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Humeral Torsion Revisited: A Functional and Ontogenetic Model for Populational Variation

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ABSTRACT Anthropological interest in humeral torsion has a long history, and several functional explanations for observed variation in the orientation of the humeral head have been proposed. Recent clinical studies have revived this topic by linking patterns of humeral torsion to habitual activities such as overhand throwing. However, the precise functional implications and ontogenetic history of humeral torsion remain unclear. This study examines the ontogeny of humeral torsion in a large sample of primarily immature remains from six different skeletal collections ($n = 407$). The results of this research confirm that humeral torsion displays consistent developmental variation within all populations of growing children; neonates display relatively posteriorly oriented humeral heads, and the level of torsion declines steadily into adulthood. As in adults, variation in the angle of humeral torsion in immature individuals varies by population, and these differences arise early in development. However, when examined in the context of the developing muscles of the shoulder complex, it becomes apparent that variation in the angle of humeral torsion is not necessarily related to *specific* habitual activities. Variability in this feature is more likely caused by a generalized functional imbalance between muscles of medial and lateral rotation that can be produced by a wide variety of upper limb activity patterns during growth. Am J Phys Anthropol 134:472–480, 2007. © 2007 Wiley-Liss, Inc.

Individual variation in the degree of torsion of the humeral head has been widely discussed within anthropological literature over the course of the 20th century, and patterns of variation by population, side, and sex have been documented. This feature, defined as the angle formed between the proximal midhumeral axis and the distal articular axis of the humerus, has received renewed attention due to more recent research in the field of sports medicine, which has linked the development of a posteriorly oriented humeral head to the habitual activity of overhand throwing in professional and collegiate baseball and handball players (Pieper, 1998; Crockett et al., 2002; Osbahr et al., 2002; Reagan et al., 2002).

While the association of humeral torsion with a specific habitual activity is suggestive of an underlying functional cause for this morphological pattern, it does not entirely clarify the precise biomechanical and muscular forces acting during ontogeny that produce variation in this feature. This research specifically tests the hypothesis that levels of humeral torsion vary throughout ontogeny in six skeletal samples of immature humeri. The results of this analysis are then combined with information on the mechanics of the shoulder girdle musculature during growth in order to develop a new explanatory model that draws together both functional and ontogenetic perspectives for interpretation of adult variation in humeral torsion.

CURRENT AND HISTORICAL PERSPECTIVES ON HUMERAL TORSION

While the first description of humeral torsion dates to the 18th century, more thorough analyses were not undertaken until later in the 19th and 20th centuries (Bertin, 1754; Winslow, 1763; Meyer, 1856; Martins, 1857; Gegenbaur, 1868; Albrecht, 1875; Broca, 1881; Durand de Gros, 1887; LeDamany, 1903; Braus, 1906; Grunewald, 1919; Rouffiac, 1924; Martin, 1933, 1958; Evans and Krahl, 1945; Krahl and Evans, 1945; Krahl, 1947, 1976; Kate, 1968). Historically, much attention has been focused on documenting differences in degrees of humeral torsion between populations. Reported means for adult populations vary from a low of 3° to a high of 55°, but most populations fall closer to the middle of this range (~25°–35°) (Broca, 1881; Martin, 1933, 1958; Krahl and Evans, 1945; Kate, 1968; Kronberg et al., 1990; Edelson, 2000). In the few studies that summarize data from multiple groups, several patterns can be discerned. Generally, urban western Europeans tend to have more medially oriented humeral heads, while posteriorly oriented humeral heads are found in physically active populations, such as Melanesians and Australian Aborigines (Broca, 1881; Martin, 1933, 1958; Krahl and Evans, 1945). When sex differences are examined, males often possess more posteriorly oriented humeral heads than females (Broca, 1881; Martin, 1933, 1958; Krahl and Evans, 1945; Edelson, 1999). Lastly, side differences have been observed, with the right humeral head tend-

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ing to be more posteriorly oriented in comparison to the left (Broca, 1881; Krahl and Evans, 1945; Martin, 1958; Kronberg et al., 1990).

Despite the diversity of available data describing variation in humeral torsion, no consensus has been reached as to the ultimate anatomical and functional factors that produce the documented patterns, and little agreement exists regarding how this feature should be interpreted in archaeological samples. However, a wide variety of possible causes have been suggested. Albrecht (1875) and Braus (1906) argued that humeral torsion was initiated by embryological rotation of the forearm, and that the present location and orientation of the humerus was simply a byproduct of a 180° rotation of the radius around the ulna during limb development. Several researchers have claimed that the development of humeral torsion is triggered by the dorso-ventral flattening of the thorax and an accompanying dorsal migration of the scapula during growth (Fick, 1904; Grunwald, 1919; Braus, 1929), or that variation in humeral torsion angles is partially a product of scapular orientation and thorax shape (Vandermeersch and Trinkaus, 1995; Churchill, 1996). More recently, a possible link between variation in the angle of humeral torsion and the shape and width of the deltoid tuberosity has been suggested (Carretero et al., 1997). Other researchers, however, have preferred a more explicitly functional approach to the issue, although much of this research has viewed humeral torsion as a consequence of muscular contractions operating in opposing directions on the proximal and distal ends of the humerus, resulting in "twisting" of the element (LeDamany, 1903; Rouffiac, 1924; Martin, 1933; Kate, 1968). Krahl (1947) suggested that the medial and lateral rotators might play a role in the production of variation in humeral torsion.

