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News and views Humeral torsion and throwing proficiency in early human evolution

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Background

In their recent paper, "Clavicle length, throwing performance and the reconstruction of the *Homo erectus* shoulder," Roach and Richmond (2015) test the hypothesis that relative clavicular length predicts scapular position and explore whether or not variation in relative clavicular length in a sample of modern humans from northwestern Kenya is correlated to throwing performance. Since the impetus to undertake these analyses is in part based on supposed claims I have made in my research on hominin shoulder evolution, I feel compelled to correct some misrepresentations they make of my work.

The shoulder of *H. erectus*

The references I have made to relative clavicular length in my investigation of hominin shoulder evolution (Larson et al., 2007; Larson, 2007, 2009, 2013) concern a potential means of functionally interpreting the very low degree of humeral torsion typifying early hominins and early *Homo*. Contrary to the claim of Roach and Richmond (2015:108). I have not suggested that a more lateral position for the scapula in early *Homo* and an anterior facing shoulder joint was "necessary to allow early *H. erectus* to overcome deficits in internal shoulder rotation caused by very low humeral torsion." What I have argued is that the very low degree of humeral

torsion that has been documented for all early hominins and early *Homo* would result in a reduced range of internal shoulder rotation if these taxa had a dorsal scapular position similar to that of modern humans. The difference here concerns what is cause and what is effect. I contend that given our current understanding of the factors influencing humeral torsion, the very low degree of torsion in early *H. erectus* is surprising, and to explain why I believe this to be the case I will digress briefly with the following overview.

Humeral torsion

Humeral torsion refers to the orientation of the proximal articular surface relative to the distal end of the humerus (Fig. 1). The use of the distal humerus as a reference is not simply a convenience. The elbow in virtually all mammals is a unidirectional hinge joint with little if any rotational mobility. What flexibility in hand positioning that exists in a taxon depends on the range of motion available at the shoulder coupled with forearm pronation/ supination mobility. Therefore, the functional plane of elbow flexion/extension depends on the configuration of the glenohumeral joint. Intuitively, an elevated degree of humeral torsion (humeral head facing more inward) in humans and apes is related to the dorsal position of their scapulae since this results in more laterally facing glenoid fossae. The shift from a laterally positioned scapula on a dorsoventrally deep thorax typical of monkeys to a dorsal position on a broad thorax in hominoids is generally understood to be related to a greatly expanded range of motion at the shoulder due to the lateral reorientation of the shoulder joint. It is not actually known, however, whether selection for this increased range of motion caused the change in thoracic shape and scapular position, or if an enhanced range of motion was the fortuitous result of thoracic shape change bringing about scapular repositioning.

Modern humans and extant African apes are characterized by a high degree of humeral torsion compared to other primates (Fig. 2), and for many years this was counted as a shared derived feature of hominoids (e.g., Le Gros Clark, 1969; Andrews, 1985; Martin, 1986; Harrison, 1987). However, as Fig. 2 shows, Asian apes have a much lower degree of torsion, though all apes have dorsally positioned scapulae. In 1988 I reported that the very low humeral torsion displayed by gibbons was likely related to the extreme degree of external shoulder rotation they exhibit during arm-swinging







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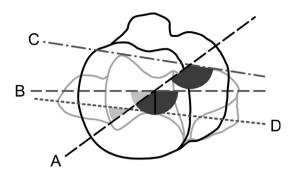


Figure 1. Humeral torsion measurements. A: axis of the humeral head; B: axis of the distal articular surface. In anthropology and other fields of morphological study, the primitive condition for humeral head orientation is assumed to be directly posterior (solid black line), and is expressed as either 0° or 90° relative to the articular surface (B). Increasing humeral torsion values reflect more inward orientations of the humeral head (dark gray angles). Some studies use a different distal reference axis, like the anterior surface of the distal articular surface (C; e.g., Van Dongen, 1963; Edelson, 1999, 2000) or the transepicondylar axis (D; e.g., Osbahr et al., 2002; Reagan et al., 2002; Chant et al., 2007), that can affect the direct comparability of reported torsion values. In contrast, the human clinical and sports literature view a directly inward facing humeral head as the default condition and report posterior deviations from this orientation as increasing retroversion refers to decreasing humeral torsion and vice versa. To avoid confusion, all reported retroversion values from studies use have been converted into torsion angles. Figure adapted from Larson et al. (2007).

