ramsay, 1980), how it presents in the skeleton throughout growth is unclear. However, based on what is understood of biomechanics and the fluctuating hand preference in young children, it was predicted that non-adult skeletons would exhibit different patterns of bilateral asymmetry than their adult counterparts. It was hypothesized that this could be observed as either left-sided dominance or symmetry between the two humeri. Alternately, if there was no difference in bilateral asymmetry between the adult and non-adult segments of the populations this could suggest that the trait is subject to strong genetic control. This does not necessarily negate the well-established hypothesis that hand preference is genetically determined

(Annett, 2002; Corballis, 1997; Francks et al., 2007; Hopkins, 2006), it merely suggests that asymmetry of the humerus does not reflect this genetic predisposition.

General Asymmetry Trends

As previously outlined, approximately 90% of individuals exhibit a preference for using their right hand. Therefore, if skeletal asymmetry of the upper limb directly reflects handedness we would expect right-sided asymmetry in 90% of observed individuals. The correlation between these two traits is not 1:1 however, due to complicating factors such as activity related skeletal change. Interestingly, not all measurements reflect hand preference with equal accuracy and in many individuals one measurement will suggest right-handedness while another will indicate left-handedness. Results from the present study indicate that maximum length of the humerus may be the most accurate predictor of hand preference, as 82.8% of all individuals in the pooled sample (British and North American) were right dominant for this trait. This measurement most closely resembled actual handedness proportions, especially those for relative hand skill (Annett & Kilshaw, 1983), followed by midshaft circumference and midshaft diameter. Head diameter and epicondylar breadth were the least consistent with known handedness proportions. This is somewhat contrary to work by Auerbach and Ruff (2006) which found diaphyseal breadth to be a better predictor of hand preference than humeral length. Such discrepancies could result from sample variation.

Length is affected by biomechanical forces throughout growth but ceases to be influenced by these environmental factors once skeletal maturity is reached (Steele & Mays, 1995). Midshaft dimensions, however, are very susceptible to biomechanical

modification throughout life. As such, these measurements are a direct reflection of ongoing physical activity and, hence, a right-hand preference. Finally, although the epicondylar breadth and head diameter (the two measurements which represent the distal and proximal ends respectively) are not as strongly right-sided as the other measurements, they still exhibit less left-sided asymmetry than would be expected through chance. It is possible that this reflects different patterns of activity that affect these areas of the humerus rather than the midshaft. Activities affecting the head of the humerus include anything requiring use of the muscles around the shoulder, including those of the rotator cuff. It should be noted though, that articular surface dimensions do remain relatively unchanged once epiphyseal fusion has occurred (Ruff et al., 1991; Humphrey, 1998; Lieberman et al., 2001) The epicondylar breadth is affected by movements of the elbow, such as flexion, extension, pronation, and supination. Therefore, these results could reflect a trend towards using the right arm less frequently in movements which place strain on the distal and proximal ends. In future research it may be more beneficial to divide the epicondylar breadth into articular and non-articular areas so that the medial and lateral epicondyles and the trochlea and capitulum are examined independently. In this manner it may be possible to discern differences in asymmetry resulting from muscle attachments (epicondyles) and those related to joint action (trochlea and capitulum). As articular surfaces tend to change little once physical maturity is reached (Knüsel, 2000a), it would be predicted that the non-articular areas would exhibit more asymmetry related to handedness, especially in adult skeletons.

More detailed analyses of the results of this study will lend some interesting insights with respect to age, sex, and activity patterns. Identifying the manner in which

these variables affect bilateral asymmetry of the humerus will, by proxy, help our understanding of how handedness presents in the skeleton.

Age-related Asymmetry Trends

When examining mean asymmetry for each measurement by age category, a statistically significant trend was observed between the younger and older age categories. For mean length and circumference the sampled skeletal populations exhibited left-sidedness from the foetal stage until the end of the first month, and until the end of the first year according to the epicondylar breadth. A similar trend is present in the median data although it demonstrates symmetry until approximately 1-12 months for all measurements except epicondylar breadth which is left-sided. While some previous studies (both skeletal and behavioural) have found right-sided asymmetry early in development (Bareggi et al., 1994; Pande & Singh, 1971), much of that research is based on samples younger (i.e. embryonic) than those found in the current work.

Interestingly, results are not inconsistent with what is known about the development of behavioural handedness exhibited in young children. In general, children tend to begin demonstrating hand preference between 18 and 24 months of age. This coincides with the development of spoken language and suggests a correlation between this trait and handedness (Butterworth & Hopkins, 1993; Ramsay, 1980). Although results from the metric analysis demonstrate a change from left-sidedness to right-sidedness before 18-24 months, it is noteworthy that following this change asymmetry goes through a period which does not deviate greatly from zero (symmetry). From a biomechanical perspective, this is precisely what would be expected if there was no hand

preference or if that preference continually shifted back and forth during a short period of time, which is exactly what occurs in young children. Furthermore, the changes in asymmetry throughout growth indicate that this trait is most likely based on biomechanical modifications rather than being genetically based. It does not, however, rule out the possibility that asymmetry could be influenced by certain intrinsic forces, such as hormonal changes altering set-points (Frost, 1987), occurring throughout growth and development, and indeed, this research does not serve as a direct test of these intrinsic factors.

Further investigation of age-related changes in bilateral asymmetry was performed using 3D data. Results from both the mean and median data were found to both corroborate and refine those trends identified with traditional circumference measurements, by demonstrating left-sidedness between birth and 8 years. Two aspects of this trend are of particular note. The first is the lack of left-sided asymmetry among the foetal age category which is most probably due to the fact that this group only consists of 2 individuals as compared to 20 in the traditional measurements. Therefore, it is possible that if the sample size was increased, left-sidedness would be observable among the foetal category as well. The presence of left-sided asymmetry until the 5-8 year age category also warrants further attention. Based on what was discussed regarding the onset of handedness in children, it would seem that at a population level this is far too late to be exhibiting anything other than right-handedness. However, it has been demonstrated that while hand preference first emerges towards the end of the second year, it can fluctuate until the age of 8 years (Corballis, 1983). This strongly supports the conclusions previously reached, specifically that skeletal asymmetry matches what can be observed in

children behaviourally because of biomechanical influences. Additionally, in medieval Britain males over the age of 12 years were subjected to all the physical demands of adulthood (Härke, 1997), so these results could also reflect a change from child to adult behaviour. It was possible to refine these results because the measurements obtained from the 3D data are more precise than those obtained from traditional measurement techniques, with 3D measurements being taken to 2 decimal places and traditional circumference measurements only to the nearest millimetre. Because of this increased precision, we again have osteological evidence that supports behavioural evidence of handedness.

The final aspect of humeral morphology that was examined with regard to age related changes was shape. This analysis focused specifically on the transition between 5-8 and 9-12 year olds as this is a key time in the development of handedness and bilateral asymmetry. Although there is no significant difference in shape between the left and right sides within age categories, the right humeri varies in shape between the older and younger age categories. These results indicate that asymmetry of size and shape may be related, although they do not appear to be perfectly correlated otherwise shape differences would exist among the other variables as well. However, this does suggest that once right-handedness is strongly established, as it is in the 9-12 year olds, this trait can be detected in shape differences. While it might be expected that differences in shape should exist in the left humerus also, as it exhibits size dominance in the 5-8 year olds, it is possible that left-hand usage is less consistent and, subsequently, does not result in significant shape changes. So, while biomechanical influences may result in size asymmetry, shape asymmetry remains relatively constant, at least in the age categories

examined. Unfortunately, the current work is limited in that it cannot make inferences regarding shape change throughout growth and development in its entirety.

There is one alternate possibility for why there is increased left-sidedness in infants and young children. This trend could support the hypothesis that bilateral asymmetry is caused by what has been termed “pathological left-handedness” (O’Callaghan et al., 1993a; 1993b; Satz et al., 1985). As pathological left-handedness is correlated with factors such as low birth weight, these infants would be less likely to survive, especially in the past when medical care was poor. Therefore, left-sidedness would be expected in foetal and neonate skeletons just as is demonstrated in the present study, although the persistence of left-sidedness into older ages seems anomalous. However, pathological left-handedness is not synonymous with death but it certainly would be associated with decreased fitness and, as such, these individuals would be more likely to die at younger ages. This is consistent with the fact that, by their very nature, these individuals represent the non-survivors of their respective groups and may not be representative of the typical population. The Native Point sample has the potential to overcome this obstacle as evidence suggests that the Sadlermiut may have been practicing female infanticide (Holland, 2007). If this was indeed the case, then this population can be considered free of the complicating factor of pathological left-handedness. As predicted, results indicate that the Sadlermiut exhibit similar patterns of bilateral asymmetry as seen in the British populations, indicating that the asymmetry patterns observed early in growth and development may not be the result of pathology. It must be cautioned, however, that accurately assigning sex to non-adult skeletal remains is problematic as much sexual dimorphism does not occur until puberty (Scheuer & Black,

2004). Holland (2007) also points out that if high infant mortality resulted from infanticide one would expect a larger number of individuals to be neonates, rather than being pooled in the 1-12 month age category. Because of these issues, the effects of pathological left-handedness cannot be definitively ruled out.