Recent clinical studies have revived discussion of this topic by linking patterns of humeral torsion to habitual activities such as overhand throwing in baseball, further supporting the idea that a functional approach to understanding humeral torsion is appropriate. Several studies have found that, in contrast to nonthrowing control groups, individuals who engage in overhand throwing activity during adolescence and young adulthood display high levels of bilateral asymmetry in their angle of humeral torsion, with the dominant throwing arm possessing a more posteriorly oriented humeral head (Pieper, 1998; Crockett et al., 2002; Osbahr et al., 2002; Reagan et al., 2002). Pieper (1998) found that the difference in humeral torsion between the dominant throwing and contralateral arms in professional handball players averaged 9.4°, with a side-to-side difference of up to 29°. In contrast, no statistically significant differences were found between right and left arms in the nonthrowing control groups (Pieper, 1998; Crockett et al., 2002).

In light of this research, new attempts have recently been made to integrate modern methods of analysis with the recent body of medical literature in order to better understand variation in proximal humeral morphology in archaeological skeletal samples (Rhodes, 2002, 2006; Gjerdrum et al., 2003; Rhodes and Knüsel, 2005). Rhodes (2006) tested the hypothesis that humeral torsion is an adaptation to repetitive upper limb use in several British medieval skeletal samples and a modern cadaver-derived assemblage. Given the humeral alterations characteristic of the professional throwing athlete, Rhodes suggested that medieval populations known to be engaging in strenuous weapons training might display similar changes in humeral architecture. While statistically significant differences were found between the samples analyzed, the results were not congruent with expectations based on behavior patterns. The cadaver-derived sample, which was predicted to be the least strenuously active group, had more posteriorly oriented humeral heads than three of the medieval samples, and statistically significant sex differences were detected in only two of the five samples analyzed despite expected differences in the sexual division of labor. Rhodes suggested that an individual rather than population-based approach to the study of humeral torsion is needed, as population behavioral heterogeneity can obscure individual variation in activity patterns.

In addition to the lack of compatibility between observed patterns of humeral torsion and documented habitual behaviors, attempts to correlate humeral torsion with other measures of habitual upper limb use have yielded complex results. Rhodes and Knüsel (2005) examined the relationship between cross-sectional geometric properties and humeral torsion angles in medieval individuals with and without osteological evidence of blade-induced trauma. While humeral torsion is correlated with diaphyseal robusticity, the direction of the correlation does not vary in a consistent fashion. Among blade-injured individuals, as the angle of humeral torsion increases, humeral diaphyseal robusticity decreases. The opposite was found in the non blade-injured sample: humeral torsion and cross-sectional properties exhibited a positive correlation, with the angle of humeral torsion increasing with diaphyseal robusticity.

RESEARCH OBJECTIVES

To better understand variability in adult levels of humeral torsion, a comprehensive functional and developmental approach to this question should be employed. Although a few studies have noted variability in humeral torsion during ontogeny (Gegenbaur, 1868; Krahl, 1947; Edelson, 2000), the developmental trajectories of humeral torsion have not yet been investigated in multiple populations. The goal of this article is to investigate for the first time the relationship between humeral torsion and growth in multiple samples of immature individuals. Specifically, several research questions will be addressed:

1a. What is the pattern of variation in humeral torsion during growth?
 b. When are adult levels of humeral torsion attained?
2a. Does the pattern of variation in humeral torsion differ by population during growth?
 b. If so, when do populational differences in levels of humeral torsion emerge?
3. Does bilateral asymmetry in humeral torsion vary with age?
4a. Does the pattern of variation in humeral torsion differ by sex during growth?
 b. If so, when do sex differences in levels of humeral torsion emerge?

The results of this analysis will be interpreted in the context of current medical literature in order to present a more complete picture of the functional and developmental processes that produce adult populational and individual variation in this feature. On the basis of information derived from an approach combining both ontogenetic and biomechanical approaches, a model explaining the populational variation in this feature is proposed.

MATERIALS AND METHODS

Quantification of humeral torsion

The measurement of humeral torsion in adults has been previously defined as the angle formed by the proximal midhumeral axis and the distal articular axis (Evans and Krahl, 1945; Rhodes, 2006). In mature humeri, the proximal midhumeral axis bisects the proximal articular surface, dividing it into anterior and posterior halves, and the distal articular axis passes through the center of the capitulum and trochlea (Evans and Krahl, 1945; Kate, 1968; Rhodes, 2006). Recently, confusion has resulted from the wide variety of methods used to quantify and report this measurement within the historical anthropological and recent clinical literature (Larson, 2007; Rhodes, 2007). Unlike previous anthropological research, this study does not take an evolutionary approach to the investigation of humeral torsion, and follows the standard of measurement set by Rhodes (2006). Thus, the acute angle between the distal and proximal axes is reported, and greater angles of humeral torsion are indicative of a more posteriorly oriented humeral head. The values reported here are then more similar to those in the clinical literature on humeral "retroversion," but are perhaps not directly comparable to measurements taken on living individuals (Pieper, 1998; Crockett et al., 2002; Osbahr et al., 2002; Reagan et al., 2002; van der Sluijs et al., 2002).