(Larson, 1988). The ability to achieve this degree of external rotation. however, incurred a certain cost in that it results in a "lateralset" to their elbow joint that requires elevated recruitment of subscapularis as a medial shoulder rotator to overcome. In a subsequent study, I attempted to determine if the high level of torsion seen in modern humans and African apes was indeed a synapomorphy or was due to functional convergence by estimating the degree of humeral torsion displayed by the early hominin humeri known at the time, none of which were complete (Larson, 1996). My estimates of torsion for these incomplete humeri indicated much lower torsion than that of either modern humans or African apes, supporting an explanation of convergence for their similarity. In the years that have followed, several nearly complete hominin humeral specimens have been recovered [ARA-VP-1/4 and ARA-VP-7/2 (Ardipithecus ramidus; Lovejoy et al., 2009), MH1 and MH2 (Australopithecus sediba; Churchill et al., 2013), LB1/50 (Homo floresiensis; Morwood et al., 2005; Larson et al., 2007), and H. erectus KNM-WT15000 (Walker and Leakey, 1993; Larson et al., 2007), D2680, and D4507 (Lordkipanidze et al., 2007)], and these specimens confirm that very low humeral torsion characterized early hominins (Fig. 2).

The amount of humeral torsion displayed by an individual is a product of both development and function. Torsion increases from birth to maturity (Krahl, 1947; Edelson, 2000; Cowgill, 2007; see Fig. 3), and it is thought that variation in the degree of torsion between individuals may simply be a product of when this developmental trajectory ends (Yamamoto et al., 2006). Humeral torsion varies across different human groups, is often lower in males than in females, and is often lower in the dominant arm than the nondominant arm (Martin, 1933; Krahl and Evans, 1945; Churchill, 1994; Edelson, 1999; see Fig. 4). Logically, the orientation of the humeral head and glenoid fossa must be related to some degree, but all modern humans share a dorsally placed scapula, although little is known about how differences in overall body form, shoulder breadth, chest size, or chest shape may subtly influence scapular position, which in turn might be correlated to variation in humeral torsion (a small amount of variation in glenoid orientation relative to the rest of the scapula-glenoid version-has been reported, but it does not appear to be correlated to humeral torsion; Matsumura et al., 2014). Nonetheless, "normal" glenohumeral configurations among humans apparently include a broad range of humeral torsion values. Functionally, this variation in humeral torsion has been associated with needed ranges of internal/external humeral rotation related to habitual activity patterns, with higher levels of torsion conferring an increase in the range of internal rotation, and lower torsion increasing the range of external rotation. Since the total range of rotational motion at the shoulder doesn't change, an increase in range of motion in one direction is bought at the expense of a loss in the other. Hence the "lateral-set" to the gibbon shoulder due to their very low humeral torsion (Larson, 1988).

It was in the light of this developmental plasticity and functional adaptability that I found the unusually low degree of humeral torsion in fossil hominin taxa perplexing. In particular, it would have seemed likely that the shoulder of early *H. erectus* should display features related to manual manipulation of objects, reflecting a growing dependence on material culture for survival. With a dorsal scapula and laterally facing glenoid fossa, manipulation entails some amount of active internal shoulder rotation depending on the degree of humeral torsion. Since early *Homo* did not need the enhanced range of external humeral rotation for armswinging as gibbons do, it seems logical that the developmental plasticity of humeral torsion.

The fact that all the nearly complete early hominin humeri uniformly display very low torsion (I have come to suspect that my estimates of torsion for proximal humeral fragments alone, i.e., A.L. 288-1r. OMO119-73-2718, and STS7, are too high) didn't make sense if they all possessed a human-like scapular position. While there is evidence that the earliest hominins maintained a shoulder positioned high above the thorax as in modern apes and presumably the last common ancestor (LCA), the scapulae of early H. erectus display more human-like characteristics, suggesting they had moved to a lower position on the thorax. The simplest scenario would have been for the scapula to move inferiorly while maintaining its dorsal position, in which case the adaptability of humeral torsion should have resulted in an increase in torsion to accommodate a laterally facing glenoid fossa. The fact that early H. erectus nonetheless still displayed very low humeral torsion led to my hypothesis that in the course of this change in position, the pectoral girdle underwent a transitional phase in which the scapula moved not only inferiorly, but also somewhat anteriorly (Larson, 2007; Larson et al., 2007). Since the resulting more laterally positioned scapula did not appear to offer any particular advantage, I proposed that it might simply have been due to a clavicle that had not yet undergone the relative elongation observed in modern humans, by constraining scapular repositioning as it moved inferiorly on a flaring thoracic cavity. I suggested that the anterior shift in scapular position reported for people born with pathologically short clavicles (hypoplastic clavicle syndrome; Milgram, 1942; Guidera et al., 1991; Beals, 2000; Beals and Sauser, 2006) supported the plausibility of this scenario. As Roach and Richmond (2015) emphasize, this is indeed evidence that clavicular length can influence scapular position. However, to me, influencing scapular position does not necessarily imply being able to predict scapular position in humans, and I hope to now be able to correct this unintended extrapolation from my proposal. In fact I agree with Roach and Richmond (2015) that factors like thoracic shape and body build mitigate the likelihood of this being the case. In regard to the incidental complaint I noted by people with hypoplastic clavicles that they don't throw well (Guidera et al., 1991; Beals, 2000), their poor throwing proficiency has more to do with the restricted range of glenohumeral motion that results from their lateral scapular position and anteriorly Download English Version:

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