Population Variations in Asymmetry

When examining bilateral asymmetry in skeletal populations it is important to take the nature of the population into account. As outlined above, Blackburn (2004) demonstrated the necessity of considering what types of activities the population would have been engaged in. This is an important factor to be aware of as bilateral asymmetry is easily influenced by activity, but it is difficult to identify exactly what type of activity was actually performed. For example, with the exception of pathologically induced asymmetry, strong bilateral asymmetry suggests a high level of physical activity, a hypothesis which was supported by work with a modern population where both handedness and activity level were known (Blackburn & Knüsel, 2006). It seems reasonable to assume then, that a lack of asymmetry would indicate a somewhat inactive lifestyle. However, weak bilateral asymmetry can also be caused by using both arms almost equally as would occur in an individual who is either naturally ambidextrous or forced to use both of their arms in certain repetitive tasks. Because of these contradictory explanations, any conclusions drawn from bilateral asymmetry must remain tentative and interpretations are much more reliable when the context of the skeletal population is understood.

The majority of the samples in the present study are from British archaeological sites, spanning a period from the 1st century B.C. to the 19th century A.D., although most date to the medieval era. Therefore, the greatest part of this skeletal population can be considered genetically homogeneous, with the exception of the Sadlermiut sample from Nunavut. A comparative analysis of all skeletal populations was performed, the implications of which shed some light on how bilateral asymmetry presents in different environments and time periods.

The most obvious comparison is between the British populations and the Sadlermiut, not only because of differing ancestral backgrounds, but because the two groups would have had wholly different lifestyles and activity patterns. Furthermore, Merbs (1983) describes the Sadlermiut as performing a variety of left-handed tasks. This included “the apparent use of the left hand and wrist as a pivot in kayak-paddling by the males, use of the left hand in cutting skins by the females, and the holding of skins in the left hand by the women while they softened them with their teeth” (Merbs, 1983:184). However, analysis revealed no significant difference in standardized asymmetry between the two groups. Perhaps a more adult-inclusive study would have demonstrated results consistent with the activities Merbs (1983) described. Not only is the present study focused on non-adults, but the large majority of the Native Point sample consists of individuals less than one year of age, with the exception of head diameter and epicondylar breadth measurements for which most individuals were either adult or older than 5 years. Therefore, much of the sample would have been far too young to engage in anything other than typical infant behaviour. Nevertheless, these results support the notion that all human populations have a propensity for right-handedness, irrespective of

ancestry or environment (Coren & Porac, 1977; Faurie *et al.*, 2005). Although skeletal asymmetry is not as direct as observation of modern populations, or historical depictions of right-hand use (Coren & Porac, 1977), it does provide strong evidence in support of this hypothesis.

Comparing the British and Sadlermiut populations in terms of absolute asymmetry reveals that for most measurements there is no difference between the two groups. However, degree of asymmetry in the epicondylar breadth and midshaft circumference does differ significantly, with the British being more asymmetrical than the Sadlermiut. This suggests that the Sadlermiut may have been performing more bimanual activities whereas the British populations were favouring one hand. The humeral midshaft is strongly influenced by biomechanical forces and serves as the attachment site for the deltoid muscle which is involved shoulder movement and rotation. In the distal humerus, the medial and lateral epicondyles serve as attachment sites for the ulnar collateral ligament, pronator quadratus, pronator teres, the common flexor tendon, supinator, and the common extensor tendon. Therefore, this region of the humerus is strongly influenced by movements of the hand and wrist. As the epicondylar breadth appears to have been better preserved in older individuals, in both the British and Sadlermiut samples, this measurement was primarily obtained from adolescents and adults. Therefore, these asymmetry trends were not caused by infant behaviour, as predicted in the hypotheses. The Sadlermiut remain a somewhat poorly understood population, but historical accounts coupled with archaeological evidence, including harpoons, kayak rests, and kayak lances, points to a strong emphasis on marine subsistence (Boas, 1901; Comer, 1910; Lyon, 1825; Mathiassen, 1927). The motions

associated with paddling a kayak could be enough to produce the type of asymmetry present in this group, with both arms being subject to a considerable amount of activity. Although it might be expected that the epicondylar breadth should be left-sided based on the historical descriptions of kayak use (i.e. using the left-hand as a pivot) the trend towards symmetry may actually be more consistent with a population who consistently uses their left hand for certain specialized tasks but is otherwise right-handed. Therefore, a lack of asymmetry in both the midshaft circumference and the epicondylar breadth could quite possibly have been caused by kayak paddling. However, it should be noted that while the pooled British sample has more asymmetrical epicondylar breadths than the Sadlermiut, when examined independently, several individual sites (Ancaster, Wharram Percy) exhibit a similar level of asymmetry as the Native Point sample. As stated previously, any attempt to link skeletal asymmetry to specific activities must be done tentatively.

To identify any patterns of asymmetry that may be temporally based, both the traditional measurement and 3D circumference data for the British populations was collapsed under two main categories: pre-industrial and industrial. With regard to the traditional metric data, a t-test indicates a significant difference in midshaft circumference with the industrial population being more strongly right-sided than the pre-industrial population. Although t-test or Mann-Whitney U-test results did not indicate any significant temporal differences with respect to absolute asymmetry, a slight trend toward stronger asymmetry in the industrial population (Wolverhampton) for all measurements except head diameter was noted. Interestingly, these results are contrary to what was

hypothesized, with asymmetry expected to be less pronounced in the industrial population.

The same analysis using the 3D circumference data demonstrated the same trends as noted above, with the industrial group being more asymmetrical than the pre-industrial population. Although a statistically significant difference between time periods is not present, it is possible that this results from a small sample size among the industrial group. As such, the trends noted suggest that the later population was performing laborious unimanual tasks. During the pre-industrial period, technology and lifestyle would have remained much the same and, subsequently, the activities performed would have changed little. Commencing in the 18th century however, the Industrial Revolution transformed the face of Britain and resulted in drastic changes in lifestyle, occupation, and health. Populations moved out of rural areas and crowded into towns and cities, often living in squalid conditions (Steckel & Floud, 1997). In Wolverhampton, mining of limestone and iron prevailed as a staple in the local economy until mechanization increased, leading to many individuals, both adults and children, being employed in factories. Health among this population was quite poor, most likely resulting from a combination of filthy living conditions in the town and unsafe work environments (Arabaolaza et al., 2006). This pronounced alteration in lifestyle can be seen not only in skeletal pathology and high infant mortality (Arabaolaza et al., 2006), but in a change in bilateral asymmetry of the humerus. Undoubtedly individuals working either in mines or factories are subject to a large amount of physical labour. Furthermore, many individuals commenced this type of work as children, which would result in even more skeletal change. This is consistent with what has been documented in people who play racquet sports or engage in physical

labour before reaching skeletal maturity. Individuals who begin these activities when they are children exhibit much more pronounced bilateral asymmetry than individuals who start later in adolescence or adulthood (Bass et al., 2000; Blackburn & Knüsel, 2006; Kannus, 1994; Ruff, 1992). Overall, degree of bilateral asymmetry seems to reflect the monumental changes that occurred in Britain during the Industrial Revolution, although these differences are subtle and are not readily apparent in traditional measurements. This study would benefit from additional skeletal samples dating to industrial Britain and future research could focus on the differences in asymmetry that occur during this significant period in history.

Sex-related Variations in Adolescent and Adult Asymmetry

Although this study focuses primarily on the development of bilateral asymmetry in non-adults, it is important to examine how this trait is affected by intrinsic characteristics, such as sex. Therefore, examining how bilateral asymmetry varies according to sex can reveal important insights into differences in how the male and female skeleton responds to biomechanical forces, as well as sex-related activity patterns. Research regarding biomechanical modifications to the skeleton has shown that there is a difference in robusticity between males and females, partially resulting from a delay in epiphyseal fusion and the adolescent growth spurt in males (Humphrey, 1998). It has been demonstrated that when exposed to similar biomechanical loading of the skeleton, males will experience more compensatory bone growth than females. For example, male tennis players will have greater bilateral asymmetry in their upper limbs than females (Jones et al, 1977). Based on this knowledge it would be expected that males should be more

asymmetrical than females. Both traditional circumference and midshaft diameter measurements and 3D circumference data do indeed display a significant difference with males being far more asymmetrical than females.

With respect to the traditionally obtained midshaft circumference, although both males and females are right-sided for this measurement, males exhibit approximately twice the asymmetry as females. In the most general terms this indicates that females were performing less strenuous activity with their right arms than males, although as stated above, the male skeleton responds more strongly to biomechanical forces. Therefore, it is possible that males and females could have been engaged in similar amounts of activity, but the male skeletons would exhibit this activity to a greater degree. As the majority of this sample were from rural, medieval settings, it is probable that both sexes would have been engaged in a very physical lifestyle as compared to most modern individuals. Härke (1997) has proposed that Anglo-Saxon England is comparable to colonial societies where females perform heavy work similar to males. Furthermore, at certain times of the year, such as haymaking and harvesting, medieval agriculture required great efforts by all able-bodied family members and neighbours (Dyer, 2002).

Despite the potential for similarities in male and female tasks, there still would have been differences between the activities they performed. Blackburn (2004) demonstrated a tendency for left-sidedness in the humeral head of females, a trait which was potentially linked to infant-carrying. Although a similar trend is not present in the current study, it is possible that the smaller degree of right-handedness in females results from performing left-handed activities. While these were not repetitive or strenuous enough to create left-sided asymmetry, they could have served to weaken the right-sided

asymmetry. As proposed above, infant-carrying could create this effect as observation of modern females has shown that they prefer holding children on their left side, while males do not appear to have a preference (Calvin, 1983). As with all speculations regarding the activities of past populations, hypotheses must remain cautious as it is impossible to know exactly what tasks were being performed and how they would have affected bilateral asymmetry of the upper limbs.