Due to missing epiphyses in the immature humeri of the skeletal collections analyzed, the exact orientation used to measure adult humeri cannot be replicated with unfused humeral diaphyses. Care was taken, however, to ensure that the measurements generated from immature humeri were as equivalent as possible to those taken from fully fused adult elements. The angle of humeral torsion in immature, unfused humeri is defined here as the acute angle between the axis bisecting the proximal metaphyseal surface, and the transverse axis of the distal metaphyseal surface (Fig. 1). The distal metaphyseal axis was determined using a transverse line evenly dividing the distal metaphyseal surface into anterior and posterior halves. The distal ends of the unfused humeri were oriented along this axis using reference lines marked on graph paper. The proximal metaphyseal axis passed through the maximum diameter of the proximal metaphyseal surface, and bisected the elliptical surface of the proximal metaphysis into two even segments. This axis was identified and marked as a straight line on the proximal metaphysis, using clear tape to protect the surface of the bone. The level of intraobserver error produced by this measurement technique was assessed using a subset of 10 immature humeri ranging in age from 6 months to 15 years, which were measured twice on two consecutive days. Differences between the first and second measurements ranged between 1° and 4°.

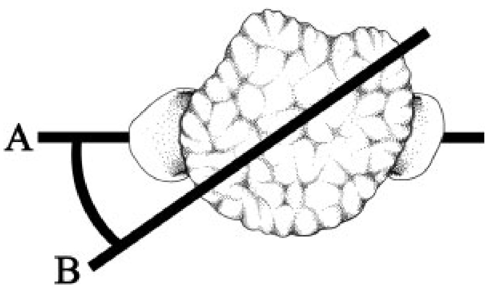

Fig. 1. Superior view of an unfused humerus illustrating the axes of orientation for the measurement of humeral torsion in immature individuals. Line A is the approximate location of the transverse axis of the distal metaphyseal surface. Line B is the axis bisecting the proximal metaphyseal surface. The angle of humeral torsion is the acute angle formed by these two axes.

Despite the similarity of the earlier measurement to the conventional quantification of humeral torsion in adults, the angles of humeral torsion taken on mature versus immature humeri are not directly comparable. Discrepancies between the two methods are produced by slight differences in the orientation of the distal axis in fused and unfused humeri; the trochlea and capitulum fuse to the distal humeral metaphysis at a slightly different angle from that of the transverse axis of the metaphyseal surface. Five adolescent humeri with fusing proximal and distal epiphyses but still retaining clear lines of epiphyseal union were measured twice using the two orientations in order to quantify the difference between the two methods. First, the specimen was oriented using a transverse line through the distal metaphyseal surface, and second, the humerus was positioned using the articular axis bisecting the newly fused trochlea and capitulum. Values from humeri oriented based on the fused distal articular axis were, on average, 10° greater than values based on orientation with the distal metaphyseal surface (range: 7°–14°). To maintain constancy across all ages, all adolescent humeri, regardless of the state of fusion of the distal end, were oriented based on the distal metaphyseal surface.

Samples

Six skeletal collections containing a total of 407 individuals were used for this analysis (Table 1). The majority of the sample is comprised of individuals between the ages of birth and 17.9 years ($n = 369$). In addition, humeral torsion was measured in a small subsample of individuals between 18 and 30 years in order to estimate the approximate level of adult humeral torsion in each sample ($n = 38$). While it is difficult to know specific details of habitual patterns of upper limb use, these samples were selected in order to represent a probable diverse selection of lifeways and activity patterns. Four of the six samples are from nonurban, nonmechanized societies (Mistihalj, Indian Knoll, Point Hope, and California Amerindian), and of these, the latter three derive from semi-sedentary foraging populations. In contrast, the Dart collection material is an ethnically mixed, both urban and nonurban sample of Sub-Saharan Africans, and the Lúis Lopes collection is comprised of urban, 20th century Portuguese. The angle of humeral torsion of the right humerus was recorded for all individuals in the six samples. In both the Lúis Lopes and Indian Knoll samples, humeral torsion for both right and left humeri was collected. Since both the Lúis Lopes and Dart collections are cadaver-derived samples, data indicating sex of the individuals was also available.

For five of the six samples, lateral mandibular radiographs were taken from associated dental material when available, and crown and root formation standards following Smith (1991) and Liversidge and Molleson (2004) were used to assess developmental age for each individual. The Lúis Lopes collection was not dentally aged, as it is associated with reliable known ages from civil registrations of birth and death (Cardoso, 2005). Among the five samples for which age was unknown, it was possible to dentally age 74% of the individuals. When associated

TABLE 1. Sample description, sizes, and location. Percentage of each sample dentally aged, and the r^2 *for the age-prediction regression based on femur or tibia length*

Sample	Sample description	Location	*N*	Percentage dentally aged	r^2 for age regression
Dart collection	20th century, ethnically mixed southern Africans	University of Witwatersrand, Johannesburg, South Africa	94	88.0%	0.890
Mistihalj	Medieval eastern Europeans from Serbia	Harvard Peabody Museum	49	85.7%	0.877
Indian Knoll	North American Archaic period Native Americans from Kentucky	University of Kentucky at Lexington	96	77.3%	0.922
Point Hope	Pre- and proto-historic Alaskan Inuits	American Museum of Natural History	44	68.2%	0.888
California Amerindian	Mixed sample of Native American remains from multiple sites in Northern California	Phoebe Hearst Museum, University of California, Berkeley	89	57.3%	0.928
Luis Lopes collection	20th century, urban western Europeans from Lisbon, Portugal	Bocage Museum, Lisbon, Portugal	35	Known age	Known age
Total			407	74.4%	

dental material was not available, age was assessed using a population-specific least squares regression of femur or tibia length against age. Percentage of individuals dentally aged in each sample and r^2 for the age-prediction regression formulae are listed in Table 1.

To address research questions 1b, 2b, and 4b, the immature sample was collapsed into age categories. It is necessary that these categories be narrow enough to have biological relevance, but broad enough to account for any potential aging errors and encompass individuals of roughly similar developmental stages. For the analyses utilizing a larger number of individuals (1b and 2b), skeletal age categories are 0–1.9 years, 2–5.9 years, 6–9.9 years, 10–13.9 years, 14–17.9 years, and adults. Because of the limited number of available individuals of known sex, the age categories for research question 4b must be somewhat broader: 0–5.9 years, 6–11.9 years, 12–17.9 years, and adults.

Statistical analysis

Right humeral torsion was regressed on age in order to evaluate the pattern of variation in humeral torsion during growth (research question 1). Reduced major axis (RMA) regression was chosen over Least Squares regression due to the probability of error in both dependent and independent variables (Sokal and Rohlf, 1981). The sample was then subdivided into smaller age categories, and age category means and confidence intervals were used to determine when adult levels of humeral torsion are attained (research question 1b).

Unstandardized residuals from the regression of right humeral torsion on age were used to test for population differences between samples (research question 2 and 2b). Analysis of variance (ANOVA) was used to assess population differences across all age groups; due to small and uneven sample sizes in subdivided age categories, nonparametric statistics (Kruskal-Wallis) were used to evaluate population differences in specific age categories and to determine the age at which population differences arise.

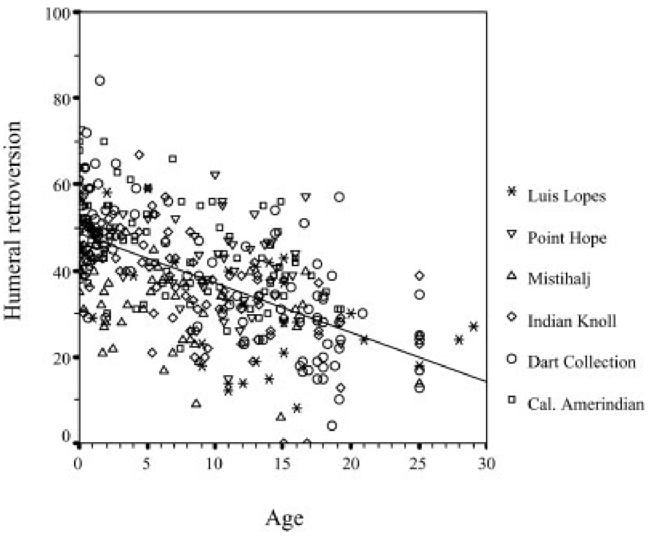

Fig. 2. RMA regression of right humeral torsion on age.

To determine how bilateral asymmetry varies with age (research question 3), asymmetry in the angle of torsion was calculated as the absolute difference between the two sides. RMA regression of bilateral asymmetry on age was used to analyze the relationship between these variable during growth. Differences between males and females in the degree of humeral torsion were assessed using *t*-tests of unstandardized residuals from the regression of humeral torsion on age (research question 4 and 4b).

RESULTS

Humeral torsion decreases with age, with infants between birth and 2 years postnatal displaying the highest values (HUM RETRO = (AGE × −2.01) + 48.78,