Methodological Issues

The method of calculating directional asymmetry was one of several that could have been utilized in this research, and was chosen because of its use in other studies of handedness in skeletal populations (Blackburn & Knüsel, 2006; Steele & Mays, 1995). However, this method does not take fluctuating asymmetry into account and, while it is likely to be of a relatively small magnitude, fluctuating asymmetry can influence directional asymmetry. This is especially true as directional asymmetry itself is often very small. Further analysis of these data could use a bootstrapping method for estimating directional asymmetry which accounts for the effects of fluctuating asymmetry (Richtsmeier et al., 2005), although it is beyond the scope of the current work.

As with any emerging technology, there are unexpected issues that must be overcome, especially when applying it to new problems and disciplines, such as physical anthropology. In the current study, challenges were encountered from the initial stages of 3D data acquisition and processing to the final steps in analysis. The Polhemus handheld laser scanner is a powerful tool that can capture 3D point data of an object's surface, and its portability made it particularly useful in the present study. However, the proficient use

of this machine requires a considerable amount of time, as well as proper laboratory conditions (i.e. no metallic objects may be in close proximity to the scanned object), and the potential for producing poor quality images is high. As such, a portion of the 3D dataset acquired in this study was eliminated from analysis because it was deemed to be unusable. However, the hole-repairing method described in Chapter 3 did successfully salvage a large amount of data without sacrificing the reliability of the results.

The specific reason for the poor quality of some of the 3D models remains unknown, although several possibilities exist. As mentioned above, the presence of metallic objects can greatly affect the accuracy of the surface data obtained, and this cannot be ruled out as a factor. In many instances though, the problems with the data were much more subtle than would have been produced by metal interference. Therefore, it is likely that other causes were in play, including the possibility that the scanned element moved slightly during acquisition or the scanner sensitivity was not set at the most appropriate level (the level can be manually adjusted for each scan and this information is not recorded). It is probable that the issues encountered in this study resulted from the interplay of several factors.

Another challenge was encountered when determining how to reliably estimate positions to place cross-sections on the 3D models. As scans were taken with the element secured upright, the distal end was often obscured, making it difficult to accurately determine the midshaft position. Scanning each side of the element separately and then registering them together would have solved the issue of obscured ends. However, this was determined not to be feasible as non-adult humeri are fairly amorphous making it extremely difficult to identify analogous points at which to stitch the images together.

The use of equipment which captures data both in colour and at a higher resolution, such as the NextEngine Desktop Scanner, could potentially eliminate many of these problems. Not only does the NextEngine rotate 360° around an object, meaning the data would not need to be registered, but a small coloured adhesive could be temporarily placed at the midshaft of the element, making the need for visual estimation unnecessary. Furthermore, this technique would also make it possible to identify pseudolandmarks, something which was not possible in the present study due to the amorphous nature not only of non-adult humeri, but humeral diaphyses in general. Assigning pseudolandmarks to diaphyseal cross-sections could expand this type of study by making it possible to apply landmark-based analyses, such as Euclidean Distance Matrix Analysis (Richtsmeier et al., 2002).

In the present study, Elliptic Fourier Analysis was used to perform an outline analysis. Although this method did indeed provide some interesting insights into humeral shape, it was quite limited in the types of questions that could be addressed because of both sample size and protocol restrictions, described below. These issues made it impossible to analyse shape change throughout all age categories, as size changes throughout growth affected the number of coordinate points present, and an equal number of points must be used for comparison. Additionally, a certain number of individuals must be present in a sample, specifically, the number of coordinate points must not exceed the total number of cases analysed, and in many instances small sizes in certain age categories did not allow for analysis to be performed. An initial attempt was made to combine several age categories, but this was deemed unfeasible as too many coordinates would have to be deleted from the larger (older) individuals, resulting in a loss of important morphological attributes. Because of these limitations, this study is not as comprehensive as would have

been possible if the entire dataset had been useable, and the ability to examine shape change throughout all age categories may have demonstrated important variations during growth. Such changes were demonstrated in the traditional metric analysis, pointing to the continued usefulness of these techniques, especially in the face of technological challenges. Nevertheless, this work did successfully contribute to how 3D data can be used to examine bilateral asymmetry of the humerus, and while it demonstrates a need for more refined methodology, the challenges encountered will prove invaluable for the development of future research.

Conclusions

Despite eliciting a great deal of curiosity and subsequent research, handedness remains a relatively enigmatic phenomenon. However, the current work has led to a better understanding of this characteristic by demonstrating the following:

- Bilateral asymmetry of the humerus goes through a progression from either left-sided or symmetrical to right-sided throughout growth and development, as was predicted in the hypotheses
- Bilateral asymmetry is strongly influenced by biomechanical forces that are consistent with behavioural observations of children during growth
- The right humerus exhibits a shape change in the circumference between the ages of 5-8 and 9-12 years
- Differences in lifestyle and activity patterns can be detected in asymmetry of the humerus

- The use of 3D data holds the potential to answer more questions about asymmetry than traditional measurement techniques

This study used bilateral asymmetry of the humerus as a proxy for handedness in order to better understand the presence of this unique trait in humans. Although it is well-established that adults are predominantly right-handed, what was not well-understood was the pattern of asymmetry exhibited in non-adult individuals. It was unclear whether bones of the upper limb displayed asymmetry early in development or if this only became apparent later in life. Studies of hand preference in living children suggested that this trait appears after 18 months of age (Bradshaw & Rogers, 1993), however, evidence also demonstrated that handedness may be present prior to birth (Hepper et al., 1991). A correlation has also been observed between the emergence of handedness and the development of speech. The onset of handedness tends to coincide with an infant's first two-syllable words (Ramsay, 1980). As such, the gradual appearance of hand dominance may be related to increasing cerebral lateralization. Interestingly, there is evidence that handedness and language co-evolved. Corballis (2002) proposed that language began with hand gestures and these eventually came to be augmented with vocalizations. As a result, language started to become vocal rather than primarily gestural. Speech must represent a high degree of adaptive significance in human evolution as it has many behavioural advantages over gestural language, such as the ability to communicate in the dark. Undoubtedly, the development of language was a pivotal point in our history and without it our species would have assumed a much different role in the world. Based on Corballis' (2002) hypothesis, language is closely related to gesture which can account for

the tendency among humans for the neural centers controlling the preferred hand to be located in the same area as those that control articulate speech.

Results from the current work can support the hypothesis that handedness and language develop concurrently. Although the correlation between hand preference and bilateral asymmetry of the humerus is not perfect, this research indicates that right-handedness gradually appears throughout development, either late in infancy or around 5-8 years of age depending on which measurement is considered. This is consistent with behavioural evidence for handedness in children which indicates that while handedness first emerges around the end of the second year, it tends to fluctuate until approximately eight years of age. Therefore, the trends of bilateral asymmetry observed in the skeletal sample can be explained by increased mechanical loading of the right arm throughout growth and development. Although it was hypothesized that handedness should become apparent in the skeleton shortly after 2 years of age, its appearance several years later is most likely results from a lag between activity and its measurable effect on the skeleton, as well as continued fluctuating hand preference during early development.

The knowledge that left-sided asymmetry, extends from infancy into late childhood would not have been gained without the use of 3D data. The measurements obtained from the 3D data are more precise than those obtained from traditional measurement techniques. Without this type of precision, it would not be possible to reach many of the conclusions present in this work, including the changes and differences in asymmetry that occur as a result of lifestyle and activity patterns. Although this work supports the hypothesis that all human populations are right-handed, there are subtle differences between groups. The use of 3D circumference data indicates that British

populations became more asymmetrical following the Industrial Revolution. With the drastic changes that would have occurred during this time, it is encouraging to find skeletal markers for these differences in lifestyle beyond those typically investigated (i.e. palaeopathology, growth profiles). Differences in degree of asymmetry between males and females were observed using the 3D data. Not only did this suggest variations in activity between the two sexes, but corroborated research demonstrating that the female skeleton does not respond as strongly to biomechanical forces as its male counterpart, consistent with what was hypothesized. Although 3D data does not exist for the Native Point population, thereby negating the possibility of examining that population with increased precision, traditional measurements did indicate a difference between the Sadlermiut and British sample. In the future, 3D data could be used to provide a more comprehensive comparative analysis of these two groups. A larger sample size would also allow for further geometric morphometric analysis, not only between populations, but in order to fill in the gaps in the growth and development portion of this research. Finally, these techniques hold great promise for increasing our understanding of how handedness evolved in humans, which is perhaps one of the most mysterious aspects of this trait. By examining bilateral asymmetry in the upper limbs of early human ancestors with the increased precision permitted by 3D technology, it may be possible to detect when handedness appears in the fossil record. As it has been hypothesized that handedness and language co-evolved with the development of increased cerebral lateralization (Corballis, 2002), evidence for right-handedness would suggest the presence, or at least potential, for complex communication, a factor that is pivotal in human evolution.

Overall, this work successfully demonstrated that bilateral asymmetry of the humerus is a useful tool for observing how handedness presents in the skeleton throughout growth and development. Interestingly, this trait presents in a manner which strongly parallels what is observed in children behaviourally, indicating that biomechanics strongly influences asymmetry. As these biomechanical influences continue over the course of one's life, bilateral asymmetry of the upper limbs also possesses the potential to uncover variation correlated with factors such as temporal period or sex. Although any proposals regarding what specific tasks individuals performed must be made conservatively, an understanding of how asymmetry presents in populations whose activity patterns are known will make it possible to extend more reliable interpretations to skeletal populations whose context is less clear.