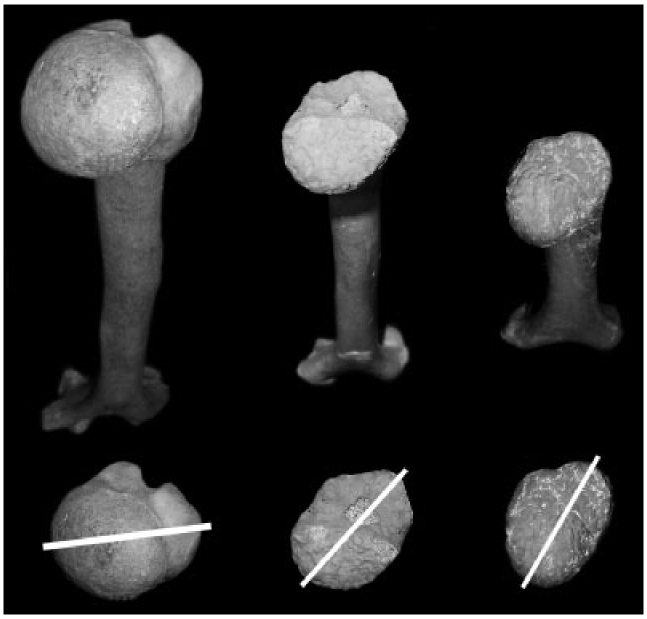

Fig. 3. Age series of approximate levels of humeral torsion in an adult, an adolescent, and an infant (not to scale).

TABLE 2. Age category means, samples sizes, ranges, and confidence intervals for angle of humeral torsion

Age	Sample size	Mean	Confidence interval	Range
Category 1 (0–1.9 years)	107	48.5°	46.5°–50.6°	21°–84°
Category 2 (2–5.9 years)	65	45.9°	43.4°–48.4°	21°–67°
Caregory 3 (6–9.9 years)	66	36.2°	33.4°–39.0°	9°–66°
Category 4 (10–13.9 years)	69	34.4°	31.5°–37.3°	12°–62°
Category 5 (14–17.9 years)	62	32.2°	29.0°–35.5°	0°–57°
Category 6 (Adults)	38	25.1°	21.9°–28.2°	4°–57°

$P < 0.001$, $r^2 = 0.331$). Humeral torsion decreases linearly until adulthood in all six immature samples (Figs. 2 and 3). Age category means, sample sizes, ranges, and confidence intervals are shown in Table 2.

Comparison of residuals from the regression of humeral torsion on age indicates that populations do differ in their level of humeral torsion during ontogeny ($P < 0.001$). Specific differences between populations are shown in Table 3. The order of the samples, from highest to lowest degree of humeral torsion, is Point Hope, California Amerindian, Dart collection, Indian Knoll, Mistihalj and Lúis Lopes, respectively. In general, the analysis of variance reflects this, with most of the statistically significant differences found between the Lúis Lopes and Mistihalj samples, on one hand, and the Point Hope, California Amerindian, Indian Knoll, and Dart collection samples, on the other.

TABLE 3. Tukey HSD results showing sample specific means and P-values in analysis of humeral torsion residuals

Sample	Compared with	*P*-value
California Amerindian (Residual mean = 3.94)	Dart	0.645
	Indian Knoll	0.003*
	Mistihalj	0.645
	Point Hope	0.968
	Luis Lopes	0.001*
Dart Collection (Residual mean = 1.61)	California Amerindian	0.645
	Indian Knoll	0.219
	Mistihalj	<0.001*
	Point Hope	0.645
	Luis Lopes	0.040*
Indian Knoll (Residual mean = −1.75)	California Amerindian	0.003*
	Dart	0.219
	Mistihalj	0.003*
	Point Hope	0.002*
	Luis Lopes	0.784
Mistihalj (Residual mean = −8.56)	California Amerindian	<0.001*
	Dart	<0.001*
	Indian Knoll	0.003*
	Point Hope	<0.001*
	Luis Lopes	0.448
Point Hope (Residual mean = 5.45)	California Amerindian	0.968
	Dart	0.321
	Indian Knoll	0.002*
	Mistihalj	<0.001*
	Luis Lopes	<0.001*
Luis Lopes (Residual mean = −4.40)	California Amerindian	0.001*
	Dart	0.040*
	Indian Knoll	0.784
	Mistihalj	0.448
	Point Hope	<0.001*

* Indicates values signifcant at $\alpha = 0.05$.

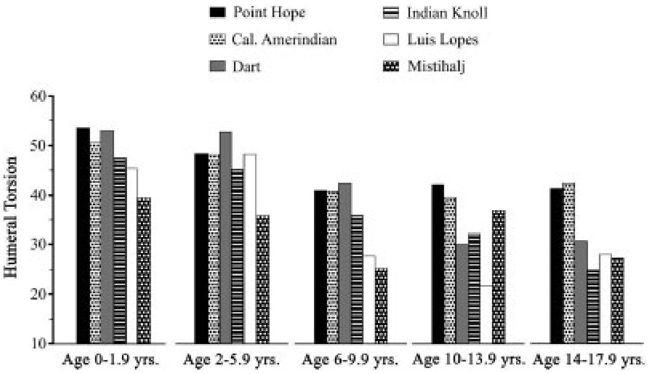

Fig. 4. Bar graph of humeral torsion age category means by population.

These populational differences exist throughout ontogeny and, despite small sample sizes in some of the age categories, statistically significant differences between the six samples are present from birth to 17.9 years. Although there are a few minor fluctuations in the pattern likely due to small sample sizes within age categories, the relative level of humeral torsion within a given population is generally stable throughout ontogeny (Fig. 4). Age category means, sample sizes, confidence intervals, and *P*-values for the nonparametric test of population differences in specific age categories are shown in Table 4.

While there is a slight positive correlation between bilateral asymmetry and age when adults are included in the regression ($P = 0.012$), this relationship disappears when adults are removed from the analysis. There is no relationship between age and the level of bilateral asymmetry in humeral torsion under the age of eighteen ($P = 0.912$). *T*-tests of residuals from the regression of humeral torsion on age for males and females indicate that while males do display higher levels of humeral torsion across all age categories (male $\bar{X} = 1.17$, female $\bar{X} = -1.96$), this difference is

TABLE 4. Age category, sample-specific humeral torsion means, samples sizes, confidence intervals, Kruskal-Wallis P*-values*

	Samples						
Age Category	California Amerindian	Dart	Indian Knoll	Mistihalj	Point Hope	Luis Lopes	*P*-value
0–1.9 years							
Mean	50.5°	53°	47.5°	39.4°	53.6°	45.3°	>0.001
N	26	29	24	19	6	3	
C.I	46.5°–54.4°	53.0°–57.2°	44.2°–50.8°	35.1°–43.7°	42.9°–64.3°	9.1°–1.5°	
2–5.9 years							
Mean	48.2°	52.7°	45.2°	35.8°	48.3°	48.2°	0.013
N	19	6	18	10	6	6	
C.I	43.6°–52.8°	43.1°–62.2°	40.1°–50.3°	30.0°–41.6°	42.8°–53.7°	38.5°–57.8°	
6–9.9 years							
Mean	40.7°	42.4°	35.9°	25.1°	40.8°	27.7°	0.004
N	17	7	21	11	7	3	
C.I	34.8°–46.6°	34.1°–50.7°	31.2°–40.5°	19.1°–31.1°	34.0°–47.6°	−3.9°–59.1°	
10–13.9 years							
Mean	39.5°	30.0°	32.2°	37.0°	42.0°	21.7°	0.002
N	13	11	17	2	17	9	
C.I	34.1°–45.0°	25.5°–34.4°	28.8°–35.6°	−1.1°–75.1°	35.7°–48.3°	9.0°–34.3°	
14–17.9 years							
Mean	42.3°	30.6°	24.8°	27.2°	41.3°	28.0°	0.002
N	11	19	11	5	7	9	
C.I	38.1°–46.4°	24.8°–36.3°	15.9°–33.7°	11.4°–43.0°	32.7°–49.9°	18.9°–37.1°	

not statistically significant ($P = 0.481$). It remains possible, however, that the lack of statistically significant results in these analyses is partially be a reflection of the relatively smaller available sample sizes.

DISCUSSION

While humeral torsion does decrease by ~25° from birth to adulthood, it is difficult to determine when adult levels of torsion are attained. The adult mean and confidence interval ($\bar{X} = 25.1°$, CI = 21.9°–28.2°) does not overlap with that of the 14 to 18-year-olds ($\bar{X} = 32.2°$, CI = 29.0°–35.5°). Previous research with limited samples has suggested that ontogenetic change in the angle of humeral torsion ceases between 16 and 20 years of age (Krahl, 1947; Edelson, 2000), and it remains possible that the age category used in this study is too broad to detect this. In addition, individual variation in humeral torsion is great (Rhodes, 2006). The adult range of values (4°–57°) is so large that it actually encompasses the mean of all the age categories, including the relatively high values of individuals between birth and 1.9 years.

Population differences coincide with expectations based on activity level, although there are some discrepancies. Levels of humeral torsion are generally elevated in the populations predicted to be participating in high levels of strenuous activity and lower in less active, more urban groups. Higher levels of humeral torsion in the Point Hope and California Amerindian populations are consistent with this prediction, as are the relatively lower values of the urban Portuguese from the Luis Lopes sample. The Mistihalj sample, however, is derived from a nonmechanized medieval agricultural population, and it is perhaps surprising that this group possesses the lowest angles of humeral torsion, falling below the more urban samples. The overall pattern, however, does not drastically depart from expectations, and the deviation of the Mistihalj sample may reflect inaccurate predictions of actual upper limb use from the broad subsistence categories used here.

On the other hand, these differences may partially be explained by the early onset of populational differences in the level of humeral torsion. While the analysis of populational differences in humeral torsion by age category does suffer from low sample sizes in some of the age groups, it is clear that these differences manifest at an early age during growth. Differences in the level of humeral torsion are already present between birth and 1.9 years, with the three samples that display the lowest levels of humeral torsion overall (Indian Knoll, Mistihalj, and Luis Lopes) already demonstrating lower age-specific means in the youngest age categories. Although childhood activities and/or play are likely important to the production of developmental variation in humeral torsion, it seems improbable that these factors are strongly influencing individuals prior to the age of two. Therefore, while the presence of bilateral asymmetry in adult humeral torsion angles implies a strong functional influence, the early manifestation of populational differences suggests a genetic component to group differences in humeral torsion.

Functional models for changes in humeral torsion during growth

In order to understand populational patterns of variation in humeral torsion, the results of the earlier analyses should be combined with previous research in both anthropology and medicine. Placing what is currently known about this feature in the context of development and functional morphology may provide insight into why previous analyses have experienced difficulty in consistently correlating levels of humeral torsion with specific activities.