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Appendix

Post hoc tests:

Bonferroni - Uses t tests to perform pairwise comparisons between group means, but controls overall error rate by setting the error rate for each test to the experimentwise error rate divided by the total number of tests. Hence, the observed significance level is adjusted for the fact that multiple comparisons are being made.

Tamhane's T2 - Conservative pairwise comparisons test based on a t test. This test is appropriate when the variances are unequal.

Standardized asymmetry of British sample for factor = age

Test of Homogeneity of Variances

	Levene Statistic	df1	df2	Sig.
Stand. Asymm. Length	1.872	7	235	.075
Stand. Asymm. MS Diam	2.620	7	404	.012
Stand. Asymm. MS Circ	2.378	7	403	.022
Stand. Asymm. Epi.Breadth	1.307	7	108	.254

Multiple Comparisons

Bonferroni

Dependent Variable	(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
Length	Foetus	Birth - 1mo	.033794	.116906	1.000
		1 - 12mo	-.137706	.139298	1.000
		1 - 4yrs	-.127856	.084930	1.000
		5 - 8yrs	-.223367	.081231	.180
		9 - 12yrs	-.269134	.086721	.060
		13 - 17yrs	-.529506(*)	.096770	.000
		Adult 18+	-.391536(*)	.080749	.000
		Birth - 1mo	Foetus	-.033794	.116906
	1 - 12mo		-.171500	.151483	1.000
	1 - 4yrs		-.161650	.103713	1.000
	5 - 8yrs		-.257161	.100707	.316
	9 - 12yrs		-.302929	.105185	.122
	13 - 17yrs		-.563300(*)	.113612	.000
	Adult 18+		-.425331(*)	.100318	.001
	1 - 12mo		Foetus	.137706	.139298
		Birth - 1mo	.171500	.151483	1.000
		1 - 4yrs	.009850	.128426	1.000
		5 - 8yrs	-.085661	.126010	1.000
		9 - 12yrs	-.131429	.129617	1.000
		13 - 17yrs	-.391800	.136545	.126

		Adult 18+	-.253831	.125700	1.000
	1 - 4yrs	Foetus	.127856	.084930	1.000
		Birth - 1mo	.161650	.103713	1.000
		1 - 12mo	-.009850	.128426	1.000
		5 - 8yrs	-.095511	.060728	1.000
		9 - 12yrs	-.141279	.067896	1.000
		13 - 17yrs	-.401650(*)	.080336	.000
	5 - 8yrs	Adult 18+	-.263681(*)	.060082	.000
		Foetus	.223367	.081231	.180
		Birth - 1mo	.257161	.100707	.316
		1 - 12mo	.085661	.126010	1.000
		1 - 4yrs	.095511	.060728	1.000
		9 - 12yrs	-.045768	.063208	1.000
		13 - 17yrs	-.306139(*)	.076415	.002
	9 - 12yrs	Adult 18+	-.168170	.054728	.066
		Foetus	.269134	.086721	.060
		Birth - 1mo	.302929	.105185	.122
		1 - 12mo	.131429	.129617	1.000
		1 - 4yrs	.141279	.067896	1.000
		5 - 8yrs	.045768	.063208	1.000
		13 - 17yrs	-.260371(*)	.082227	.049
	13 - 17yrs	Adult 18+	-.122402	.062587	1.000
		Foetus	.529506(*)	.096770	.000
		Birth - 1mo	.563300(*)	.113612	.000
		1 - 12mo	.391800	.136545	.126
		1 - 4yrs	.401650(*)	.080336	.000
		5 - 8yrs	.306139(*)	.076415	.002
		9 - 12yrs	.260371(*)	.082227	.049
	Adult 18+	Adult 18+	.137969	.075902	1.000
		Foetus	.391536(*)	.080749	.000
		Birth - 1mo	.425331(*)	.100318	.001
		1 - 12mo	.253831	.125700	1.000
		1 - 4yrs	.263681(*)	.060082	.000
		5 - 8yrs	.168170	.054728	.066
		9 - 12yrs	.122402	.062587	1.000
		13 - 17yrs	-.137969	.075902	1.000
Epicondylar Breadth	Foetus	Birth - 1mo	.507700	.334279	1.000
		1 - 12mo	.393400	.472742	1.000
		1 - 4yrs	-.214933	.315161	1.000
		5 - 8yrs	-.453100	.256709	1.000
		9 - 12yrs	-.571600	.246023	.617
		13 - 17yrs	-.364886	.252691	1.000
	Birth - 1mo	Adult 18+	-.294080	.211417	1.000
		Foetus	-.507700	.334279	1.000
		1 - 12mo	-.114300	.510620	1.000
		1 - 4yrs	-.722633	.369560	1.000
		5 - 8yrs	-.960800	.321165	.096

	9 - 12yrs	-1.079300(*)	.312690	.022
	13 - 17yrs	-.872586	.317963	.199
	Adult 18+	-.801780	.286260	.169
1 - 12mo	Foetus	-.393400	.472742	1.000
	Birth - 1mo	.114300	.510620	1.000
	1 - 4yrs	-.608333	.498314	1.000
	5 - 8yrs	-.846500	.463562	1.000
	9 - 12yrs	-.965000	.457731	1.000
	13 - 17yrs	-.758286	.461349	1.000
	Adult 18+	-.687480	.440099	1.000
1 - 4yrs	Foetus	.214933	.315161	1.000
	Birth - 1mo	.722633	.369560	1.000
	1 - 12mo	.608333	.498314	1.000
	5 - 8yrs	-.238167	.301216	1.000
	9 - 12yrs	-.356667	.292162	1.000
	13 - 17yrs	-.149952	.297800	1.000
	Adult 18+	-.079147	.263683	1.000
5 - 8yrs	Foetus	.453100	.256709	1.000
	Birth - 1mo	.960800	.321165	.096
	1 - 12mo	.846500	.463562	1.000
	1 - 4yrs	.238167	.301216	1.000
	9 - 12yrs	-.118500	.227885	1.000
	13 - 17yrs	.088214	.235069	1.000
	Adult 18+	.159020	.190004	1.000
9 - 12yrs	Foetus	.571600	.246023	.617
	Birth - 1mo	1.079300(*)	.312690	.022
	1 - 12mo	.965000	.457731	1.000
	1 - 4yrs	.356667	.292162	1.000
	5 - 8yrs	.118500	.227885	1.000
	13 - 17yrs	.206714	.223350	1.000
	Adult 18+	.277520	.175297	1.000
13 - 17yrs	Foetus	.364886	.252691	1.000
	Birth - 1mo	.872586	.317963	.199
	1 - 12mo	.758286	.461349	1.000
	1 - 4yrs	.149952	.297800	1.000
	5 - 8yrs	-.088214	.235069	1.000
	9 - 12yrs	-.206714	.223350	1.000
	Adult 18+	.070806	.184540	1.000
Adult 18+	Foetus	.294080	.211417	1.000
	Birth - 1mo	.801780	.286260	.169
	1 - 12mo	.687480	.440099	1.000
	1 - 4yrs	.079147	.263683	1.000
	5 - 8yrs	-.159020	.190004	1.000
	9 - 12yrs	-.277520	.175297	1.000
	13 - 17yrs	-.070806	.184540	1.000

* The mean difference is significant at the .05 level.

Multiple Comparisons
Tamhane

Dependent Variable	(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
MS Diam	Foetus	Birth - 1mo	.103355	.478189	1.000
		1 - 12mo	.216541	.463815	1.000
		1 - 4yrs	-.099196	.449325	1.000
		5 - 8yrs	-.285163	.446496	1.000
		9 - 12yrs	.084356	.473540	1.000
		13 - 17yrs	-.305500	.455083	1.000
		Adult 18+	-.313941	.445368	1.000
		Birth - 1mo	Foetus	-.103355	.478189
	1 - 12mo		.113186	.254602	1.000
	1 - 4yrs		-.202550	.227137	1.000
	5 - 8yrs		-.388518	.221487	.926
	9 - 12yrs		-.018998	.271915	1.000
	13 - 17yrs		-.408855	.238324	.937
	Adult 18+		-.417296	.219205	.853
	1 - 12mo		Foetus	-.216541	.463815
		Birth - 1mo	-.113186	.254602	1.000
		1 - 4yrs	-.315737	.195064	.961
		5 - 8yrs	-.501704	.188455	.238
		9 - 12yrs	-.132185	.245757	1.000
		13 - 17yrs	-.522041	.207983	.331
		Adult 18+	-.530482	.185768	.149
		1 - 4yrs	Foetus	.099196	.449325
	Birth - 1mo		.202550	.227137	1.000
	1 - 12mo		.315737	.195064	.961
	5 - 8yrs		-.185967	.149281	.999
	9 - 12yrs		.183552	.217177	1.000
	13 - 17yrs		-.206304	.173281	.999
	Adult 18+		-.214746	.145874	.987
	5 - 8yrs		Foetus	.285163	.446496
		Birth - 1mo	.388518	.221487	.926
		1 - 12mo	.501704	.188455	.238
		1 - 4yrs	.185967	.149281	.999
		9 - 12yrs	.369519	.211261	.914
		13 - 17yrs	-.020337	.165806	1.000
		Adult 18+	-.028778	.136910	1.000
		9 - 12yrs	Foetus	-.084356	.473540
	Birth - 1mo		.018998	.271915	1.000
	1 - 12mo		.132185	.245757	1.000
	1 - 4yrs		-.183552	.217177	1.000
	5 - 8yrs		-.369519	.211261	.914
	13 - 17yrs		-.389856	.228851	.933
	Adult 18+		-.398298	.208868	.823
13 - 17yrs	Foetus		.305500	.455083	1.000
	Birth - 1mo	.408855	.238324	.937	

		1 - 12mo	.522041	.207983	.331
		1 - 4yrs	.206304	.173281	.999
		5 - 8yrs	.020337	.165806	1.000
		9 - 12yrs	.389856	.228851	.933
	Adult 18+	Adult 18+	-.008441	.162745	1.000
		Foetus	.313941	.445368	1.000
		Birth - 1mo	.417296	.219205	.853
		1 - 12mo	.530482	.185768	.149
		1 - 4yrs	.214746	.145874	.987
		5 - 8yrs	.028778	.136910	1.000
		9 - 12yrs	.398298	.208868	.823
		13 - 17yrs	.008441	.162745	1.000
MS Circ	Foetus	Birth - 1mo	-.439100	.359024	.999
		1 - 12mo	-.661495	.356572	.884
		1 - 4yrs	-1.041456	.338219	.136
		5 - 8yrs	-.974429	.335026	.201
		9 - 12yrs	-1.008907	.335908	.164
		13 - 17yrs	-1.288575(*)	.346299	.027
	Adult 18+	Adult 18+	-1.287929(*)	.331985	.023
		Foetus	.439100	.359024	.999
	Birth - 1mo	1 - 12mo	-.222395	.225516	1.000
		1 - 4yrs	-.602356	.195206	.096
		5 - 8yrs	-.535329	.189621	.191
		9 - 12yrs	-.569807	.191175	.130
		13 - 17yrs	-.849475(*)	.208894	.005
	Adult 18+	Adult 18+	-.848829(*)	.184195	.002
		Foetus	.661495	.356572	.884
	1 - 12mo	Birth - 1mo	.222395	.225516	1.000
		1 - 4yrs	-.379961	.190658	.762
		5 - 8yrs	-.312934	.184936	.939
		9 - 12yrs	-.347412	.186528	.856
		13 - 17yrs	-.627080	.204650	.082
	Adult 18+	Adult 18+	-.626435(*)	.179368	.025
		Foetus	1.041456	.338219	.136
	1 - 4yrs	Birth - 1mo	.602356	.195206	.096
		1 - 12mo	.379961	.190658	.762
		5 - 8yrs	.067027	.146457	1.000
		9 - 12yrs	.032549	.148462	1.000
		13 - 17yrs	-.247119	.170675	.990
	Adult 18+	Adult 18+	-.246473	.139360	.900
		Foetus	.974429	.335026	.201
	5 - 8yrs	Birth - 1mo	.535329	.189621	.191
		1 - 12mo	.312934	.184936	.939
		1 - 4yrs	-.067027	.146457	1.000
		9 - 12yrs	-.034478	.141038	1.000
		13 - 17yrs	-.314146	.164258	.819
	Adult 18+	Adult 18+	-.313500	.131423	.403
		Foetus	1.008907	.335908	.164
	9 - 12yrs				

	Birth - 1mo	.569807	.191175	.130
	1 - 12mo	.347412	.186528	.856
	1 - 4yrs	-.032549	.148462	1.000
	5 - 8yrs	.034478	.141038	1.000
	13 - 17yrs	-.279668	.166049	.941
	Adult 18+	-.279022	.133654	.671
13 - 17yrs	Foetus	1.288575(*)	.346299	.027
	Birth - 1mo	.849475(*)	.208894	.005
	1 - 12mo	.627080	.204650	.082
	1 - 4yrs	.247119	.170675	.990
	5 - 8yrs	.314146	.164258	.819
	9 - 12yrs	.279668	.166049	.941
	Adult 18+	.000646	.157963	1.000
Adult 18+	Foetus	1.287929(*)	.331985	.023
	Birth - 1mo	.848829(*)	.184195	.002
	1 - 12mo	.626435(*)	.179368	.025
	1 - 4yrs	.246473	.139360	.900
	5 - 8yrs	.313500	.131423	.403
	9 - 12yrs	.279022	.133654	.671
	13 - 17yrs	-.000646	.157963	1.000

* The mean difference is significant at the .05 level.

Absolute asymmetry of British sample for factor = age
Test of Homogeneity of Variances

	Levene Statistic	df1	df2	Sig.
Ab.Asymm.Length	3.887	7	235	.001
Ab.Asymm. MS Diam	2.369	7	404	.022
Ab.Asymm. MS Circ	3.300	7	403	.002
Ab.Asymm. Epi. Breadth	2.888	7	108	.008

Multiple Comparisons
Tamhane

Dependent Variable	(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.	
Length	Foetus	Birth - 1mo	.112206	.083468	.997	
		1 - 12mo	.091706	.086911	1.000	
		1 - 4yrs	.080256	.065971	1.000	
		5 - 8yrs	-.017562	.068698	1.000	
		9 - 12yrs	-.117094	.069629	.957	
		13 - 17yrs	-.238094	.125487	.858	
		Adult 18+	-.135142	.070439	.856	
	Birth - 1mo	Foetus	Birth - 1mo	-.112206	.083468	.997
		1 - 12mo	1 - 12mo	-.020500	.080684	1.000
		1 - 4yrs	1 - 4yrs	-.031950	.057521	1.000
		5 - 8yrs	5 - 8yrs	-.129768	.060629	.768
		9 - 12yrs	9 - 12yrs	-.229300	.061682	.059
		13 - 17yrs	13 - 17yrs	-.350300	.121258	.193
		Adult 18+	Adult 18+	-.247347(*)	.062595	.033
	1 - 12mo	Foetus	1 - 12mo	-.091706	.086911	1.000
		Birth - 1mo	Birth - 1mo	.020500	.080684	1.000
		1 - 4yrs	1 - 4yrs	-.011450	.062412	1.000
		5 - 8yrs	5 - 8yrs	-.109268	.065288	.984
		9 - 12yrs	9 - 12yrs	-.208800	.066266	.336
		13 - 17yrs	13 - 17yrs	-.329800	.123653	.317
		Adult 18+	Adult 18+	-.226847	.067117	.237
	1 - 4yrs	Foetus	1 - 4yrs	-.080256	.065971	1.000
		Birth - 1mo	Birth - 1mo	.031950	.057521	1.000
		1 - 12mo	1 - 12mo	.011450	.062412	1.000
		5 - 8yrs	5 - 8yrs	-.097818	.032576	.092
		9 - 12yrs	9 - 12yrs	-.197350(*)	.034495	.000
		13 - 17yrs	13 - 17yrs	-.318350	.109949	.222
		Adult 18+	Adult 18+	-.215397(*)	.036103	.000
	5 - 8yrs	Foetus	5 - 8yrs	.017562	.068698	1.000
		Birth - 1mo	Birth - 1mo	.129768	.060629	.768
		1 - 12mo	1 - 12mo	.109268	.065288	.984
		1 - 4yrs	1 - 4yrs	.097818	.032576	.092
		9 - 12yrs	9 - 12yrs	-.099532	.039461	.319
		13 - 17yrs	13 - 17yrs	-.220532	.111607	.829
		Adult 18+	Adult 18+	-.117580	.040874	.126

MS Diam	9 - 12yrs	Foetus	.117094	.069629	.957		
		Birth - 1mo	.229300	.061682	.059		
		1 - 12mo	.208800	.066266	.336		
		1 - 4yrs	.197350(*)	.034495	.000		
		5 - 8yrs	.099532	.039461	.319		
		13 - 17yrs	-.121000	.112182	1.000		
	13 - 17yrs	Adult 18+	-.018047	.042420	1.000		
		Foetus	Foetus	.238094	.125487	.858	
			Birth - 1mo	.350300	.121258	.193	
			1 - 12mo	.329800	.123653	.317	
			1 - 4yrs	.318350	.109949	.222	
			5 - 8yrs	.220532	.111607	.829	
	9 - 12yrs		.121000	.112182	1.000		
	Adult 18+	Adult 18+	.102953	.112687	1.000		
		Foetus	Foetus	.135142	.070439	.856	
			Birth - 1mo	.247347(*)	.062595	.033	
			1 - 12mo	.226847	.067117	.237	
			1 - 4yrs	.215397(*)	.036103	.000	
			5 - 8yrs	.117580	.040874	.126	
	9 - 12yrs		.018047	.042420	1.000		
	Foetus	13 - 17yrs	-.102953	.112687	1.000		
		Birth - 1mo	.659891	.334515	.820		
		1 - 12mo	.597262	.324613	.899		
		1 - 4yrs	.618293	.318792	.850		
		5 - 8yrs	.583192	.317834	.905		
		9 - 12yrs	.553484	.343813	.971		
		13 - 17yrs	.530600	.321185	.965		
		Adult 18+	.570763	.316729	.919		
		Birth - 1mo	Foetus	-.659891	.334515	.820	
			1 - 12mo	-.062629	.164259	1.000	
			1 - 4yrs	-.041598	.152432	1.000	
			5 - 8yrs	-.076699	.150418	1.000	
			9 - 12yrs	-.106407	.199536	1.000	
			13 - 17yrs	-.129291	.157375	1.000	
		Adult 18+	Adult 18+	-.089127	.148069	1.000	
			Foetus	Foetus	-.597262	.324613	.899
				Birth - 1mo	.062629	.164259	1.000
				1 - 4yrs	.021032	.129262	1.000
	5 - 8yrs			-.014069	.126882	1.000	
	9 - 12yrs			-.043777	.182450	1.000	
	13 - 17yrs	-.066662		.135056	1.000		
	1 - 12mo	Adult 18+	-.026498	.124088	1.000		
Foetus		Foetus	-.618293	.318792	.850		
		Birth - 1mo	.041598	.152432	1.000		
		1 - 12mo	-.021032	.129262	1.000		
		5 - 8yrs	-.035101	.111145	1.000		
		9 - 12yrs	-.064809	.171878	1.000		
	13 - 17yrs	-.087693	.120393	1.000			