Obstetrical brachial plexus injuries in infants and children. Information on growth pathologies of the shoulder complex in infants and children can provide insight into the normal muscular forces acting on the humerus during development. Although the measurements used to quantify shoulder girdle pathologies in the clinical literature differ from those used here, examples derived from growth under abnormal conditions may provide a useful heuristic device for understanding normal developmental processes. Brachial plexus injuries during birth affect as many as 0.4% of births in populations with poor medical facilities (Hardy, 1981; Narakas, 1987). Injury to the brachial plexus of the infant can result from extreme lateral traction of the infant's head and shoulder during the last phase of delivery, stretching or avulsing the nerve roots of C5 through T1 (Narakas, 1987; Clarke and Curtis, 1995). If the injury only affects the upper roots of the brachial plexus (C5, C6, and sometimes C7, e.g. Erb's palsy), the injury manifests as adduction and internal rotation of the shoulder, extension of the elbow, pronation of the forearm, and flexion of the wrist and fingers (Clark and Curtis, 1995). In more severe cases, the entire brachial plexus is affected, which presents as complete atonia of the arm (Clark and Curtis, 1995). In cases of permanent neurological damage, skeletal changes to the affected shoulder result. The humeral head of the shoulder affected by the obstetrical brachial plexus injury is significantly more retroverted and subluxated than the humeral head of the normal shoulder on the contralateral side (Waters et al., 1998; van der Sluijs et al., 2002).

These changes to the humeral architecture in the injured shoulder are produced by a muscular imbalance between the muscles of medial and lateral rotation (L'Episcopo, 1934; Birch, 1998). The primary muscles affected by obstetrical brachial plexus birth injury are adductors and lateral rotators, creating a functional imbalance where the less affected medial rotators overpower the atrophied lateral rotators, resulting in increased humeral torsion on the injured side (Birch, 1998; van der Sluijs et al., 2002). MRI studies of the rotator cuff in infants with obstetrical brachial plexus damage indicate that all the muscles of the rotator cuff are atrophied, and that the degree of rotator cuff atrophy is positively correlated with posterior displacement of the humeral head (Pöyhiä et al., 2005). Clinicians have actively used this knowledge to treat the osteological deformities on the injured side; a common surgical procedure used to correct the posteriorly oriented humeral head is transplantation of tendons from the latissimus dorsi and teres major muscles to the insertions sites of the rotator cuff, essentially transforming medial rotators to lateral rotators and correcting the imbalance (L'Episcopo, 1934; Waters, 1999; Waters and Bae, 2005).

This balance between medial and lateral rotators appears to be critical for the normal pattern of development and the decrease in humeral torsion with age illustrated in the earlier analyses. In the absence of normal rotator cuff activity, medial rotation of the humeral head does not occur during growth. Without normally functioning muscles of lateral rotation, pectoralis major, latissimus dorsi, and teres major, which act to medially rotate the humeral diaphysis, are exerting the primary muscular force on the growing humerus. Unopposed, this force results in a more anterioposterior orientation of the proximal midhumeral axis of the humeral head (Fig. 5B). In an individual with normal muscular balance, the muscles of the rotator cuff (particularly the primary lateral rotators infraspinatus and teres minor) exert a counterbalancing force that rotates the humeral diaphysis laterally, and result in a more mediolateral orientation of the proximal midhumeral axis of the humeral head (Fig. 5A). Under the influence of medial rotators without antagonistic lateral rotators, the humeral head on the injured side of infants with brachial plexus injuries remains posteriorly oriented, while the undamaged humeral head on the contralateral side continues to undergo a normal developmental trajectory.

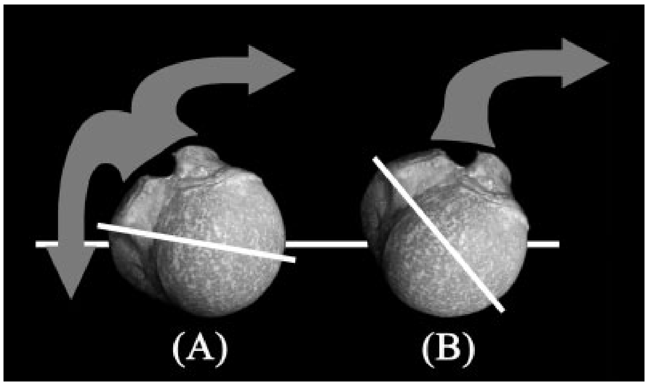

Fig. 5. Illustration of muscular forces acting on the left humeral head in a normal individual (**A**) and an individual with a functional imbalance between medial and lateral rotators (**B**). Horizontal line represents the orientation of the transverse axis of the distal metaphyseal surface. Lines bisecting the humeral head illustrate the contrasting degrees of humeral torsion. In the normal individual (A), balanced forces of medial and lateral rotators produce a modest degree of humeral torsion. In the individual with a functional imbalance (B), unopposed forces of medial rotators results in a more posterior orientation of the humeral head.