		Adult 18+	-.047530	.107944	1.000
	5 - 8yrs	Foetus	-.583192	.317834	.905
		Birth - 1mo	.076699	.150418	1.000
		1 - 12mo	.014069	.126882	1.000
		1 - 4yrs	.035101	.111145	1.000
		9 - 12yrs	-.029708	.170095	1.000
		13 - 17yrs	-.052592	.117833	1.000
		Adult 18+	-.012429	.105082	1.000
	9 - 12yrs	Foetus	-.553484	.343813	.971
		Birth - 1mo	.106407	.199536	1.000
		1 - 12mo	.043777	.182450	1.000
		1 - 4yrs	.064809	.171878	1.000
		5 - 8yrs	.029708	.170095	1.000
		13 - 17yrs	-.022884	.176277	1.000
		Adult 18+	.017279	.168021	1.000
	13 - 17yrs	Foetus	-.530600	.321185	.965
		Birth - 1mo	.129291	.157375	1.000
		1 - 12mo	.066662	.135056	1.000
		1 - 4yrs	.087693	.120393	1.000
		5 - 8yrs	.052592	.117833	1.000
		9 - 12yrs	.022884	.176277	1.000
		Adult 18+	.040163	.114819	1.000
	Adult 18+	Foetus	-.570763	.316729	.919
		Birth - 1mo	.089127	.148069	1.000
		1 - 12mo	.026498	.124088	1.000
		1 - 4yrs	.047530	.107944	1.000
		5 - 8yrs	.012429	.105082	1.000
		9 - 12yrs	-.017279	.168021	1.000
		13 - 17yrs	-.040163	.114819	1.000
MS Circ	Foetus	Birth - 1mo	.548036	.279884	.825
		1 - 12mo	.396584	.274807	.993
		1 - 4yrs	.380208	.265954	.994
		5 - 8yrs	.400615	.261980	.985
		9 - 12yrs	.425470	.261833	.971
		13 - 17yrs	.168250	.264780	1.000
		Adult 18+	.222180	.259330	1.000
	Birth - 1mo	Foetus	-.548036	.279884	.825
		1 - 12mo	-.151452	.165131	1.000
		1 - 4yrs	-.167828	.149935	1.000
		5 - 8yrs	-.147421	.142768	1.000
		9 - 12yrs	-.122566	.142497	1.000
		13 - 17yrs	-.379786	.147843	.327
		Adult 18+	-.325856	.137845	.495
	1 - 12mo	Foetus	-.396584	.274807	.993
		Birth - 1mo	.151452	.165131	1.000
		1 - 4yrs	-.016376	.140229	1.000
		5 - 8yrs	.004031	.132539	1.000
		9 - 12yrs	.028886	.132247	1.000

		13 - 17yrs	-.228334	.137990	.952
		Adult 18+	-.174404	.127221	.995
	1 - 4yrs	Foetus	-.380208	.265954	.994
		Birth - 1mo	.167828	.149935	1.000
		1 - 12mo	.016376	.140229	1.000
		5 - 8yrs	.020407	.113043	1.000
		9 - 12yrs	.045262	.112701	1.000
		13 - 17yrs	-.211958	.119388	.899
		Adult 18+	-.158028	.106758	.986
	5 - 8yrs	Foetus	-.400615	.261980	.985
		Birth - 1mo	.147421	.142768	1.000
		1 - 12mo	-.004031	.132539	1.000
		1 - 4yrs	-.020407	.113043	1.000
		9 - 12yrs	.024855	.102975	1.000
		13 - 17yrs	-.232365	.110253	.659
		Adult 18+	-.178435	.096434	.853
	9 - 12yrs	Foetus	-.425470	.261833	.971
		Birth - 1mo	.122566	.142497	1.000
		1 - 12mo	-.028886	.132247	1.000
		1 - 4yrs	-.045262	.112701	1.000
		5 - 8yrs	-.024855	.102975	1.000
		13 - 17yrs	-.257220	.109903	.457
		Adult 18+	-.203290	.096033	.645
	13 - 17yrs	Foetus	-.168250	.264780	1.000
		Birth - 1mo	.379786	.147843	.327
		1 - 12mo	.228334	.137990	.952
		1 - 4yrs	.211958	.119388	.899
		5 - 8yrs	.232365	.110253	.659
		9 - 12yrs	.257220	.109903	.457
		Adult 18+	.053930	.103799	1.000
	Adult 18+	Foetus	-.222180	.259330	1.000
		Birth - 1mo	.325856	.137845	.495
		1 - 12mo	.174404	.127221	.995
		1 - 4yrs	.158028	.106758	.986
		5 - 8yrs	.178435	.096434	.853
		9 - 12yrs	.203290	.096033	.645
		13 - 17yrs	-.053930	.103799	1.000
Epi. Breadth	Foetus	Birth - 1mo	-.400700	.558457	1.000
		1 - 12mo	-.099600	.413455	1.000
		1 - 4yrs	.122733	.225000	1.000
		5 - 8yrs	.076746	.186369	1.000
		9 - 12yrs	-.049100	.172931	1.000
		13 - 17yrs	.101543	.181315	1.000
		Adult 18+	.025280	.160774	1.000
	Birth - 1mo	Foetus	.400700	.558457	1.000
		1 - 12mo	.301100	.660764	1.000
		1 - 4yrs	.523433	.562396	1.000
		5 - 8yrs	.477446	.548086	1.000

	9 - 12yrs	.351600	.543663	1.000
	13 - 17yrs	.502243	.546388	1.000
	Adult 18+	.425980	.539919	1.000
1 - 12mo	Foetus	.099600	.413455	1.000
	Birth - 1mo	-.301100	.660764	1.000
	1 - 4yrs	.222333	.418761	1.000
	5 - 8yrs	.176346	.399336	1.000
	9 - 12yrs	.050500	.393244	1.000
	13 - 17yrs	.201143	.397002	1.000
	Adult 18+	.124880	.388051	1.000
1 - 4yrs	Foetus	-.122733	.225000	1.000
	Birth - 1mo	-.523433	.562396	1.000
	1 - 12mo	-.222333	.418761	1.000
	5 - 8yrs	-.045987	.197861	1.000
	9 - 12yrs	-.171833	.185259	1.000
	13 - 17yrs	-.021190	.193109	1.000
	Adult 18+	-.097453	.173966	1.000
5 - 8yrs	Foetus	-.076746	.186369	1.000
	Birth - 1mo	-.477446	.548086	1.000
	1 - 12mo	-.176346	.399336	1.000
	1 - 4yrs	.045987	.197861	1.000
	9 - 12yrs	-.125846	.135754	1.000
	13 - 17yrs	.024797	.146285	1.000
	Adult 18+	-.051466	.119885	1.000
9 - 12yrs	Foetus	.049100	.172931	1.000
	Birth - 1mo	-.351600	.543663	1.000
	1 - 12mo	-.050500	.393244	1.000
	1 - 4yrs	.171833	.185259	1.000
	5 - 8yrs	.125846	.135754	1.000
	13 - 17yrs	.150643	.128728	1.000
	Adult 18+	.074380	.097694	1.000
13 - 17yrs	Foetus	-.101543	.181315	1.000
	Birth - 1mo	-.502243	.546388	1.000
	1 - 12mo	-.201143	.397002	1.000
	1 - 4yrs	.021190	.193109	1.000
	5 - 8yrs	-.024797	.146285	1.000
	9 - 12yrs	-.150643	.128728	1.000
	Adult 18+	-.076263	.111867	1.000
Adult 18+	Foetus	-.025280	.160774	1.000
	Birth - 1mo	-.425980	.539919	1.000
	1 - 12mo	-.124880	.388051	1.000
	1 - 4yrs	.097453	.173966	1.000
	5 - 8yrs	.051466	.119885	1.000
	9 - 12yrs	-.074380	.097694	1.000
	13 - 17yrs	.076263	.111867	1.000

* The mean difference is significant at the .05 level.

Standardized asymmetry of 3D circumference data for factor = age

Test of Homogeneity of Variances

Levene Statistic	df1	df2	Sig.
2.195	7	183	.037

Multiple Comparisons

Tamhane

(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
Foetus	Birth - 1 month	3.833258	.822075	.146
	1-12 months	2.305896	.581695	.136
	1-4 years	2.242817	.504970	.193
	5-8 years	2.438367	.433873	.335
	9-12 years	1.754458	.402598	.743
	13-17 years	1.020508	.407434	.973
	Adult 18+	1.278151	.370461	.966
Birth - 1 month	Foetus	-3.833258	.822075	.146
	1-12 months	-1.527361	.887485	.977
	1-4 years	-1.590441	.839199	.956
	5-8 years	-1.394891	.798440	.985
	9-12 years	-2.078800	.781886	.745
	13-17 years	-2.812750	.784387	.382
	Adult 18+	-2.555107	.765834	.515
1-12 months	Foetus	-2.305896	.581695	.136
	Birth - 1 month	1.527361	.887485	.977
	1-4 years	-.063079	.605655	1.000
	5-8 years	.132471	.547785	1.000
	9-12 years	-.551438	.523362	1.000
	13-17 years	-1.285388	.527091	.473
	Adult 18+	-1.027745	.499063	.783
1-4 years	Foetus	-2.242817	.504970	.193
	Birth - 1 month	1.590441	.839199	.956
	1-12 months	.063079	.605655	1.000
	5-8 years	.195550	.465504	1.000
	9-12 years	-.488359	.436502	1.000
	13-17 years	-1.222309	.440966	.212
	Adult 18+	-.964666	.407050	.496
5-8 years	Foetus	-2.438367	.433873	.335
	Birth - 1 month	1.394891	.798440	.985
	1-12 months	-.132471	.547785	1.000
	1-4 years	-.195550	.465504	1.000
	9-12 years	-.683909	.351831	.808
	13-17 years	-1.417859(*)	.357354	.006
9-12 years	Adult 18+	-1.160216(*)	.314549	.017
	Foetus	-1.754458	.402598	.743

13-17 years	Birth - 1 month	2.078800	.781886	.745
	1-12 months	.551438	.523362	1.000
	1-4 years	.488359	.436502	1.000
	5-8 years	.683909	.351831	.808
	13-17 years	-.733950	.318656	.506
	Adult 18+	-.476307	.269779	.912
	Foetus	-1.020508	.407434	.973
Adult 18+	Birth - 1 month	2.812750	.784387	.382
	1-12 months	1.285388	.527091	.473
	1-4 years	1.222309	.440966	.212
	5-8 years	1.417859(*)	.357354	.006
	9-12 years	.733950	.318656	.506
	Adult 18+	.257643	.276944	1.000
	Foetus	-1.278151	.370461	.966
	Birth - 1 month	2.555107	.765834	.515
	1-12 months	1.027745	.499063	.783
	1-4 years	.964666	.407050	.496
	5-8 years	1.160216(*)	.314549	.017
9-12 years	.476307	.269779	.912	
13-17 years	-.257643	.276944	1.000	

* The mean difference is significant at the .05 level.

Absolute asymmetry of 3D circumference data for factor = age

Test of Homogeneity of Variances

Levene Statistic	df1	df2	Sig.
1.288	7	183	.258

Multiple Comparisons

Bonferroni

(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
Foetus	Birth-1month	.007500	.771868	1.000
	1-12 months	.597265	.689654	1.000
	1-4 years	.524542	.678985	1.000
	5-8 years	.848464	.675244	1.000
	9-12 years	1.168638	.674467	1.000
	13-17 years	.587242	.673062	1.000
	Adult 18+	.943936	.664103	1.000
Birth-1month	Foetus	-.007500	.771868	1.000
	1-12 months	.589765	.469349	1.000
	1-4 years	.517042	.453526	1.000
	5-8 years	.840964	.447906	1.000
	9-12 years	1.161138	.446735	.283
	13-17 years	.579742	.444610	1.000

1-12 months	Adult 18+	.936436	.430927	.870
	Foetus	-.597265	.689654	1.000
	Birth - 1 month	-.589765	.469349	1.000
	1-4 years	-.072723	.292453	1.000
	5-8 years	.251200	.283659	1.000
	9-12 years	.571373	.281806	1.000
	13-17 years	-.010023	.278426	1.000
1-4 years	Adult 18+	.346672	.256009	1.000
	Foetus	-.524542	.678985	1.000
	Birth - 1 month	-.517042	.453526	1.000
	1-12 months	.072723	.292453	1.000
	5-8 years	.323923	.256632	1.000
	9-12 years	.644096	.254582	.343
	13-17 years	.062700	.250835	1.000
5-8 years	Adult 18+	.419395	.225694	1.000
	Foetus	-.848464	.675244	1.000
	Birth - 1 month	-.840964	.447906	1.000
	1-12 months	-.251200	.283659	1.000
	1-4 years	-.323923	.256632	1.000
	9-12 years	.320174	.244429	1.000
	13-17 years	-.261222	.240525	1.000
9-12 years	Adult 18+	.095472	.214177	1.000
	Foetus	-1.168638	.674467	1.000
	Birth - 1 month	-1.161138	.446735	.283
	1-12 months	-.571373	.281806	1.000
	1-4 years	-.644096	.254582	.343
	5-8 years	-.320174	.244429	1.000
	13-17 years	-.581396	.238336	.439
13-17 years	Adult 18+	-.224702	.211716	1.000
	Foetus	-.587242	.673062	1.000
	Birth - 1 month	-.579742	.444610	1.000
	1-12 months	.010023	.278426	1.000
	1-4 years	-.062700	.250835	1.000
	5-8 years	.261222	.240525	1.000
	9-12 years	.581396	.238336	.439
Adult 18+	Adult 18+	.356694	.207196	1.000
	Foetus	-.943936	.664103	1.000
	Birth - 1 month	-.936436	.430927	.870
	1-12 months	-.346672	.256009	1.000
	1-4 years	-.419395	.225694	1.000
	5-8 years	-.095472	.214177	1.000
	9-12 years	.224702	.211716	1.000
	13-17 years	-.356694	.207196	1.000

* The mean difference is significant at the .05 level.

Standardized asymmetry of all populations with Wharram Percy excluded for factor = age

Test of Homogeneity of Variances

	Levene Statistic	df1	df2	Sig.
Stand. Asymm. Length	1.517	7	146	.166
Stand. Asymm. MS Diam	.844	7	343	.551
Stand. Asymm. MS Circ	2.338	7	342	.024
Stand. Asymm. Epi.Breadth	2.115	7	85	.050

Multiple Comparisons

Bonferroni

Dependent Variable	(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
Length	Foetus	Birth - 1mo	-.003750	.211879	1.000
		1 - 12mo	-.046400	.164121	1.000
		1 - 4yrs	-.066474	.164839	1.000
		5 - 8yrs	-.201409	.162873	1.000
		9 - 12yrs	-.250667	.165634	1.000
		13 - 17yrs	-.508063	.167505	.080
		Adult 18+	-.303118	.155586	1.000
		Birth - 1mo	Foetus	.003750	.211879
	1 - 12mo		-.042650	.164121	1.000
	1 - 4yrs		-.062724	.164839	1.000
	5 - 8yrs		-.197659	.162873	1.000
	9 - 12yrs		-.246917	.165634	1.000
	13 - 17yrs		-.504312	.167505	.086
	Adult 18+		-.299368	.155586	1.000
	1 - 12mo		Foetus	.046400	.164121
		Birth - 1mo	.042650	.164121	1.000
		1 - 4yrs	-.020074	.095994	1.000
		5 - 8yrs	-.155009	.092577	1.000
		9 - 12yrs	-.204267	.097352	1.000
		13 - 17yrs	-.461663(*)	.100503	.000
		Adult 18+	-.256718(*)	.079056	.040
		1 - 4yrs	Foetus	.066474	.164839
	Birth - 1mo		.062724	.164839	1.000
	1 - 12mo		.020074	.095994	1.000
	5 - 8yrs		-.134935	.093844	1.000
	9 - 12yrs		-.184193	.098558	1.000
	13 - 17yrs		-.441589(*)	.101672	.001
	Adult 18+		-.236644	.080536	.107
5 - 8yrs	Foetus		.201409	.162873	1.000
	Birth - 1mo	.197659	.162873	1.000	
	1 - 12mo	.155009	.092577	1.000	

		1 - 4yrs	.134935	.093844	1.000
		9 - 12yrs	-.049258	.095233	1.000
		13 - 17yrs	-.306653	.098452	.062
		Adult 18+	-.101709	.076431	1.000
	9 - 12yrs	Foetus	.250667	.165634	1.000
		Birth - 1mo	.246917	.165634	1.000
		1 - 12mo	.204267	.097352	1.000
		1 - 4yrs	.184193	.098558	1.000
		5 - 8yrs	.049258	.095233	1.000
		13 - 17yrs	-.257396	.102955	.379
		Adult 18+	-.052451	.082150	1.000
	13 - 17yrs	Foetus	.508063	.167505	.080
		Birth - 1mo	.504312	.167505	.086
		1 - 12mo	.461663(*)	.100503	.000
		1 - 4yrs	.441589(*)	.101672	.001
		5 - 8yrs	.306653	.098452	.062
		9 - 12yrs	.257396	.102955	.379
		Adult 18+	.204945	.085861	.512
	Adult 18+	Foetus	.303118	.155586	1.000
		Birth - 1mo	.299368	.155586	1.000
		1 - 12mo	.256718(*)	.079056	.040
		1 - 4yrs	.236644	.080536	.107
		5 - 8yrs	.101709	.076431	1.000
		9 - 12yrs	.052451	.082150	1.000
		13 - 17yrs	-.204945	.085861	.512
MS Diam	Foetus	Birth - 1mo	-.743083	.449953	1.000
		1 - 12mo	-.657894	.398959	1.000
		1 - 4yrs	-1.042716	.399369	.264
		5 - 8yrs	-.959154	.402152	.493
		9 - 12yrs	-.742375	.410116	1.000
		13 - 17yrs	-1.179798	.408486	.115
		Adult 18+	-1.160318	.394101	.097
	Birth - 1mo	Foetus	.743083	.449953	1.000
		1 - 12mo	.085189	.285131	1.000
		1 - 4yrs	-.299632	.285705	1.000
		5 - 8yrs	-.216071	.289583	1.000
		9 - 12yrs	.000708	.300545	1.000
		13 - 17yrs	-.436714	.298316	1.000
		Adult 18+	-.417234	.278294	1.000
	1 - 12mo	Foetus	.657894	.398959	1.000
		Birth - 1mo	-.085189	.285131	1.000
		1 - 4yrs	-.384821	.195801	1.000
		5 - 8yrs	-.301260	.201417	1.000
		9 - 12yrs	-.084481	.216882	1.000
		13 - 17yrs	-.521904	.213782	.424
		Adult 18+	-.502423	.184818	.193
	1 - 4yrs	Foetus	1.042716	.399369	.264
		Birth - 1mo	.299632	.285705	1.000