Balance of medial and lateral rotators in throwing athletes. As noted previously, the other population in which increased humeral torsion has been well documented is the professional throwing athlete (Pieper, 1998; Crockett et al., 2002; Osbahr et al., 2002; Reagan et al., 2002). A closer inspection of the sport medicine literature illustrates that professional throwing athletes experience the same imbalance of medial and lateral rotators that are characteristic of individuals with obstetric brachial plexus injuries. In this case, however, this imbalance seems to be a product of a slight reduction in the power of the muscles of lateral rotation in combination with a dramatic increase in the power of muscles in medial rotation. In comparison to nonthrowing controls, throwing athletes display relatively stronger muscles of medial rotation (Cook et al., 1987; Brown et al., 1988; Hinton, 1988; Ellenbecker and Mattalino, 1997; Donatelli et al., 2000; Falla et al., 2003; Nofal, 2003; Mulligan et al., 2004) and slightly weaker muscles of lateral rotation (Cook et al., 1987; Hinton, 1988; Wilk et al., 1993; Mikesky et al., 1995; Donatelli et al., 2000).

In particular, the ratio of medial to lateral rotation strength in throwers is higher than nonthrowing controls and athletes in other sports (Cook et al., 1987; Wilk et al., 1993; Codine et al., 1997; Nofal, 2003). Due to their greater number and size, medial rotator strength is always greater than lateral rotator strength, with a ratio ranging from 1.3 to 1.5 in normal, nonthrowing adults (Ivey et al., 1985; Murry et al., 1985). Baseball players, however, display ratios higher than the general population and other athletes, possibly reflecting both increased medial rotation strength and decreased lateral rotation strength. When Codine et al. (1997) compared the ratio of medial to lateral rotation strength in baseball players, tennis players, runners, and nonathletes, the baseball players showed consistently higher ratios of medial to lateral rotation strength, with values ranging from 1.69 to 1.81, in contrast to both nonathletes and runners, whose ratios were between 1.28 and 1.32. In addition, throwing athletes also exhibit a difference in strength ratios between their dominant and nondominant arms, with higher ratios of medial to lateral rotation strength on the dominant side, which reflects the pattern of humeral torsion seen in this group (Cook et al., 1987; Hinton, 1988; Ellenbecker and Mattalino, 1997; Donatelli et al., 2000; Mulligan et al., 2004).

Interpreting variation in humeral torsion in adult skeletal samples. Evidence from the clinical literature clearly indicates that habitual overhand throwing results in a muscular imbalance between medial and lateral rotators and thus, in high levels of humeral torsion. Therefore, it is entirely plausible that repetitive overhand throwing had an influence on proximal humeral architecture in past populations. The application of this research hypothesis to the analysis of archaeological and paleontological samples may indeed be fruitful, particularly if information is known about the relative homogeneity of the given population's subsistence activities.

It is still valuable, however, to consider the broader patterns of humeral growth and functional morphology of the proximal humerus, and their relationship to the production of humeral torsion. During growth, it appears that individuals with more posteriorly oriented humeral heads possess relatively powerful muscles of medial rotation that have essentially stopped the developmental medial rotation of the humeral head. Despite the link between overhand throwing and elevated levels of humeral torsion, it may remain difficult to link high levels of humeral torsion in a given population to any one specific activity, as they could be produced by a wide range of upper limb activity patterns. It is not the activity of throwing *per se* which results in the higher angles of humeral torsion; all repetitive activities during growth that create a functional imbalance resulting in relatively more powerful muscles of medial rotation can produce this morphology.

In addition, the early onset of population differences in proximal humeral morphology indicates a probable genetic influence on humeral torsion, which could contribute to difficulties detecting populational differences in upper limb usage with this feature. Caution should therefore be taken when drawing conclusions about upper limb activities across genetically diverse samples based on levels of humeral torsion. More success in correlating this feature with patterns of activity may be achieved if the genetic variability of populations in a given analysis is sufficiently limited, and the diversity of upper limb activities that result in elevated levels of humeral torsion is kept in mind. Nonetheless, while humeral torsion may indeed have a genetic component, the high levels of bilateral asymmetry and clear association between this feature and specific patterns of muscular balance indicates that much of the variation in humeral torsion is epigenetic, and that valuable insight into patterns of upper limb usage may still be gained through the analysis of this feature.

CONCLUSION

This research has highlighted several issues important to the interpretation of variation in humeral torsion in skeletal samples. First, humeral torsion decreases linearly with age between birth and adulthood, and populations differ in their relative levels of humeral torsion over this time period. Second, population-level differences in degree of humeral torsion appear very early during growth, suggesting there may be a genetic component to this feature. Third, these innate differences are likely enhanced by differences in upper limb use over the life of the individual. Although high or low levels of humeral torsion in the adult cannot be tied to a specific repetitive activity, they are likely a product of activity patterns that result in a functional imbalance between muscles of medial and lateral rotation. The wide range of possible habitual upper-limb activities that could potentially result in elevated levels of humeral torsion should be considered when interpreting skeletal variation in this feature.

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