		1 - 12mo	.384821	.195801	1.000
		5 - 8yrs	.083562	.202228	1.000
		9 - 12yrs	.300341	.217636	1.000
		13 - 17yrs	-.137082	.214547	1.000
		Adult 18+	-.117602	.185703	1.000
	5 - 8yrs	Foetus	.959154	.402152	.493
		Birth - 1mo	.216071	.289583	1.000
		1 - 12mo	.301260	.201417	1.000
		1 - 4yrs	-.083562	.202228	1.000
		9 - 12yrs	.216779	.222702	1.000
		13 - 17yrs	-.220644	.219684	1.000
		Adult 18+	-.201164	.191615	1.000
	9 - 12yrs	Foetus	.742375	.410116	1.000
		Birth - 1mo	-.000708	.300545	1.000
		1 - 12mo	.084481	.216882	1.000
		1 - 4yrs	-.300341	.217636	1.000
		5 - 8yrs	-.216779	.222702	1.000
		13 - 17yrs	-.437423	.233945	1.000
		Adult 18+	-.417943	.207811	1.000
	13 - 17yrs	Foetus	1.179798	.408486	.115
		Birth - 1mo	.436714	.298316	1.000
		1 - 12mo	.521904	.213782	.424
		1 - 4yrs	.137082	.214547	1.000
		5 - 8yrs	.220644	.219684	1.000
		9 - 12yrs	.437423	.233945	1.000
		Adult 18+	.019480	.204574	1.000
	Adult 18+	Foetus	1.160318	.394101	.097
		Birth - 1mo	.417234	.278294	1.000
		1 - 12mo	.502423	.184818	.193
		1 - 4yrs	.117602	.185703	1.000
		5 - 8yrs	.201164	.191615	1.000
		9 - 12yrs	.417943	.207811	1.000
		13 - 17yrs	-.019480	.204574	1.000

* The mean difference is significant at the .05 level.

Tamhane

Dependent Variable	(I) Age	(J) Age	Mean Difference (I-J)	Std. Error	Sig.
MS Circ	Foetus	Birth - 1mo	-.512403	.636792	1.000
		1 - 12mo	-.799004	.630729	1.000
		1 - 4yrs	-1.179177	.627093	.947
		5 - 8yrs	-1.191702	.626206	.942
		9 - 12yrs	-1.233000	.629719	.924
		13 - 17yrs	-1.332244	.629857	.866
		Adult 18+	-1.453855	.624911	.771
		Birth - 1mo	.512403	.636792	1.000
	Birth - 1mo	Foetus	.512403	.636792	1.000
		1 - 12mo	-.286602	.198669	.991

		1 - 4yrs	-.666774(*)	.186806	.029
		5 - 8yrs	-.679299(*)	.183808	.022
		9 - 12yrs	-.720597(*)	.195440	.019
		13 - 17yrs	-.819841(*)	.195885	.004
		Adult 18+	-.941452(*)	.179344	.000
	1 - 12mo	Foetus	.799004	.630729	1.000
		Birth - 1mo	.286602	.198669	.991
		1 - 4yrs	-.380172	.164958	.479
		5 - 8yrs	-.392698	.161554	.377
		9 - 12yrs	-.433996	.174675	.340
		13 - 17yrs	-.533240	.175173	.081
		Adult 18+	-.654850(*)	.156457	.002
	1 - 4yrs	Foetus	1.179177	.627093	.947
		Birth - 1mo	.666774(*)	.186806	.029
		1 - 12mo	.380172	.164958	.479
		5 - 8yrs	-.012525	.146720	1.000
		9 - 12yrs	-.053823	.161054	1.000
		13 - 17yrs	-.153067	.161594	1.000
		Adult 18+	-.274678	.141088	.788
	5 - 8yrs	Foetus	1.191702	.626206	.942
		Birth - 1mo	.679299(*)	.183808	.022
		1 - 12mo	.392698	.161554	.377
		1 - 4yrs	.012525	.146720	1.000
		9 - 12yrs	-.041298	.157565	1.000
		13 - 17yrs	-.140542	.158117	1.000
		Adult 18+	-.262153	.137093	.814
	9 - 12yrs	Foetus	1.233000	.629719	.924
		Birth - 1mo	.720597(*)	.195440	.019
		1 - 12mo	.433996	.174675	.340
		1 - 4yrs	.053823	.161054	1.000
		5 - 8yrs	.041298	.157565	1.000
		13 - 17yrs	-.099244	.171501	1.000
		Adult 18+	-.220855	.152335	.990
	13 - 17yrs	Foetus	1.332244	.629857	.866
		Birth - 1mo	.819841(*)	.195885	.004
		1 - 12mo	.533240	.175173	.081
		1 - 4yrs	.153067	.161594	1.000
		5 - 8yrs	.140542	.158117	1.000
		9 - 12yrs	.099244	.171501	1.000
		Adult 18+	-.121611	.152906	1.000
	Adult 18+	Foetus	1.453855	.624911	.771
		Birth - 1mo	.941452(*)	.179344	.000
		1 - 12mo	.654850(*)	.156457	.002
		1 - 4yrs	.274678	.141088	.788
		5 - 8yrs	.262153	.137093	.814
		9 - 12yrs	.220855	.152335	.990
		13 - 17yrs	.121611	.152906	1.000
Epi.Breadth	Foetus	Birth - 1mo	1.276000	.923895	1.000

	1 - 12mo	.143417	.338682	1.000
	1 - 4yrs	-.049619	.369754	1.000
	5 - 8yrs	-.310000	.363084	1.000
	9 - 12yrs	.075238	.363319	1.000
	13 - 17yrs	-.165933	.337936	1.000
	Adult 18+	-.158358	.327649	1.000
Birth - 1mo	Foetus	-1.276000	.923895	1.000
	1 - 12mo	-1.132583	.878951	1.000
	1 - 4yrs	-1.325619	.891385	1.000
	5 - 8yrs	-1.586000	.888639	.998
	9 - 12yrs	-1.200762	.888735	1.000
	13 - 17yrs	-1.441933	.878663	.999
	Adult 18+	-1.434358	.874758	1.000
1 - 12mo	Foetus	-.143417	.338682	1.000
	Birth - 1mo	1.132583	.878951	1.000
	1 - 4yrs	-.193036	.235988	1.000
	5 - 8yrs	-.453417	.225393	.843
	9 - 12yrs	-.068179	.225772	1.000
	13 - 17yrs	-.309350	.182134	.957
	Adult 18+	-.301774	.162251	.906
1 - 4yrs	Foetus	.049619	.369754	1.000
	Birth - 1mo	1.325619	.891385	1.000
	1 - 12mo	.193036	.235988	1.000
	5 - 8yrs	-.260381	.269842	1.000
	9 - 12yrs	.124857	.270159	1.000
	13 - 17yrs	-.116314	.234916	1.000
	Adult 18+	-.108739	.219860	1.000
5 - 8yrs	Foetus	.310000	.363084	1.000
	Birth - 1mo	1.586000	.888639	.998
	1 - 12mo	.453417	.225393	.843
	1 - 4yrs	.260381	.269842	1.000
	9 - 12yrs	.385238	.260955	.993
	13 - 17yrs	.144067	.224271	1.000
	Adult 18+	.151642	.208447	1.000
9 - 12yrs	Foetus	-.075238	.363319	1.000
	Birth - 1mo	1.200762	.888735	1.000
	1 - 12mo	.068179	.225772	1.000
	1 - 4yrs	-.124857	.270159	1.000
	5 - 8yrs	-.385238	.260955	.993
	13 - 17yrs	-.241171	.224651	1.000
	Adult 18+	-.233596	.208856	1.000
13 - 17yrs	Foetus	.165933	.337936	1.000
	Birth - 1mo	1.441933	.878663	.999
	1 - 12mo	.309350	.182134	.957
	1 - 4yrs	.116314	.234916	1.000
	5 - 8yrs	-.144067	.224271	1.000
	9 - 12yrs	.241171	.224651	1.000
	Adult 18+	.007576	.160689	1.000

Adult 18+	Foetus	.158358	.327649	1.000
	Birth - 1mo	1.434358	.874758	1.000
	1 - 12mo	.301774	.162251	.906
	1 - 4yrs	.108739	.219860	1.000
	5 - 8yrs	-.151642	.208447	1.000
	9 - 12yrs	.233596	.208856	1.000
	13 - 17yrs	-.007576	.160689	1.000

* The mean difference is significant at the .05 level.